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# Duality of stochasticity and natural selection shape the ecology-driven pattern of social interactions: the fall of Hamilton's rule

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# Duality of stochasticity and natural selection shape the ecology-driven pattern of social interactions: the fall of Hamilton's rule

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## Abstract

Both competition and cooperation are pervasive at all levels of biological organization. Traditionally, the theory of evolution, understood as “red in tooth and claw” is challenged by the mere existence of cooperation. As a plausible explanation of this conundrum, Hamilton’s rule has dominated sociobiology for 50 years, but its genetic component (relatedness) is increasingly questioned. On the other hand, there is no doubt that social interactions are regulated by ecological (cost-benefit) factors.

Hamilton’s rule, like Darwin’s theory, implicitly assumes a stable environment. Stable environments favor selfish individuals that are selected to maximize their fitness. Hamilton’s rule allegedly explains the paradox of altruism, that selfish individuals forego their own reproductive opportunities to help close kin to reproduce. Kin selection/inclusive fitness was Hamilton’s explanation for this conundrum. But abiotic and biotic environments are not stable, but variable, often unpredictable. Particularly, biotic environments with their manifold conflicts, Red Queen coevolutionary arms races, and density- and frequency-dependence of fitness have often chaotic dynamics. Environmental stochasticity, resulting in uncertain, unpredictable reproductive success, changes fundamentally the rules for the “gamble of life”. A cybernetic model of evolution revealed the duality of stochasticity and natural selection at input and output levels of the evolutionary Black Box, resulting in multilevel selection of social behavior (Heininger, 2013, 2015). From microbes to mammals, cooperation is selected-for in harsh, uncertain and unpredictable environments. In stochastic environments, cooperation trades individual fitness maximization for less variability and greater reliability of evolutionary outcomes. Thus, the evolution of cooperation is a bet-hedging (risk spreading) strategy of risk-averse individuals. The biological default setting of individuals is neither selfish nor cooperative but ecologically context-dependent and dynamic. Competition and cooperation are threshold traits of nonlinear complex systems on a continuum of

ecological variables. The frequent kin structure of communities is not the predominant reason for cooperation/altruism but the result of limited dispersal. Limited dispersal and the evolution of cooperation share environmental stochasticity as common cause resulting in spurious relationships. The environmental conditions that favor cooperativity discourage dispersal and promote philopatry, thus shaping the preferential kinship structure of cooperative communities. Under more adverse ecological conditions, kin competition can strongly antagonize the benefits of kin cooperation and inhibit the evolution of cooperation in viscous populations. Not kinship but context-dependent, pleiotropic processes shape the dynamic sociobiological behavior of populations.

The ecological conditions and genetic “fossil record” of social behavior in both prokaryotic and eukaryotic microbes hold the key to understand the evolutionary present of cooperation in higher taxa. In microbes, cooperative behavior is induced by adverse conditions, particularly starvation, leading to social aggregations with the formation of complex patterns such as fruiting bodies and biofilms. In colonies of metabolically stressed clonal cells the competition for scarce resources is decided by a fair lottery. Experiments with bacteria and social amoeba suggest that cell fate ‘decisions’ (either survival as spores or cell death whose remains fuel the metamorphosis of spores) are stochastic, and moreover that these ‘decisions’ are controlled by genetically-encoded probabilities that are evolvable. Behind the “veil of ignorance”, the competitors are not “aware” of their relative position in the competitive hierarchy. This hierarchy is determined stochastically through a variety of cellular processes with inherent noise that render the cells heterogeneous and the lotteries fair.

The vast majority of cooperative systems are characterized by dominance hierarchies with asymmetric conflicts between dominants and subordinates over limited reproductive opportunities. Eusocial societies, the Holy Grail of kin selection theory, are despotic Orwellian societies that only serve the reproductive needs of selfish Big Sisters and Brothers that for this purpose enslave, police, and suppress their worker castes by aggression and

chemical agents. In this respect they resemble a unitary metazoan organism with its reproductive monopoly of the germline. Punishment allows the evolution of cooperation (or anything else) in sizable groups; thus neither altruism nor inclusive fitness gains are behaviorally or causally involved in these despotic systems. Intriguingly, queen pheromones are even able to suppress reproductive activity across species boundaries e.g. from honeybees to fruit flies. The existence of this oppressive system clearly argues against the role of inclusive fitness in the evolution of eusociality. Nestmate recognition, the eusocial version of the immune system and histocompatibility complex, has the function to ensure the reproductive monopoly. Within my alternative conceptual framework of colony fitness a joint genetic-physiological-behavioral-ecological hypothesis of eusociality in insects is presented.

In stochastic environments, reproductive success is unpredictable and highly variable. In taxa without parental brood care, particularly insects, survivorship to reproductive maturity is extremely low. Even in eusocial insects with independent colony foundation, the vast majority of attempts to establish a colony will fail. The extent to which immediate gains are preferred over future rewards is known as future discounting. Individuals who grow up in environments where resources are scarce, competition is intense, and mortality is high should discount the future with its uncertain benefits more heavily than individuals who grow up in abundant, supportive, long-lived habitats. On the other hand, an uncertain, unpredictable environment selects for evolutionary gambling, and either conservative or diversifying bet-hedging as individual- or population-level insurance to individual risk. The deterministic Hamilton's rule is hardly compatible with the stochasticity of reproductive success in uncertain, unpredictable environments. If the basic assumptions of kin selection/inclusive fitness theory would be right, eusociality should have evolved in (i) less adverse environments with less unpredictable reproductive success, and (ii) in taxa with more predictable reproductive success and, hence, less uncertain inclusive fitness benefits.

The insight that cooperation is a selected-for trait in stochastic environments unifies the so-far distinct concepts of cooperation, mutualism, symbiosis and cooperation in mating systems. Cooperation emerges as a self-organized behavior of complex systems. Phenomena such as swarm-behavior and -intelligence and division of labor emerge from the interplay of both stochastic and deterministic forces, generating order from disorder through self-organization. Responding to

the uncertainties of lotteries with insurance policies, populations engage in nest/burrow building, social contracts with assured fitness returns and social queuing. Via the law of large numbers evolution generated a form of automatic biological insurance against idiosyncratic risk.

From a systems biology perspective Hamilton's rule is simplistic, biased by observation selection, static, and parochial (ignoring the world outside its limited scope, i.e., both the huge majority of cooperative behaviors targeted to nonkin and to other species and being blind to epistemological inputs e.g. from complexity theory and neurobiology). Hamilton's rule was (and many mathematical models still are) shaped by an egalitarian worldview in which autonomous individuals "decide" to forego their reproduction and help their kin to ensure the representation of their genes in the next generation. In nature, however, the vast majority of cooperative systems are characterized by dominance hierarchies with asymmetric conflicts. The "decision" of subordinates to help is not self-determined but enforced by despotic dominants and the prevailing environmental conditions that limit the subordinates' options for independent reproduction. In a world of nonlinear biological processes and social interactions, complex emergent behavior, and probabilistic theories, Hamilton's linear and deterministic rule is a plausibility-based anachronism (one of Gould and Lewontin's "just-so stories") rooted in Newtonian thinking. Increasingly, "expanded" definitions of altruism and indirect fitness have been used to rescue the concept. The sociobiological definition of altruism, as one of an outcome, does not say how this outcome has been achieved. In sociobiological parlance, definitions such as fitness transfer by force, "enforced altruism", as a result of mere luck "coin-flipping altruism", or the mutual exchange of commodities "reciprocal altruism", pervert the common sense definition of altruism. In its last consequence, kin selection theory is a fascistoid concept, emphasizing the cohesive value of genetic homogeneity for a population tied together by parochial altruism. Parochial altruism promotes group conflict and may coevolve with warfare. On the other hand, mutualism causes partners to become increasingly dependent on each other as a basis for peaceful coexistence in societies.

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## 1. Introduction

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*The challenge to any approach purporting to replace inclusive fitness theory is to explain the same phenomena without using the insights or concepts of the theory.*

Bourke (2011a)

### Summary

**At its heart, evolutionary theory has an economic algorithm, a cost–benefit calculation. The theory of evolution by Natural Selection predicts that individuals will be selfish rather than cooperative. But the world is cooperative and this dilemma has vexed biologists since Darwin. Hypotheses regarding the origin and maintenance of social behavior emphasize the role of ecology and relatedness. While the role of ecology in the evolution of social behavior is not in doubt, recent controversy concerns the role of relatedness.**

A growing consensus suggests that ecological/evolutionary and economic theories are ultimately indistinguishable (Boulding, 1978; Hirschliefer, 1977; Real & Caraco, 1986; Noë & Hammerstein, 1994, 1995; Noë et al., 2001; Gandolfi et al., 2002; Hodgson, 2002; Orr, 2007; Yaari & Solomon, 2010; Okasha & Binmore, 2012). At its heart, evolutionary theory has an economic algorithm, a cost–benefit calculation: if a trait is beneficial for fitness, it will be selected for, when it is costly, it will be selected against (Maderspacher, 2011). Costs represent the flipside of direct benefits (e.g., see Lee & Hays 2004) For a focal genotype of interest to increase in frequency in a population, carriers must, on average, end up with more net direct fitness benefits than average population members. This net direct fitness must account not only for any costs and/or benefits to the focal carrier due to its own behavior associated with the trait, but also for any fitness benefits received from other individuals (related or not; Queller, 1985; Fletcher & Zwick, 2006). In particular, any trait that causes carriers via their own behaviors to put themselves at a disadvantage compared with those they interact with, will only increase if the benefits received from others are sufficient to make up for this disadvantage (Fletcher & Doebeli, 2009).

Robert May began his last presidential address to the Royal Society on 30th November 2005 by saying: “The most important unanswered question in evolutionary biology, and more generally in the social sciences, is how cooperative behaviour evolved and can be maintained in human or other animal groups and societies”. Darwin’s theory of evolution by Natural Selection predicts a nature “red in tooth and claw” (Ruse, 1999). In such a nature individuals will be selfish rather than cooperative (Darwin, 1859; Fisher, 1930). How then, can genetically prescribed selfless behavior arise by natural selection, which is seemingly its antithesis? This problem has vexed biologists since Darwin, who in *The Origin of Species* declared the paradox—in particular displayed by ants—to be the most important challenge to his theory. The hypotheses regarding the origin and maintenance of social behavior can be categorized into three classes (Slobodchikoff & Shields, 1988): (i) Genetic hypotheses assume that high levels of kinship among group members are necessary and sufficient to explain the kind of society being investigated (Hamilton, 1964; Alexander, 1974; Trivers, 1985). (ii) Ecological hypotheses assume that nongenetic environmental factors are necessary and sufficient to explain an observed social system (Crook, 1965, 1970; Lack, 1968, Emlen, 1982a). (iii) A phylogenetic hypothesis assumes that a social system evolved in the context of conditions occurring earlier in the evolutionary history of the lineage in question and does not represent an adaptation to current conditions (Wilson EO, 1975).

Allegedly, Hamilton's rule (Hamilton, 1963, 1964) provides a tool for understanding a range of social interactions, including altruism, aggression, selfishness and spite. It states that altruism (or less aggression) is favored when  $rb - c > 0$ , where  $c$  is the fitness cost to the altruist,  $b$  is the fitness benefit to the beneficiary and  $r$  is their genetic relatedness. The basic idea of the kin selection theory is that of inclusive fitness, a concept that breaks through the limitation imposed by the so-called Darwinian fitness, in which for a characteristic to have adaptive value it must favor its bearer's ability to reproduce. According to inclusive fitness theory, a gene which codes for behavior that is costly to the individual who carries it, but benefits his genetic relatives, e.g. sharing food with siblings, will increase in frequency by natural selection—because the individual's relatives are likely to carry copies of the gene in question themselves. Altruism can evolve, Hamilton concluded, so long as the cost incurred by the altruist is offset by a sufficient amount of benefit to sufficiently closely related relatives. Kin selection theory is widely accepted

among evolutionary biologists as the most plausible way of explaining the evolution of altruism from a Darwinian perspective (Cronin, 1991; Okasha, 2002). In the kin selection equation (Hamilton, 1964) relatedness is deeply intertwined with ecology (cost-benefit) so that both are essential (Crozier, 2008). While the role of ecology in the evolution of social behavior is not in doubt, recent controversy concerns the role of relatedness. Nowak et al. (2010) argued that the narrow focus on relatedness often fails to characterize the underlying biology and prevents the development of multiple competing hypotheses. This work has received some support (Doebeli, 2010; Gadagkar, 2010; van Veelen et al., 2010a) but, not surprisingly, has been angrily rebuffed by more than 150 prominent advocates of inclusive fitness theory (Abbot et al., 2011; Boomsma et al., 2011; Bourke, 2011a; Ferriere & Michod, 2011; Gardner et al., 2011; Herre & Wcislo, 2011; Marshall, 2011; Ratnieks et al., 2011; Rousset & Lion, 2011; Strassmann et al., 2011a). Edward O. Wilson (in response to R. Dawkins' recension of "The Social Conquest of Earth" [Prospect Magazine 195, 24th May 2012]) answered that "It should be born in mind that if science depended on rhetoric and polls, we would still be burning objects with phlogiston and navigating with geocentric maps."

In the following, I will argue that, from a systems biology perspective, the kin selection/inclusive fitness theory is simplistic, biased by observation selection, static and parochial. The result of my comprehensive literature study is an ecological-evolutionary scenario in which the omnipresent dualism of environmental stochasticity and natural selection shaped the evolutionary pattern of cooperation and competition. The complexity of the sociobiological regulation is reflected by the argumentation and hence the paper is no easy reading. I have tried to assist the reader by providing short summaries at the beginning of the chapters. This assistance may abet a rather saltatory style of reading with intermittent full text reading depending on the reader's focus of interest. Taking the potentially saltatory style of reading and the complexity of the topic into account there is some inbuilt redundancy of argumentation both to keep track and stress the consistency and consilience of data.

## 2. The shortcomings of observation selection and linear thinking

*It is theory which decides what we can observe*  
Einstein to Heisenberg, 1926 (Heisenberg, 1971)

*Mathematical descriptions of nature are not fundamental truths about the world, but models. There are good models and bad models and indifferent models, and what model you use depends on the purposes for which you use it and the range of phenomena which you want to understand [...] reductionist rhetoric ... claims a degree of correspondence between deep underlying rules and reality that is never justified by any actual calculation or experiment.*

Cohen & Stewart, 1994, p. 410

### Summary

**The reductionist approach to science today remains largely the dominant model. Reductionist and linear thinking have brought tremendous progress in our knowledge of biological processes and their networks. But reductionist thinking fails in the quest to understand complex systems. The observation selection related to the reductionist approach fails to appreciate biological phenomena in their wider context.**

The nineteenth-century American poet John Saxe told the story of the blind men from Industan and the elephant (1892):

It was six men from Industan, to learning much inclined,  
Who went to see the elephant (though all of them were blind),  
That each by observation might satisfy his mind...

Not surprisingly, each blind man felt a different part of the elephant, so that the one touching its legs thought they were tree trunks, the one touching its tail thought it was a snake, and so on (Gandolfi et al., 2002). By the end, they

Disputed loud and long, each in his opinion stiff and strong,

Though each was partly in the right, and all of them were wrong.

The same issue was approached by Bostrom (2003) from a different perspective. He asked: "How big is the smallest fish in the pond? You take your wide-meshed fishing net and catch one hundred fishes, every one of which is greater than six inches long. Does this evidence support the hypothesis that no fish in the pond is much less than six inches long? Not if your wide-meshed net can't actually catch smaller fish.

The limitations of your data collection process affect the inferences you can draw from the data. In the case of the fish-size-estimation problem, a selection effect—the net's being able to sample only the big fish—invalidates any attempt to extrapolate from the catch to the population remaining in the water. Had

your net had a finer mesh, allowing it to sample randomly from all the fish, then finding a hundred fishes all greater than a foot long would have been good evidence that few if any fish remaining were much smaller.

In the fish net example, a selection effect is introduced by the fact that the instrument you used to collect data sampled from only a subset of the target population. Analogously, there are selection effects that arise not from the limitations of the measuring device but from the fact that all observations require the existence of an appropriately positioned observer. These are known as observation selection effects."

Traditional linear thinking approaches work against an understanding of how the different parts of a system work together and underplay or ignore the multifaceted nature of complex problems. Gould and Lewontin (1979) criticized the adaptationist "just-so stories", that break an organism into unitary 'traits', either behavioral or physical, and propose an adaptive story for each trait considered separately. Instead of speculations about how a trait might possibly have been selected they advocated a holistic approach, to analyze organisms as integrated wholes. Naturally, with any research program that requires theory to be integrated with data, there is an inevitable tension between experimental biologists, who deal daily with the complexity of real biological systems, and theoretical biologists, who "simplify, simplify, simplify" in the name of tractability (Rouzine et al., 2001). All models, by definition, are simplified representations of natural systems or processes and out of necessity, must be abstractions from reality. It has been stressed (Kingsland, 1985; Clark & Yoshimura, 1993) that only the naïve believe that any particular mathematical model can provide more than a partial view of the complexity inherent in any biological system. Thus, all models are wrong in some respect by design (or more commonly, by accident) (Bentley, 2009). Theoreticians noted that when only a few components of a complex system are analyzed in isolation, conceptual mistakes commonly arise (e.g. Frank, 1996; Melbourne & Hasting, 2008; Stover et al., 2012). Byrne & Callaghan (2014) even noted that the development of systems of equations, however sophisticated, may well have very little to tell us about the social world. In the same vein of thought, Wilbur et al. (1974) remarked that attempts to explain life histories as outcomes of single selective pressures, however simple and appealing, have obscured rather than elucidated the evolution of life histories. Most studies of the genetics of adaptation rely on a separation of timescales of evolution and ecology (Orr, 2010). In many cases, this might be a severe oversimplification (e.g. Hairston et al., 2005;

Heininger, 2013). Indeed, recent developments on the establishment of beneficial mutations in changing environments reveal that this separation can lead to qualitatively different results (Uecker & Hermisson, 2011).

Hamilton's rule is an extreme example of linear thinking. The early models of social behavior assumed that altruistic and selfish behaviors are caused directly by corresponding genes, which means that the only way for groups to vary behaviorally is for them to vary genetically. Although this was assumed in the models primarily to simplify the mathematics, hardly anyone regards such strict genetic determinism as biologically realistic (Wilson & Wilson, 2007). Van Veelen et al. (2010b) concluded that the tendency to form groups and the tendency to cooperate interact; either looking at the two traits in isolation or allowing them to evolve together can give predictions that differ from each other (van Veelen et al., 2010b). In a similar vein of thought, Mitchell (2009, p. 114) argued for an "integrative pluralism which attempts to do justice to the multilevel, multicomponent, evolved character of complex systems". Models of social queuing (see chapter 17.2) that take into account even the smallest individual quality differences, which are probably plentiful in nature, result in individuals using queuing strategies completely different from those in models that assume qualitatively equal competitors (van de Pol et al., 2007). Generally it can be stated that even the most extensive models do not capture the complexity that can be demonstrated in real systems (Clark & Yoshimura, 1993; Sheldon, 2002).

The reductionist approach to science today remains largely the dominant model. It fosters the detailed study of limited domains in individual subdisciplines within the vast tree of science. The decline of *Partula* snails on a Pacific island, the flow of viscoelastic fluids within porous media, antibiotic resistance in the dihydropteroate synthase enzyme, and the search for the Higgs boson are examples of the degree of specialization in research. That the traditional epistemological approach of reductionism is not sufficient to explain complexity and self-organization is a view increasingly shared among scientists (Coveney, 2003). Systems thinking, on the other hand, offers an integrative way of appreciating all the major dimensions of a complex problem (Bosch et al., 2013). Theoretically, systems biology adopts a holistic, integrative view (Institute of Systems Biology website: [www.systemsbiology.org](http://www.systemsbiology.org)). In practice, however, it is usually large-scale reductionism: it takes a bottom-up approach, using information from complex interactions among lower level (molecular) processes to explain

the functioning of cells and organisms. This is crucially different from life history evolution, which uses a top-down approach, starting at the level where selection acts (typically the individual organism), and moving down the organisational hierarchy to eventually find a mechanistic explanation. Both approaches have their advantages and disadvantages and should be used in a complementary manner (Pijpe, 2007).

In this work, to remain in the metaphor of Saxe, I do not argue that the “snake” has hairs and cannot be a snake. Instead, I embark to retrieve as many data as available to identify the huge, context-dependent, ecological scenario into which cooperation is embedded, finally trying to discern the silhouette and body of the “elephant”.

### 3. What is altruism?

#### Summary

**The sociobiological definition of altruism, characterized by the costly transfer of fitness, is, in its actual version, the one of an outcome. It does not specify how this outcome has been achieved. This led to the strange situation that in sociobiological parlance definitions are used such as fitness transfer by force, “enforced altruism”; as a result of mere luck “coin-flipping altruism”; or the mutual exchange of commodities “reciprocal altruism”, that pervert the common sense definition of altruism as is e.g. expressed by the Oxford Dictionary definition. As in sociobiology “altruism” is an anthropocentric, intentional term replete with moral implications and teleological connotations, I will use it in quotation marks when I have to use it to refer to the argumentation of other authors but apart from that will avoid the term whenever possible.**

The Oxford Dictionary defines altruism as: “disinterested and selfless concern for the well-being of others”. A common definition in sociobiology describes altruism as behavior that simultaneously entails fitness costs to the behaving individual and fitness benefits to individuals on the receiving end of the behavior (Bourke & Franks, 1995; Sober & Wilson, 1998; Kerr et al., 2004). The term “altruism” has been used in different ways by different authors, generating considerable confusion and ambiguity (Grafen, 1984; Nunnery, 1985; Wilson, 1990; Uyenoyama & Feldman, 1992; Wilson & Dugatkin, 1992). Moreover, the behavior labeled “cooperation” by evolutionary game theorists is the same as that discussed in the evolution of altruism literature (Sober & Wilson, 1998; Worden &

Levin, 2007). A fundamental difficulty with the evaluation of acts of commodity/service transfer is that the outside observer can only observe the outcome of fitness transfer but has no knowledge of the specific motives and mechanisms. Basically, a net transfer of commodities can take place due to voluntary intent, cheating, coercion, or be the result of a lottery. For example, altruistic acts involve the actor voluntarily donating fitness to beneficiaries. Parasitic acts, on the other hand, involve the actor extracting benefit from others at net cost to the donors (Doncaster et al., 2013). Both behaviors may have the same direct net-cost transferral of fitness from donor to beneficiary; the key difference between parasitism and altruism is thus who drives the interaction. Identifying the evolutionary driver is not always straightforward in practice, yet it is crucial in determining the conditions necessary to sustain such fitness exchange (Doncaster et al., 2013).

Social interactions are often represented by a quadrant system (e.g. West et al., 2007c), the quadrants being defined by the positive and negative effects on both actor and recipient. Hamilton's rule stands and falls with the role of kinship in the manifestation of altruism; two of the quadrants representing mutualism and selfishness clearly do not require kinship for their manifestation. And spite is an unproven theoretical concept (Hamilton, 1970) that allegedly has some empirical support (Blackman, 2004); but there are thousands of counterexamples in which, under the appropriate ecological conditions, aggression and killing are either directed indiscriminately against kin and nonkin (see chapters 5.3.2 and 10.1) or even preferentially against kin (Dunn et al., 2014). One of the major flaws of the kin selection theory is that Hamilton classified fitness transfers as act of altruism without intimate knowledge of the underlying mechanism(s). One of the objectives of this work is to correctly classify the mechanisms behind the fitness transfer/exchange and delimit cooperation from altruism. Altruism is an intentional term (Grafen, 1999) replete with moral implications and teleological connotations. Cooperation is less tainted by anthropocentric notions. Therefore, I will put “altruism” in quotation marks whenever I have to use it to refer to the argumentation of other authors but apart from that avoid the term whenever possible.

### 4. Both competition and cooperation are pervasive

*Natural selection is demanding, exacting, relentless. It*

*is intolerant of weakness, indifferent to suffering ... One might expect organisms shaped by such a force to bear its stamp... Natural selection would surely see off chivalrous self-sacrifice, selfishness should win the day.*

Cronin, 1991

### Summary

**The competitive advantage of organisms depends on their stress resilience and acquisition of limited and contested resources. As a rule, competition in nature is asymmetrical, establishing dominance hierarchies. The selection principles that work at the level of individuals are also pervasively deployed at the cellular level during development, immune surveillance and cancerogenesis. Cell competition, modulated by redox balance, is an efficient mechanism for selecting cell quality and thereby ensuring that the requisite cellular tasks will be done by the most efficient and competitive cells.**

**Cooperation including mutualism, and symbiosis is abundant at all levels of biological organization. The benefits derived from cooperations include increased feeding success, access to resources that are unavailable to solitary individuals, increased predator protection, ability to outcompete conspecifics, or ability to escape harsh environmental conditions. Cooperative breeders exert costly parenting efforts to contribute to the developmental success of an infant or juvenile that is not their own offspring. Two major selective pressures, predation risk and resource availability in both space and time influence group size. In most species, the costs and benefits associated with group living vary systematically with group size.**

**Hamilton argued that limited dispersal would lead to what he called population viscosity, elevating local relatedness sufficiently to allow altruism towards neighbors in general. Habitat heterogeneity, availability and distribution induce a cost for dispersing individuals, such as substantial increases in mortality and the risk to end up in unsuitable habitats, and thus select against dispersers. Likewise, adverse, uncertain, and unpredictable environments favor cooperative behavior (see chapters 6 and 15). The environmental conditions that favor cooperativity also discourage dispersal and promote philopatry, thus shaping the preferential kinship structure of cooperative communities. Thus, environmental heterogeneity and stochasticity may be a shared causal factor for limited dispersal and cooperation resulting in a spurious relationship.**

Biologists operating within the paradigm of evolution by natural selection have understandably found it easier to think about predation, competition and parasitism than cooperation and mutualism. A naive evolutionist would not expect individuals, which are not closely related to be 'nice' to each other (Wilkinson & Sherratt, 2001). Individuals give for two reasons. One is to get a benefit back. The other is to avoid a cost. "Cooperation" theories stress mutual benefits. "Conflict" theories stress costs (Betzig, 2004).

### 4.1 Competition

In most natural populations, the reproductive potential far exceeds the environmental opportunity, and natural selection proceeds by culling to what the habitat can support (King, 1967). As Smith (2011) put it: "In some respects natural selection is a quite simple theory, arrived at through the logical integration of three propositions (the presence of variation within natural populations, an absolutely limited resources base, and procreation capacities exceeding mere replacement numbers) whose individual truths can hardly be denied." In fact, that populations outgrow resources is the central idea of Malthus's *An Essay on the Principle of Population* (1798), that led Darwin to the conclusion that this pressure, analogous to breeder's artificial selection, was a natural form of selection (Ruse, 2009). According to MacArthur and Wilson (1967, p. 149): "Evolution ... favours efficiency of conversion of food into offspring". How resources affect individual survival and reproductive success can be described by the fitness function,  $w(x)$ , whose value is the expected number of offspring born to individuals with  $x$  units of resource (Rogers, 1992). In a similar ecological context, an energetic definition of fitness was put forward. According to the formulation of Brown et al. (1993, 2004), reproductive power is composed of two component processes: acquisition (acquiring resources and storing them in reproductive biomass) and conversion (converting reproductive biomass into offspring) (Loreau, 1998; Allen et al., 2006).

Tilman (1982) defined competition as 'an interaction between individuals brought about by a shared requirement for a resource in limited supply leading to a reduction in the survivorship, growth, and/or reproduction rates of the competing individuals concerned'. According to Welden and Slauson (1986) "competition is the induction of strain in one organism as a direct result of the use of resource items by another organism". There are several established criteria accepted as evidence of competition among populations (McLean et al., 1997; Gaudin et al., 2004). For example: (i) The presence of competitors should modify the equilibrium size of a population. (ii) The

presence of competitors should alter the dynamics of a population, e.g. the life expectancy of the individuals of the population. (iii) It should be possible to modify the equilibrium dynamics of two competing populations through the manipulation of the available resources. On all levels of biological organization, competition for limited resources is a source of conflict and arguably the most pervasive motor of evolution (Darwin, 1859; MacArthur & Levins, 1964; MacArthur, 1970; Pianka, 1974a; Lawlor & Maynard Smith, 1976; Brown, 1981; Davies, 1982; Niemitz, 2002; Winther, 2005; Kopp & Hermisson, 2006; MacLean & Gudelj, 2006; Fisher & Hoekstra, 2010; Heininger, 2012). As a rule, competition in nature is asymmetrical (Brooks & Dodson, 1965; Lawton, 1981; Lawton & Hassell, 1981; Connell, 1983; Schoener, 1983; Karban, 1986; Weiner, 1990; Callaway & Walker, 1997; Law et al., 1997; Ferriere et al., 2002), establishing dominance hierarchies (Weiner, 1990; Erlandsson, 1992; Shelley et al., 2004; Rychlik & Zwolak, 2006). Competitive asymmetry, which leads to increased individual variability in size, has been seen as one of the major processes that secure the existence of reproductive individuals, stabilize population dynamics and assure the persistence of populations (Aikio & Pakkasmaa, 2003). Natural selection generated by asymmetric competition is likely to be a persistent and continuing phenomenon in communities.

Repression of competition within social groups has been suggested as a key mechanism driving the evolution of cooperation and the major evolutionary transitions (Leigh, 1977; Alexander, 1979; 1987; Buss, 1987; Maynard Smith, 1988; Maynard Smith & Szathmáry, 1995; Szathmáry & Maynard Smith, 1995; Frank, 1995, 2003, 2009; Ratnieks et al., 2006; Gardner & Grafen, 2009). As shown in bacterial communities, repression of competition per se, as opposed to increased relatedness, is driving the observed increase in cooperation (Kümmerli et al., 2010). In bacteria, hypermutability accelerates the breakdown of cooperation due to increased sampling of genotypic space, allowing mutator lineages to generate non-cooperative genotypes (Harrison & Buckling, 2005, 2011), and cheat on the others (Vulic & Kolter, 2001), a phenomenon that also may underlie cancerogenesis (Heininger, 2001; Burt & Trivers, 2006). However, competition is also a strong coevolutionary force resulting in the selection of fitter individuals (Lawlor & Maynard Smith, 1976; Futuyma & Slatkin, 1983; Stephens & Krebs, 1986; Zambrano et al., 1993; Grover, 1997; Svanbäck & Bolnick, 2005; Araújo et al., 2011; Heininger, 2012).

#### 4.1.1 Cell competition

The possibility that cells of multicellular organisms may also compete with one another has been postulated several times over the past two centuries (Díaz & Moreno, 2005). In 1881, Wilhelm Roux proposed the idea of a cellular struggle for survival during development (Roux, 1881; Heams, 2012). Wilhelm Roux transferred Charles Darwin's theory of the struggle for existence to the fight among cells and "parts" of the organism in the process of ontogenesis. As evidence for the conflict between cell types, he referred to pathological processes in which cells of one tissue start to invade another (Roux, 1881). His idea received no acclaim, since cells within multicellular organisms were thought to display conflict mediation/repression between, and cooperation of, the different cell types because cooperation increases the fitness of the group (Michod, 1996, 2005; Frank, 2003). A common hypothesis is that the unicellular bottleneck of the germ cell acts as a conflict mediator, by increasing the kinship among cells in the organism, thereby aligning the interests of cells with the interests of the organism (Bell & Koufopanou, 1991; Maynard Smith & Szathmáry, 1995; Grosberg & Strathmann, 1998, 2007; Ostrowski & Shaulsky, 2009). Thus, an essential constituent of the cellular cooperation paradigm was the alleged clonality or high relatedness of cells (Queller, 2000; Grosberg & Strathmann, 2007; Fisher et al., 2013). However, there is now evidence for a substantial amount of genetic diversity and genetic mosaicism both between somatic and germline cells (Gill et al., 1995; Muotri et al., 2005; Flores et al., 2007; Lam & Jeffreys, 2007; Bruder et al., 2008; Liang et al., 2008; Piotrowski et al., 2008; Coufal et al., 2009; Frank, 2010; Quinlan & Hall, 2012; Li et al., 2013). Cell competition was discovered in the imaginal discs of *D. melanogaster* 40 years ago (Morata & Ripoll, 1975). It initially described a situation in which slowly dividing cells were eliminated by apoptosis from a population of more rapidly dividing cells (Morata & Ripoll, 1975; Simpson, 1979; Simpson & Morata, 1981; Moreno et al., 2002; Lolo et al., 2012), despite the fact that they would have been viable on their own (Morata & Ripoll, 1975; Simpson, 1979; Simpson & Morata, 1981; Moreno et al., 2002; de la Cova et al., 2004; Li & Baker, 2007; Moreno, 2008). Thus, competition is context-dependent? cells acquire "winner" or "loser" identity only when in confrontation; each is viable in a homotypic environment (Johnston, 2009; Baker, 2011; Lolo et al., 2012). Cellular competition also occurs in *Drosophila* tracheal branching morphogenesis (Ghabrial & Krasnow, 2006) and in postmitotic epithelial tissue repair (Tamori & Deng, 2013). It seems unlikely that such an effective mechanism to select for cell fitness

should be confined to flies (Díaz & Moreno, 2005). In fact, cell competition has now been firmly established in a variety of taxa, including mammals (Oliver et al., 2004; Oertel et al., 2006; Sansom et al., 2007; Bondar & Medzhitov, 2010; Marusyk et al., 2010; Tamori et al., 2010; Baker, 2011; Kim et al., 2011; Krueger et al., 2011; Merlo et al., 2011; Petrova et al., 2011; de Beco et al., 2012; Norman et al., 2012). Cellular selection is the ultimate consequence when repair systems fail or are overwhelmed. In vitro findings suggest that cell competition outcome is modulated by redox balance (Merlo et al., 2011) and activation of the Jun N-terminal kinase (JNK) stress-response pathway (Moreno et al., 2002; de la Cova et al., 2004; Moreno & Basler, 2004). Consistent with the role of these signaling pathways, competition intensity increases in high-intensity competitive environments (Chesson & Huntly, 1997; Violle et al., 2010; Miller et al., 2011). In all taxa, competition among cells provides an efficient mechanism for selecting cell quality and thereby ensuring that the requisite cellular tasks will be done by the most efficient cells (Abrams, 2002; Díaz & Moreno, 2005; Khare & Shaulsky, 2006; Morata & Martin, 2007; Johnston, 2009; Green, 2010; Baker, 2011; de Beco et al., 2012; Vivarelli et al., 2012).

Lynn Caporale (2009) posited that “selection must act on the mechanisms that generate variation, much as it does on beaks and bones”. On the other hand, it is variation that gives selection the raw material to work on, establishing a feedback cycle. Variation can be caused both by a variety of molecular biological processes (see Heininger, 2013, 2015). Stochasticity in gene expression gives rise to cell-to-cell variability in protein concentrations and individual cells differ widely in responsiveness to uniform physiological stimuli. Cellular oxidative stress-dependent responses, although undoubtedly programmed, are also highly variable (Heininger, 2012), at least in part based on the stochasticity of mitochondrial bioenergetic/oxidative events (Hüser et al., 1998; Genova et al., 2003; Passos et al., 2007; Wang W et al., 2008).

Quality control operates by selecting for performance in cellular functions and eliminating inferior units. Cells employ a variety of quality surveillance and assurance systems including molecular chaperones (Esser et al., 2004; McClellan et al., 2005; Bukau et al., 2006; Buchberger et al., 2010; Arias & Cuervo, 2011), the ubiquitin/proteasome pathway (Sutovsky et al., 2001; 2002; Kostova & Wolf, 2003; Sutovsky, 2003; Thompson et al., 2003; Kwon et al., 2005; Taylor & Rutter, 2011), autophagy (Jin & White, 2007; Yorimitsu & Klionsky, 2007; Lee JY et al., 2010; Lee & Yao,

2010; Arias & Cuervo, 2011; Murrow & Debnath, 2013), mitochondrial turnover (Tatsuta & Langer, 2008; Twig et al., 2008; Dagda & Chu, 2009; Luce et al., 2010), the endoplasmic reticulum (Ellgaard & Helenius, 2003; Jørgensen et al., 2003; Kostova & Wolf, 2003; Kleizen & Braakman, 2004; Groenendyk & Michalak, 2005; Buchberger et al., 2010), and apoptosis (Yin et al., 1998, 2002; Meier et al., 2000; Groenendyk & Michalak, 2005; Jin & White, 2007; Igaki, 2009). Cellular selection within multicellular organisms does not only occur within the immune system and between cancer cells (Nowell, 1976; Kisielow & von Boehmer, 1995; McLean et al., 1997; Breivik & Gaudernack, 1999; von Boehmer et al., 2003; Vineis, 2003; Frank & Nowak, 2004; Merlo et al., 2006; Moreno, 2008; Vermeulen et al., 2008; Kim et al., 2011; Tamori & Deng, 2011; Thomas et al., 2013) but, as predicted by Roux (1881), is ubiquitous in plants and animals, particularly during development (Purves, 1980; Whitham & Slobodchikoff, 1981; Buss, 1983; Antolin & Strobeck, 1985; Kupiec, 1986, 1996, 1997; Sutherland & Watkinson, 1986; Edelman, 1987; Michaelson, 1987, 1993; Klekowski, 1988, 2003; Gill et al., 1995; Otto & Orive, 1995; Møller & Pagel, 1998; Otto & Hastings, 1998; Deppmann et al., 2008; Clarke, 2011; Tamori & Deng, 2011; de Beco et al., 2012). Like in the ecological context, the cellular selection regime is driven by competition for limited resources (McLean et al., 1997; De Boer et al., 2001; Gaudin et al., 2004; Davies et al., 2012; Wright & Bourke, 2013) such as trophic factors (Harris et al., 1997; van Ooyen & Willshaw, 1999; van Ooyen, 2001) and/or some other scarce resources that are needed to promote metabolism (Montague, 1996; Thomaidou et al., 1997).

Darwin imagined, in his last paragraph of the Origin of Species, a tangled bank of competing organisms, and there is ample evidence that we can stretch his analogy to the dynamic interactions of cells that populate niches during development and repair (Green, 2010). Thus, Darwinian principles of variation and selection can be extended to sub-organismal entities, e.g. organelles, cells and the germ-soma competition (Edelman, 1987; Stoner et al., 1999; Heininger, 2001, 2002, 2012; Weiss, 2006). Within-plant competition has been demonstrated in pine trees (Honkanen & Haukioja, 1994) and in annual pea plants (Sachs & Novoplansky, 1997). It has been proposed that clones and individual plants are formed by iterated, semi-autonomous modules (e.g. ramets or shoot modules) that may respond independently to local conditions. The branch-competition hypothesis (Sachs & Novoplansky, 1997) specifically predicts that an inferior module is left out of support if more viable

sinks are available (de Kroon et al., 2005). At least two major theories are based on selectionism, even if at different levels. The clonal selection theory that was elaborated by Jerne (1955) and Burnet (1957), and later confirmed by Tonegawa (1976, 1983), states that the diversity of the antibody repertoire in dedicated immune cells is achieved by random gene recombination events, leading to a huge number of small cellular lineages (Heams, 2012). Another major selectionist theory based on cell competition is the 'selective stabilization of synapses' (Changeux et al., 1973; Changeux & Danchin, 1976), later confirmed and even explicitly named 'neural Darwinism' (Edelman & Mountcastle, 1978; Edelman, 1987).

#### 4.2 Cooperation

Cooperation is abundant at all levels of biological organization (Hammerstein, 2003; Nowak & Highfield, 2011; Weiss et al., 2011). "Cooperation is so widespread, so much widespread, that it is puzzling why scientists were not willing to easily acknowledge its ubiquitousness and importance" (Miramontes & DeSouza, 2014). Cooperation and social phenomena are present in humans, in primates and in social insects—the common examples usually given— but it is also present in unexpected places such as in plants (Callaway & Walker, 1997; Biernaskie, 2011) or bacteria (Griffin et al., 2004; Cordero et al., 2012) or even as emergent phenomena in artificial societies of robots or other creatures of the cyberspace (Maris & te Boekhorst, 1996; Langton, 1997). In some species, social interactions are confined to interactions between the sexes during mating. Species at the other extreme have complex societies in which individuals live in intimate association with nestmates, and social interactions are fundamental to all aspects of life. Interactions between organisms exist along a continuous gradation, and the lines between cooperation, mutualism, commensalism, and parasitism are not neatly delineated and rather vague (Starr, 1975; Lewis, 1985; Ewald, 1987; Hochberg et al., 2000; Thompson & Cunningham, 2002; Neuhauser & Fargione, 2004; McCreadie et al., 2005; Leung & Poulin, 2008; Pérez-Brocal et al., 2013). Facilitation has been defined as an interaction in which the presence of one species alters the environment in a way that enhances growth, survival or reproduction of a second, neighboring species. According to some definitions, facilitation can be mutualistic, antagonistic or commensal (Bronstein, 2009). These interactions can be considered as a continuous spectrum of dependence, ranging from beneficial to detrimental outcomes (Ewald, 1987; Pérez-Brocal et al., 2013).

Even linkages among mutualism, predation and

competition in natural systems have been recognized (Crowley & Cox, 2011; Assaneo et al., 2013; Afkhami et al., 2014). "Cooperation" includes any behaviors (joint resource acquisition, information exchange, communal brood care, predator defense, etc.) that, despite any individual costs, have a net beneficial effect on group members (Mesterton-Gibbons & Dugatkin, 1992; Avilés et al., 2002; Khamis et al., 2006; Garay, 2009; Krams et al., 2010). Noë (2006) draws a definitive line between mere sociality, the tendency of conspecifics to aggregate and pursue their own interests in the context of a group, and cooperation, which requires an interaction or series of interactions between or among individuals that carries a cost for the agent but which, on average, results in a net gain for all participants of the interaction. Noë intends this reading of cooperation to include 'all other terms that have been used for mutually rewarding interactions and relationships: reciprocity, reciprocal altruism, mutualism, symbiosis, collective action and so forth'. This definition will be adopted here. "Altruism", by contrast, characterizes action by one individual that benefits another (or group) at the cost of the agent's own survival, wellbeing or reproduction.

Cooperation is not limited to kin and nonkin members of the actors' species but occurs also between members of different species. Mutualism, defined as an interaction in which two or more species benefit each other, ranges from specific obligate associations to facultative interactions among free-living species (Boucher et al., 1982; Boza & Scheuring, 2004; Holland & Bronstein, 2008). Both mutualism (Boucher et al., 1982; Boucher, 1985; Doebeli & Knowlton, 1998; Frank, 1998; Herre et al., 1999; Yu, 2001; Clutton-Brock, 2002; Bronstein et al., 2006; Leigh, 2010) and long-term mutualisms, i.e. symbioses, (Kropotkin, 1902; Margulis, 1970, 1981, 1998; Harley & Smith, 1983; Boucher, 1985; Smith & Douglas, 1987; Bronstein, 1994, 2009; Klepzig et al., 2001; Ryan, 2002; Kooijman et al., 2003; Rand et al., 2004; Blüthgen et al., 2007; Douglas, 2010; Cain et al., 2011; Mittelbach, 2012) are pervasive in nature. Douglas H. Boucher (1985), in an edited volume on mutualism, pointed out that there is a long-standing debate among ecologists over the relative importance of competition and co-operation in nature, which can be traced back at least to the 1920s. He noted the remarkable fact that, despite a general bias over the years in favor of competition as the basic organizing principle of nature and a concomitant preference among theoretical ecologists for using the famed Lotka-Volterra competition model in their analyses, in fact a cooperative version of the model (involving a simple sign change) has been reinvented (evidently

independently) at least 29 times since 1935 (Corning, 1997).

Mutualisms are known in all kingdoms of organisms, and there is a tendency for the partners to come from different kingdoms (Briand & Yodzis, 1982). This is particularly true for obligate and symbiotic mutualisms, and may simply be a reflection of nutritional complementarity. Some taxa seem particularly likely to enter into mutualisms--e.g. *Nostoc*, *Trebouxia*, *Symbiodinium*, and *Chlorella* (Margulis, 1981), and at a higher level, ants, coelenterates, and legumes (Boucher et al., 1982). Some 319 species of hummingbirds live almost entirely on nectar, a dependence that has led to specialized joints in their wings that enable them to hover with pinpoint accuracy over the appropriate flower. Flower and bird are partners in a mutualistic exchange of food for the bird and assistance with fertilization for the flower. In an even tighter partnership, at least one quarter of all described fungi, an estimated 12,000 to 20,000 species, enter into associations with 40 genera of photosynthetic algae to form some 13,500 species of lichens. This strategy is so successful that lichens are the most enduring and widespread of life forms (Ryan, 2006). Virtually all species of ruminants, including some 2,000 termites, 10,000 wood-boring beetles and 200 Artiodactyla (deer, camels, antelope, etc.) are vitally dependent upon the services provided by endosymbiotic bacteria or fungi for the breakdown of the cellulose in plants into usable cellulose hydrolysis products (Price, 1991; Lynd et al., 2002). After >100 years of research it is reasonable to conclude that most, if not all, multicellular life on earth is symbiotic with microorganisms (Rodriguez & Redman, 2008). Host-associated microorganisms contribute enormously to the development of their host's immune system, nutrition, digestion, reproduction, and general wellbeing (Currie, 2001; Vance, 2001; McFall-Ngai, 2002; Dillon & Dillon, 2004; Mazmanian et al., 2005; Taylor et al., 2005; Ley et al., 2006a; Martin et al., 2008; Pais et al., 2008; Chaston & Goodrich-Blair, 2010; Kinross et al., 2011; Mattila et al., 2012). It has been argued that access to mutualistic endosymbiotic microbes is an underappreciated benefit of group living (Lombardo, 2008). A species that is relatively efficient at acquiring one resource would benefit from specialization on acquisition of that resource accompanied by trade for the other resource. The theory of relative advantage extends this prediction to show that specialization and trade confer an advantage even for species that are relatively poor resource competitors for both resources (Schwartz & Hoeksema, 1998). The formation of cooperative and mutualistic partnerships has so much in common with

the formation of reproductive partnerships that the formulation of a single basic model seems warranted (Noë & Hammerstein, 1994). In all forms of reproductive and mutualistic pair formation, and in many cases of intra-specific cooperation, the partners belong to two distinct classes, e.g. males and females, figs and fig wasps, or breeders and helpers (Noë & Hammerstein, 1994). Because mutualism causes partners to become increasingly dependent on each other, it is a basis for peaceful coexistence in societies (Clutton-Brock, 2002). In promoting peaceful coexistence, mutualism would be antagonized by kin selection (Zahavi, 1995; Clutton-Brock, 2002).

Most attention on the phenomenon of cooperation has been focused on interactions between animals. However, the same phenomenon occurs at all levels of biological organisation (Hamilton, 1972; Leigh, 1991; Maynard Smith & Szathmáry, 1995; Lehmann & Keller, 2006; West et al., 2007a). Cooperative assembly of unicellular organisms into multicellular aggregates, mounds and fruiting bodies may have occurred many times in evolution and is common in nature (Bonner, 2000). The structural complexity and degree of organization of microbial multicellular structures vary from a simple single-layer biofilm and simple aggregates to complicated structures like the fruiting bodies of myxobacteria and slime molds, complex natural biofilms (see chapter 5.3.1) and the colonies of various microbes (Palková & Váchová, 2006; Annesley & Fisher, 2009; Velicer & Vos, 2009; Cáp et al., 2012; Elias & Banin, 2012).

Multicellularity has arisen multiple times (Bonner, 1998; Cavalier-Smith, 1998; Baldauf, 2003; Adl et al., 2005; Keeling et al., 2005; Parfrey et al., 2010). A new individual entity emerges from the interaction of previously independent components. These transitions include the evolution of chromosomes, eukaryotes, sexual reproduction, multicellular organisms, and social insects (Maynard Smith & Szathmáry, 1995; Bourke, 2011b). Separate genes, which make up the genome, cooperate in what has been termed the 'parliament of the genes' (Leigh, 1971; Corning, 1996). Molecular interactions are organized in cooperative molecular networks (Weiss & Buchanan, 2009; Barabasi et al., 2011; Foster, 2011). The very existence of multicellular organisms relies upon cooperation between the eukaryotic cells that make them up. The mitochondria upon which these eukaryotic cells rely were once free-living prokaryotic cells but now live cooperative lives. The tree of life is dominated by single-celled microorganisms that appear to perform a huge range of cooperative behaviors (West et al., 2006). For example, the growth

and survival of bacteria depend upon excreted products that perform a variety of functions, such as scavenging nutrients, communication, defence and movement. The benefits of such extracellular products can be shared by neighboring cells and hence they represent a 'public good' that is open to the problem of exploitation (West et al., 2006). Almost all of the major evolutionary transitions from replicating molecules to complex animal societies have relied upon solving the problem of cooperation (Maynard Smith & Szathmáry, 1995).

In animals, selection for sociality may increase the fitness of the individual as a function of group cooperation (Whitehouse & Lubin, 2005). The benefits derived from cooperations include increased feeding success, access to resources that are unavailable to solitary individuals (Slobodchikoff, 1984; Raffa & Berryman, 1987; Dugatkin, 1997; Wyatt, 2003; Whitehouse & Lubin, 2005; Bonsall & Wright, 2012; Platt et al., 2012), increased predator protection, ability to outcompete conspecifics, or ability to escape harsh environmental conditions. Because of the efficiency of cooperation, the total productivity attained by the group tends to be larger than the sum of individual contributions (Toyoizumi, 2009). Information exchange and group foraging, for instance, are thought to allow the exploitation of patchy and ephemeral resources in colonial breeding birds (e.g., Brown et al., 1990; Berg et al., 1992; Wiklund & Andersson, 1994; Brown & Brown, 1996; Rolland et al., 1998). Female bark beetles (*Dendroctonus montanus*) use aggregation pheromones to call in conspecifics to overcome the defenses of live trees and to gain access to a resource that is not available to solitary beetles (Raffa & Berryman, 1987; Wyatt, 2003). The utilization of live trees by the tree-killing bark beetles might have followed the development of better communication systems (pheromones) to attract conspecifics during group attack (Raffa & Berryman, 1987). As female density increases, individuals have higher reproductive successes in terms of pupae per attack (until the effects of intraspecific competition increase in severity) (Raffa & Berryman, 1983; Berryman et al., 1985). Cooperative actions have also been implicated in the capture of prey by social spiders (Whitehouse & Lubin, 2005). Social and subsocial spiders cooperate in the capture of insects that are too large for single individuals to subdue (Nentwig, 1985; Ward, 1986; Rypstra, 1990; Rypstra & Tirey, 1991; Pasquet & Krafft, 1992; Jones & Parker, 2000; Kim et al., 2005). The social spider, *Anelosimus eximius*, builds communal webs and group foraging allows capture of prey of increasing size. This offsets the decline in the number of prey caught per individual as web size and

hence colony size increases. Maximum resource intake occurs at intermediate spider densities (Yip et al., 2008). Individual success rates in lion foraging are also correlated with ecological attributes such as prey type and group structure (Scheel & Packer, 1991). Groups of lions and other predators have higher success foraging than individuals (Dugatkin, 1997; Beauchamp, 2013) but this is open to exploitation by lions that refrain to engage in specific hunting bouts (Scheel & Packer, 1991).

Communal nesting in fish (Tyler, 1995) and bees (Kukuk & Sage, 1994; Kukuk et al., 1998) apparently reduces loss of offspring due to predation. Unrelated and previously unknown potential immigrants were more readily accepted if groups of the cooperatively breeding cichlid, *Neolamprologus pulcher*, were exposed to fish predators or egg predators than to herbivorous fish or control situations lacking predation risk (Zöttl et al., 2013b). Cooperation among queens in pleometrotic ant species (e.g., Bartz & Hölldobler, 1982; Rissing & Pollock, 1987; Rissing et al., 1989; Tschinkel, 1992a; Bernasconi & Strassmann, 1999) or among males in lion coalitions (Packer et al., 1991) allows the successful takeover of other conspecific associations. The exploitation of hosts by opportunistic pathogenic bacteria, such as *Bacillus thuringiensis*, involves sharing the exploits of toxin production from multiple individuals as single individuals are incapable of overcoming host defenses. The exploitation of toxin producers by cheats (non-toxin producing strains) has consequences for pathogen virulence (Raymond et al., 2007, 2009), host-pathogen epidemiology (Bonsall, 2010) and the evolution of pathogen strain specificity. By grouping, animals may reduce their individual risk of exposure to parasites by allogrooming (Hart & Hart, 1992; Mooring & Hart, 1992; Johnson et al., 2004), potentially increasing their reproductive success (Hillegass et al., 2010). In environments where night temperatures are low, birds can benefit from roosting together, thereby saving energy and reducing loss of body mass (du Plessis et al., 1994; McKechnie & Lovegrove, 2001; McGowan et al., 2006; Hatchwell et al., 2009). By huddling together in dense colonies during the bitterly cold Antarctic winter, emperor penguins (*Aptenodytes forsteri*), are able to share precious body heat and provide insulation for one another, thereby reducing their individual energy expenditures by up to 50 percent (Le Maho, 1977). These joint benefits are expected to be large enough to compensate for inevitable costs of group living, such as competition for local resources or increased parasite loads (Alexander, 1974).

#### 4.2.1 Cooperation or "altruism": direct or indirect

### fitness effects?

The evolution of cooperation/“altruism” (regarding the ambiguity of the terms see chapter 3) has often been attributed primarily to kin selection (whereby individuals gain “indirect” benefits to their fitness by assisting collateral relatives). Importantly, the distinction between acts of cooperation and “altruism” is crucially dependent on the comprehensive elucidation of direct fitness effects. The recent past has seen several examples where meticulous long-term field observations recognized direct fitness benefits of cooperative breeding (see chapters 4.2.1.1, 6 and 17.3) thus allowing behavior that was previously assumed to be “altruistic” to be re-categorized as cooperative. Jennifer Smith (2014) has given a comprehensive account of the direct benefits of communal living in mammals, often independent of any kin selection-related effects:

“Long-term studies on free-living mammals suggest that exchanges of helpful behaviors, most of which occur among kin, have cumulative direct fitness consequences for individuals (Silk & House, 2011). The accumulation of social acts, such as grooming and long-term associations, enhances both the longevity and offspring survival for the vast range of mammals. Fitness consequences of sociality have now been documented in mammalian species including humans (House et al., 1988), baboons (Silk et al., 2003; Silk et al., 2010), house mice (Weidt et al., 2008), laboratory rats, *Rattus norvegicus* (Yee et al., 2008), horses, *Equus caballus* (Cameron et al., 2009), dolphins, *Tursiops aduncus* (Frère et al., 2010), rock hyraxes, *Procavia capensis* (Barocas et al., 2011) and yellow-bellied marmots (Armitage & Schwartz, 2000; Wey & Blumstein, 2012).

Nonkin cooperation of the same species also yields direct immediate or delayed benefits. For example, spotted hyaenas withhold aggression from unrelated adult females with whom they exchange other commodities important for survival (Smith JE et al., 2007). Vervet monkeys (Seyfarth & Cheney, 1983) and baboons (Cheney et al., 2010) also solicit cooperation from recent, unrelated grooming partners, presumably because of the direct benefits that donors receive from helping nonkin. Langergraber et al. (2007) used molecular genetics to tease apart the relative effects of direct and indirect benefits in philopatric male chimpanzees at Ngogo in Kibale National Park, Uganda. Interestingly, the majority of highly affiliative and cooperative dyads (e.g. pairs that formed coalitions at the highest hourly rates) were unrelated or distantly related. A recent meta-analysis by Schino and Aureli (2010) provided similar insights about

allogrooming in nonhuman primates. By comparing the relative effects of kinship and reciprocity, they found that when both factors were evaluated simultaneously, the effects of reciprocity exceeded those of kinship in explaining grooming patterns. Similarly, meerkats gain direct benefits from sentinel behavior (Clutton-Brock et al., 1999). That is, rather than guarding only being favored by indirect benefits gained from helping kin, meerkats gain direct benefits from guarding; sentinels guard to reduce their own predation risk if no other animal is on guard and if they have recently eaten.”

There is increasing evidence that cooperation between unrelated individuals is wide-spread (Stacey & Koenig, 1990; Cockburn, 1998; Avilés et al., 2002; Clutton-Brock, 2002, 2009a; Dugatkin, 2002; Mesterton-Gibbons & Dugatkin, 1992). Studies have failed to find relatedness levels in accordance with expectations, e.g. in kingfishers (Reyer, 1984), dunnocks (Davies, 1992), fairy-wrens (Dunn et al., 1995), eider ducks (Öst et al., 2005), subdesert mesite *Monias benschi* (Seddon et al., 2005), Taiwan yuhinas (Shen, 2009), manakins (McDonald & Potts, 1994), mongooses (Creel & Waser, 1994), hyenas (Van Horn et al., 2004), coalitions of male lions (Packer & Pusey, 1982), wolves (Vucetich et al., 2004), chimpanzees (Vigilant et al., 2001; Lukas et al., 2005), greater spear-nosed bats (Bohn et al., 2009), big brown bats (Metheny et al., 2008), vampire bats (Wilkinson, 1985), oceanic delphinid species (Hayano et al., 2004; Karczmarski et al., 2005; Viricel et al., 2008; Mirimin et al., 2011), guppies (Russell et al., 2004), cichlid *Neolamprologus pulcher* (Dierkes et al., 2005), clown anemonefishes (Buston et al., 2007), the paper wasp *Polistes dominulus* (Queller et al., 2000; Zanette & Field, 2008), communal bees (Kukuk & Sage, 1994; Danforth et al., 1996; Paxton et al., 1997), and ant foundresses (Hagen et al., 1988; Sasaki et al., 1996; Bernasconi & Strassmann, 1999; Helms Cahan & Helms, 2012).

The literature often attributes non-human primate altruism and cooperation to kin selection, thus calling human cooperation with non-relatives a ‘huge anomaly’ in the animal kingdom (Fehr & Fischbacher, 2003; Gintis et al., 2003; Boyd, 2006; Melis & Semmann, 2010). Even though there is ample evidence that this claim does not hold for captive chimpanzees (de Waal, 1982, 1992, 1997a; Koyama et al., 2006), it has only recently been effectively countered for wild chimpanzees. DNA data from the field demonstrate that most of the cooperative relationships among male chimpanzees are of a reciprocal nature and concern individuals without family ties (Mitani, 2006; Langergraber et al., 2007).

Bonobos may show the same pattern, since females maintain a close cooperative network that allows them to collectively dominate the males (Furuichi, 1997; de Waal, 1997b) despite the fact that females are also the migratory sex, hence largely unrelated within each community (Kano, 1992). It seems, then, that both of our closest relatives are marked by frequent cooperation among non-relatives. Taken together, these findings suggest that kin selection is not the primary reason for animals to group together (Clutton-Brock, 2002; Valsecchi et al., 2002; Avilés et al., 2004; Russell et al., 2004; Spong & Creel, 2004; Van Horn et al., 2004; Vucetich et al., 2004; Lukas et al., 2005). Enduring relationships between nonkin, same-sex individuals occur not only in humans and non-human primates (Langergraber et al., 2007, 2009; Lehmann & Boesch, 2009; Mitani, 2009; Holt-Lunstad et al., 2010; Schulke et al., 2010; Seyfarth & Cheney, 2012) but also in various other mammals (McShea, 1990; Packer et al. 1991; Möller et al., 2001; Parker & Lee, 2003; Weidt et al., 2008; Cameron et al., 2009; Seyfarth & Cheney, 2012).

#### 4.2.1.1 Cooperative breeders

Cooperative breeding behavior has been defined as displayed by individuals exerting costly parenting effort to contribute to the developmental success of an infant or juvenile that is not their own offspring (Emlen, 1984; Stacey & Koenig, 1990). Cooperative breeders are typically divided into two general types of cooperative societies: plural breeders and singular breeders (Brown, 1987; Hauber & Lacey, 2005). In plural (communally) breeding societies, all adult group members are reproductively active and alloparental care (i.e., care of non-offspring young) is typically performed by individuals with offspring of their own. In contrast, in singular breeding societies, production of offspring is typically limited to a single male and female per group who are assisted by a variable number of non-breeding adult alloparents (“helpers at the nest”). These categories are not absolute and populations or even social groups of conspecifics may shift breeding systems (i.e., singular, plural, or non-cooperative) between or, in some cases, within years (e.g., white-fronted bee-eaters *Merops bullockoides*: Emlen & Wrege, 1992; long-tailed tits *Aegithalos caudatus*: McGowan et al., 2003; carrion crows *Corvus corone*: Baglione et al., 2002; house mice *Mus musculus*, yellow bellied marmots *Marmota flaviventris*, and voles *Microtus* spp.: Solomon & French, 1997). There is abundant evidence for a preferential help to close kin (Reyer, 1984; Curry, 1988a; Stacey & Koenig, 1990; Emlen, 1991; Russell & Hatchwell, 2001; Baglione et al., 2003; Dickinson &

Hatchwell, 2004; Hatchwell, 2009; Nam et al., 2010; McDonald & Wright, 2011; Hatchwell et al., 2014). However, cooperative breeding also occurs in some species that do not live in family groups, and more recent work has shown examples from species living in a variety of social groups where the huge variation between individuals in helping effort does not correlate with differences in genetic relatedness (Malcolm & Marten, 1982; du Plessis, 1993; Creel & Waser, 1994; Piper, 1994; Dunn et al., 1995; Hoogland, 1995; DeLay et al., 1996; Keller, 1997; Magrath & Whittingham, 1997; Heinsohn & Legge, 1999; Clutton-Brock et al., 2000, 2001a; Queller et al., 2000; Cant & Field, 2001, 2005; Clutton-Brock, 2002; Griffin & West, 2002, 2003; Field et al., 2006; Leadbeater et al., 2010; Hanson, 2013; Zöttl et al., 2013a). It has been suggested that by helping to care for unrelated young, individuals may take advantage of a kin-recognition mechanism based on associations learned by nestlings while being fed. The deceived young later may offer assistance according to its perceived relatedness to the former helper (Connor & Curry, 1995). This mechanism, termed kinship deceit, may be a form of bet-hedging in cooperative breeding systems where mortality is high, where breeders can benefit from contributions by helpers, and where helpers normally assist relatives (Connor & Curry, 1995). In 213 species of cooperatively breeding birds for which data are available, the majority of species (55%) nest in nuclear family groups, but cooperative breeding by unrelated individuals is more common than previously recognized: 30% nest in mixed groups of relatives and non-relatives, and 15% nest primarily with non-relatives. In obligately cooperative species, unaided pairs cannot rear young (e.g. dwarf mongooses, *Helogale parvula*: Creel, 1990a; African wild dogs, *Lycaon pictus*: Malcolm & Marten, 1982). Obligate cooperative breeders are far more likely to breed with non-relatives than are facultative cooperators, indicating that when constraints on independent breeding are sufficiently severe, the direct benefits of cooperative breeding—specifically, increased survival, territory inheritance and access to current or future mating opportunities—are frequently sufficient to maintain social nesting even when genetic relatedness is low (Riehl, 2013). The indirect benefits of cooperative behavior may often have been overestimated while the direct benefits of helping to the helper’s own fitness have probably been underestimated (Clutton-Brock, 2002). In general, cooperative breeders fledge their young significantly earlier and raised more broods per season than non-cooperative bird species of similar body mass. Within phylogenetic families, cooperative species have

shorter nestling periods, and the duration of the nestling period tends to decline as cooperative group size increased (Ridley & van den Heuvel, 2012).

#### 4.2.2 Group size

Although there are many ways to describe sociality, it is social group size that delineates the state space in which social systems and social complexity can evolve (Terborgh, 1983; van Schaik & van Hooff, 1983; Terborgh & Janson, 1986; Janson, 1992; Pollard & Blumstein, 2008). The general theoretical framework for explaining variation in group size assumes that there are fitness consequences associated with group size and that individuals maintain membership in groups of favorable size to maximize fitness (Wrangham, 1980). In most species, the costs and benefits associated with group living vary systematically with group size.

The individual fitness of group members as a function of group size may either consistently increase, consistently decrease or have a maximum at an intermediate group size (Brown et al., 1990). In 1931, Warder Clyde Allee proposed that populations at low numbers are affected by a positive relationship between population growth rate and density, which increases their likelihood of extinction, an idea that he later extended in his 1949 book on animal ecology (Allee, 1931; Allee et al., 1949). There is widespread evidence for the Allee effect in mammals (e.g. Komers & Curman, 2000), birds (e.g. Green, 1997) and fish (e.g. Liermann & Hilborn, 1997). Besides inbreeding depression and demographic stochasticity, a reduction in intraspecific cooperation might lead to inverse density dependence of population growth (Courchamp et al., 1999a). Factors causing an Allee effect may include dilution of predation risk at increasing group sizes (Hamilton, 1971; Treherne and Foster, 1982; Heg et al., 2004), increased predation at low population densities that follows reduced vigilance (Kenward, 1978; Berg et al., 1992), interspecific kleptoparasitism (Carbone et al., 1997), and difficulties in finding a mate (Kuussaari et al., 1998; Berec et al., 2001). The high rates of group extinction observed in obligate cooperative breeders are generated by a need for a critical number of helpers, which produce an Allee effect (Courchamp et al., 1999b; Courchamp & Macdonald, 2001). African wild dogs, *Lycaon pictus*, live in groups of up to 20 adults and their dependent young (Creel & Creel, 1995). The hunting strategy of the group usually requires a critical size to be energetically efficient (Fanshawe & Fitzgibbon, 1993; Creel & Creel, 1995; Creel, 1997). A threshold group size might also be required for hunting because of kleptoparasitism by hyenas, which can be

energetically very costly to small groups of wild dogs (Fanshawe & Fitzgibbon, 1993; Carbone et al., 1997, 2005; Gorman et al., 1998). In addition, helpers are required by the breeding female: litters are very large (up to 20 pups), and the breeding female, then the pups, need to be fed by other members of the group (Malcolm & Marten, 1982; Woodroffe et al., 1997). Group members also help by chasing predators from the den area, and by staying at the den to protect the pups while the pack is hunting (Malcolm & Marten, 1982; Woodroffe et al., 1997). There is a critical minimum threshold, below which packs face an increasing probability of extinction – an Allee effect with consequences for the conservation of this species, and of other obligate cooperators (Courchamp & Macdonald, 2001). Theoretical models (Avilés, 1999; Kokko et al., 2001a) and empirical examples (Caraco & Wolf, 1975; Nudds, 1978; Buss, 1981; Itô, 1987; Raffa & Berryman, 1987; Heinsohn, 1992; Cash et al., 1993; Komdeur, 1994; Wiklund & Andersson, 1994; Booth, 1995; Jeanne & Nordheim, 1996; Avilés & Tufiño, 1998) show that as a result of cooperation some components of individual fitness may increase as a function of colony size and underlie the positive correlation seen between the number of helpers and the number of offspring (Creel & Creel, 1991) raised in most species with communal care (coyotes: Bekoff & Wells, 1982; birds: Brown, 1987; lions: Bygott et al., 1979; wild dogs: Malcolm & Marten, 1982; jackals: Moehlman, 1979; dwarf mongooses: Rood, 1990; Creel & Creel, 1991; badgers: Kruuk, 1989). Long-term fitness considerations can explain group size regulation in meerkats. Group size distributions expected from predicted dispersal and eviction strategies matched empirical distributions most closely when emigrant survival was approximately that determined from the field study (Stephens et al., 2005).

The many factors that influence, and are influenced by, group size include predation risk (Alexander 1974; Altmann, 1974; van Schaik, 1983; van Schaik & van Hooff, 1983; Janson, 1998), resource availability and competition (Wrangham, 1980; van Schaik, 1983; van Schaik & van Hooff, 1983), foraging patch size and heterogeneity (Altmann, 1974; Leighton & Leighton, 1982; Johnson DDP et al., 2002), disease/parasite risk (Freeland, 1976; Altizer et al., 2003), body mass (Jorde & Spuhler, 1974; Clutton-Brock & Harvey, 1977; van Schaik, 1983; Janson & Goldsmith, 1995), diet (Clutton-Brock, 1975; Clutton-Brock & Harvey, 1977; Janson & Goldsmith, 1995; Williamson & Dunbar, 1999), phylogenetic inertia (Di Fiore & Rendall, 1994), life history (Wittenberger, 1980), mating opportunities (Lindenfors et al., 2004) and travel costs (Chapman &

Chapman, 2000; Sernland et al., 2003). Most of these factors can be subsumed under two major categories of selective pressures: predation risk and resource needs (Dunbar, 1988; Krause & Ruxton, 2002; Hoare et al., 2004; Caro, 2005). The classic view on the evolution of group size is that observed group sizes reflect these two major factors (Clutton-Brock & Harvey, 1977; Terborgh, 1983; van Schaik & van Hooff, 1983; Terborgh & Janson, 1986; Rodman, 1988; Janson, 1992; Wrangham et al., 1993; Janson & Goldsmith, 1995; Müller & Thalmann, 2000; Pollard & Blumstein, 2008). There is empirical evidence that group size increases with increasing risk of predation, and conversely, that more solitary individuals are found when the predation risk is low, e.g. in passerine bird colonies (Wiklund & Andersson, 1994), African penguin groups (Mori, 1999), groups of rodents (Ebensperger & Wallem, 2002), frog tadpoles (Spieler, 2003) and fish shoals (Magurran & Pitcher, 1987; Hoare et al., 2004). Evidence that dominant breeders accept additional helpers more readily with increasing benefits of help exists from pied kingfishers (*Ceryle rudis*), where experimental clutch enlargement increased helper presence (Reyer, 1980). An opposite regulatory effect was observed in the clown anemonefish (*Amphiprion percula*), where dominant group members prevent immigration when the group is saturated (Buston, 2003a). Indirect evidence for group size adjustment to demand exists from baywings (*Agelaioides badius*), where more helpers were present when nests were parasitized by cowbirds (*Molothrus spec.*), which resulted in a higher begging intensity in the nest (Ursino et al., 2011). In the cooperatively breeding cichlid, *N. pulcher*, evicted offspring can be reaccepted when competition for the territory is experimentally increased, suggesting that breeders in this species are able to estimate their need for help (Taborsky, 1985).

It is the pattern of resource availability in both space and time that influences group size (Crook, 1964; Clutton-Brock, 1975; Macdonald, 1983; Johnson DDP et al., 2002). Increases in overall resource abundance leads to increases in habitat quality per unit area, thus resulting in higher animal densities, and typically smaller ranging areas (Reiss, 1988; Powell et al., 1997). Resource abundance in itself does not necessarily affect group size, however, because rich territories are typically contracted (or split), such that individuals maintain the former per-capita intake rate (Kruuk & Macdonald, 1985). But if resources are heterogeneous in space or time, then this is no longer necessarily true – proportional increases in average resource abundance might not enable the territory to shrink, because larger areas are still needed to

encompass the temporal and spatial variability of these resources (Johnson DDP et al., 2002). Food scarcity will *decrease* optimal group size when large groups face more intense intragroup food competition (so that there is a “many eyes—many mouths” trade-off) that is not compensated by their intergroup competitive advantages (Giraldeau, 1988; Ritz, 1997). This can occur when scarcity results in less variation in food patch quality such that even the best patches are not worth defending or when food sources are less defensible (Wrangham, 1980). Food scarcity will *increase* optimal group size when resource defense benefits outweigh high intragroup feeding competition in large groups. This can occur if food scarcity increases the supply or defensibility of high-quality food patches, thus increasing intergroup competition (Pride, 2005). With greater group carrying capacities (more abundant resources), grouping and cooperative tendencies evolved in opposite directions; as the group carrying capacity increased, greater grouping but lower cooperative tendencies evolved (Avilés et al., 2002). The latter result is in agreement with findings of N-player Prisoner’s Dilemma games (e.g., Boyd & Richerson, 1988) or game-theoretic models of cooperative hunting (Packer & Ruttan, 1988) that have shown that larger groups are less stable and more susceptible to cheating. Because the costs and benefits of grouping vary as a function of group size, it can be expected that individuals will modify their choice of group size (by joining or leaving groups) as ecological conditions change to maximize their fitness (Pulliam & Caraco, 1984). One problem with this possibility is that individuals within a group may not be able to exclude solitary individuals, and consequently individuals will continue to join a group exceeding the “optimal group size” (Sibly, 1983). Thus solitary individuals, by joining a group, may increase their own fitness, but decrease that of all other group members. Theoretical considerations have revealed that optimal group size and its obvious direct-fitness benefits, but not relatedness, should determine the decision of solitary individuals to join a group (Rannala & Brown, 1994). One safe strategy for solitaries would be to only join groups that are below the optimum group size (in terms of direct fitness), and for group members of only allowing solitaries to join if the group is below the optimum size (Rannala & Brown, 1994). When the costs of grouping become greater than the benefits individuals should be expected to leave (Krause & Ruxton, 2002; Couzin & Krause, 2003). Groups fission when they become large in badgers (Da Silva et al., 1993; Newman, 2000) and other species (Macdonald, 1979; Dunbar, 1989; Baker et al., 2000). Increasing group size commonly depresses fecundity and

increases mortality of females and their offspring (Clutton-Brock et al., 1982; van Schaik et al., 1983a; Clutton-Brock, 2002, 2009b; Silk, 2007; Clutton-Brock et al., 2008; Clutton-Brock & Huchard, 2013). Where reproductive competition is intense, increases in group size are often associated with increased rates of abortion, infanticide and eviction (or dispersal), which progressively restrict recruitment and constrain the upper limits of group size (Hoogland, 1995; Stephens et al., 2005; Kappeler & Fichtel, 2011). In contrast, where increasing group size has little effect on the intensity of breeding competition between group members, females may form large groups whose size is ultimately limited by the effects of competition for resources on fecundity and survival (Prins, 1996; Moss & Lee, 2011).

#### **4.2.3 Limited dispersal**

##### **4.2.3.1 Law of Causality**

The Law of Causality states: Every event must have a cause (Hughes & Lavery, 2004). Therefore we explain particular events and general patterns by identifying the causal factors involved. Ordering two or more events in a causal order is crucial for a scientific understanding. Another order of events is their temporal order. While the temporal order is observable, outside of a controlled scientific experiment the causal order is not. This is because a complete causal account specifies the necessary and sufficient conditions for something to occur and both of these conditions involve counterfactual statements (Damer, 1995; Hughes & Lavery, 2004). Counterfactual statements are about what would have happened had the purported necessary and sufficient conditions not been satisfied. These possibilities are, by definition, not observable. For these reasons, the concept of causation must be carefully distinguished from the concept of correlation. Two events that regularly occur at the same time or in the same sequence may be both correlated and related as cause and effect or they may be correlated without being in a direct causal relationship. A correlation is observed when different events occur at the same time or occur regularly in the same sequence. With causation, one event (the cause) is responsible for, or brings about, another event (the effect). We can see the need for this distinction by considering one of the causal fallacies, common cause. Someone might notice that a sore throat is always accompanied by sinus congestion (a correlation). On the basis of this observed correlation, the sick person might fallaciously believe that the sore throat causes the sinus congestion. But really, the sore throat and the sinus congestion are both caused by a third factor, namely, a cold virus. So while the sore throat and

sinus congestion have a common cause, neither causes the other (Hughes & Lavery, 2004). There is a correlation but no causal relationship between the sore throat and the sinus congestion, while both are epiphenomena of their common cause, the cold virus. Hence, a spurious relationship is fallaciously assumed when two occurrences have no causal connection, yet it may be inferred that they do, due to a certain third, unseen factor (referred to as a "confounding factor"). Hence, causality evaluations should be based on three criteria: (i) Correlation: cause and effect must vary together; (ii) Time sequence: the cause must come before the effect; (iii) Non-spuriousness: the relationship between two events cannot be explained by any third variable.

##### **4.2.3.2 Limited dispersal and cooperation: spurious relationship?**

In his original papers on inclusive fitness theory, Hamilton pointed out that a sufficiently high relatedness to favor altruistic behaviors could accrue in two ways — kin discrimination or limited dispersal (Hamilton, 1964, 1971, 1972). He argued that limited dispersal would lead to what he called population viscosity, elevating local relatedness sufficiently to allow altruism towards neighbors in general (Queller, 1994a). There is a huge theoretical literature on the possible role of limited dispersal in kin selection (e.g. West et al., 2002a; Lehmann et al., 2008; Platt & Bever, 2009) as well as experimental evolution tests of these models (Griffin et al., 2004; Diggle et al., 2007b; Kümmerli et al., 2009b). The first study to challenge Hamilton's ideas about limited dispersal was a computer simulation based on group-selection theory (Wilson et al., 1992). Discussions of population viscosity and the evolution of cooperation have emphasized the potential for kin competition to limit the evolution of cooperation in viscous populations (West et al., 2002a; EIMouden & Gardner, 2008; Grafen & Archetti, 2008; Platt & Bever, 2009). Whereas cooperative individuals are more likely to benefit kin in viscous populations, they also compete for limiting resources with these same kin. Early theoretical work found that such kin competition can strongly antagonize the benefits of kin cooperation and inhibit the evolution of cooperation in viscous populations (Grafen, 1984; Taylor, 1992a; Queller, 1992a, 1994a; Wilson et al., 1992; West et al., 2002a). Consistent with this, empirical studies have failed to find a relationship between relatedness and aggressiveness in fig wasps (West et al., 2001) and bruchid beetle larvae (Smallegange & Tregenza, 2008), suggesting that the effects of kin competition might negate any kin-selected benefits associated with

being less aggressive toward kin. E.O. Wilson and others argue that kin selection acts more often as a 'dissolutive' than a binding force within groups (Wilson & Hölldobler, 2005; Wilson & Wilson, 2007; Nowak et al., 2010). The logic in Hamilton's argument (1964, 1971, 1972) is based on the assumption that selfishness is the evolutionary default state of every individual. Genetic relatedness may be a means to overcome this selfish "programming". But if the selfish/collaborative setting of each individual is plastic depending on the ecological conditions (as I will show below), the logic of the argument no longer holds.

The diversity of dispersal strategies is expected to be shaped by species specific characteristics and interspecific competition, which can balance the relative benefits and costs of dispersing, in interaction with the environment (Büchi & Vuilleumier, 2012). Some authors emphasize that the cost on direct fitness is small if personal reproduction after dispersing would have been unlikely, which happens if habitats are saturated and gaining a breeding position elsewhere is, therefore, difficult (the "ecological constraint" hypothesis; Selander, 1964; Brown, 1969; Emlen, 1982a, 1995). Others put more emphasis on the benefits that natal philopatry can bring about (Stacey & Ligon, 1987, 1991; Zack & Stutchbury, 1992) or on life-history traits, such as longevity, that predispose species to become cooperative (Arnold & Owens, 1998; Hatchwell & Komdeur, 2000). In some species, delayed dispersal occurs without offspring helping their parents (Gayou, 1986; Veltman, 1989; Ekman et al., 1994; Green & Cockburn, 2001; Kokko & Ekman, 2002). This suggests that direct benefits can suffice to explain delayed dispersal and serves as a useful reminder that the decision to help does not automatically follow from the decision to stay (Emlen, 1982a, 1982b; Brown, 1987; Kokko et al., 2001a). A variety of direct benefits can favor philopatry (Kokko & Ekman, 2002): subordinates may breed (females) or gain paternity (males) despite the presence of a dominant (Arnold, 1990a; Brown & Brown, 1990; Rabenold et al., 1990; Jennions & Macdonald, 1994; Sherman et al., 1995; Laranzo-Perea et al., 2000), they may eventually inherit the dominant position within the group (territorial inheritance; Woolfenden & Fitzpatrick, 1978; Zack & Stutchbury, 1992; Russell & Rowley, 1993; Ragsdale, 1999; Queller et al., 2000), or they may gain a breeding position elsewhere after having spent time in the group (Walters et al., 1988; Zack, 1990; Zack & Stutchbury, 1992; Russell & Rowley, 1993; Green & Cockburn, 2001). These advantages may co-occur with a "safe haven" mechanism, due to improved survival of offspring in the natal territory (Ekman et al., 2000). If individuals

have to wait for breeding positions, survival during the waiting period becomes an important predictor of fitness (Faaborg & Bednarz, 1990; Ekman et al., 2000; Green & Cockburn, 2001). Philopatric Siberian jay (*Perisoreus infaustus*) offspring have an odds ratio of being killed by predators 62% lower than offspring that dispersed promptly after independence to join groups of unrelated individuals (20.6% versus 33.3% winter mortality) (Griesser et al., 2006).

Dispersers typically have a phenotype allowing them to colonize unoccupied space, but this same phenotype is selectively disadvantageous under crowded conditions (e.g. Duckworth & Kruuk, 2009). Dispersal from the natal group often has high costs unless dispersing females can join other breeding groups (Berger, 1987; Van Vuren & Armitage, 1994; Nunes, 2007; Ronce, 2007; Doligez & Part, 2008; Strier, 2008; Clutton-Brock & Lukas, 2012). Dispersing meerkats have lower rates of weight gain while foraging than residents, levels of glucocorticoids rise and they suffer higher parasite load (Young & Monfort, 2009). As well as affecting survival, the energetic costs of dispersal may delay breeding and reduce reproductive potential (Ronce, 2007; Fisher et al., 2009). Under the risk of predation, subordinates of the cooperatively breeding cichlid *Neolamprologus pulcher* stay at home rather than leave and breed independently (Heg et al., 2004). Individuals that disperse to unfamiliar areas may also be more vulnerable to predators: for example, experimental studies show that dispersing white-footed mice are more susceptible than residents to predation by owls (Metzgar, 1967). In addition, they are often likely to be attacked by members of resident groups, sometimes with fatal consequences (Fritts & Mech, 1981; Packer & Pusey, 1982; Boydston et al., 2001; Creel & Creel, 2002). High rates of mortality in dispersers may be particularly common in carnivores, where attacks by residents are likely to be dangerous (Waser, 1996): for example, grey wolves making extra-territorial forays die at five times the rate of residents (Messier, 1985) while mortality rates in dispersing African wild dogs are 2.7 times higher than those of residents in females and 6.8 times higher in males (Creel & Creel, 2002). Several studies have also shown that dispersal is associated with substantial increases in mortality in many other species (Errington, 1963; Van Vuren & Armitage, 1994): for example, in red howler monkeys, 43–52% of dispersing females are suspected or known to die (Crockett & Pope, 1993).

Uncertainty can be measured as the variance of a distribution of environmental quality, and adversity as the mean (Andras et al., 2003). Both adversity and

uncertainty have been conceptualised as aspects of environmental 'risk' (Daly & Wilson, 2002). Risky environments can be expected to increase the costs of dispersal. As well as suffering the direct costs of moving between groups, dispersing females lose the potential benefits of associating with kin and this may have an important influence on the probability that they will disperse (Lambin et al., 2001; Perrin & Goudet, 2001; Silk, 2007). Studies have suggested positive effects of kin on philopatry and sociality in a wide variety of systems, including spiders (Jones & Parker, 2002), lizards (Davis, 2011), rodents (reviewed in Sherman, 1981; Lambin et al., 2001), primates (reviewed in Silk, 2002), and birds (Eikenaar et al., 2007; Hatchwell, 2009). In various mammals associating with kin can have important benefits to breeding success and/or survival (Fairbanks & Mcguire, 1987; Arnold, 1990a, b; Crockett & Pope, 1993; Lambin & Krebs, 1993; Moses & Millar, 1994; Lambin & Yoccoz, 1998; Pusenius et al., 1998; Pomeroy et al., 2000, 2001; Pavelka et al., 2002; Hacklander et al., 2003; Cheney et al., 2004; Silk, 2007; Krebs et al., 2007; Fedigan et al., 2008; Clutton-Brock & Lukas, 2012). Unconditional dispersal propensity, the baseline tendency for individuals to relocate independent of their current environment, can be favored in a stable environment as a means of reducing kin competition (Hamilton & May, 1977; Comins et al., 1980; Motro, 1983; Frank, 1986; Gandon & Michalakis, 1999; Perrin & Goudet, 2001) or the cost of demographic stochasticity (Travis & Dytham, 1998; Parvinen et al., 2003), but is disfavored by variation in fitness over space (Hastings, 1983; Holt, 1985). Ecological drivers of dispersal are environmental spatiotemporal variability and stochasticity, i.e. habitat heterogeneity, availability and distribution (Gadgil, 1971; Comins et al., 1980; Levin et al., 1984; McPeck & Holt, 1992) that induce a cost for dispersing individuals, as they face the risk to end up in unsuitable habitats (Hastings, 1983; Morris, 1991), and thus select against dispersers. In an uncertain, unpredictable environment it should be selectively favored to reduce uncertainty at least to some degree by associating with familiar individuals. Multi-species models indicate that the fraction of a community richness that comprises mutualistic versus exploitative relationships is greatest with low dispersal ability (Filotas et al., 2010a), consistent with empirical work in arid systems (Kéfi et al., 2008). Function, diversity and interspecific interactions of locally linked communities undergo a phase transition with changes in the rate of species dispersal. Low spatial interconnectedness favors the spontaneous emergence of strongly mutualistic communities which

are more stable but less productive and diverse. On the other hand, high spatial interconnectedness promotes local biodiversity at the expense of local stability and supports communities with a wide range of interspecific interactions (Filotas et al., 2010b).

At many levels of life, from plants to human societies, cooperation thrives in conditions where the environment is most adverse and unpredictable (see chapter 15.2.1). Plants at lower temperatures and higher altitudes, where abiotic stress is high, compete less and cooperate more with their neighbors (Callaway et al., 2002); bacteria and amoebae socialize in adverse environments (see chapter 5); nematodes *Caenorhabditis elegans* aggregate in response to stressors (De Bono et al., 2002); animals form more cohesive or larger groups, with consequent greater mutualistic benefits under greater predation risk (Seghers, 1974; Farr, 1975; Dunbar, 1988; Spieler, 2003; Krams et al., 2010); mole-rats, a highly social species, delay dispersion more in arid than in mesic habitats (Spinks et al., 2000); human in-group solidarity is greatest when the group is under threat or in a harsh environment (Levine & Campbell, 1972; Goody, 1991; Hogg, 1992; Hewstone et al., 2002). Likewise, adverse, uncertain, and unpredictable environments favor cooperative behavior (Andras et al., 2007). In chapter 9, I cite a text passage in which Laura Betzig (2004) succinctly highlighted the interrelationship between limited dispersal and asymmetric conflict/dominance hierarchies underlying coerced cooperation in human societies. The environmental conditions that favor cooperativity discourage dispersal and promote philopatry, thus shaping the preferential kinship structure of cooperative communities. Thus, limited dispersal and cooperation are epiphenomena of their common "confounding factor" on which both depend: environmental heterogeneity and stochasticity. This shared causal factor results in a spurious relationship.

## 5. The social games of microbes: cooperation, altruism, cheating or exploitation?

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*From the elephant to butyric acid bacterium—it is all the same!*

Albert Jan Kluyver, 1926

*Anything found to be true of E. coli must also be true of elephants.*

Jacques Monod, 1954

## Summary

Understanding the ecological conditions that favor, and the genetic “fossil record” that regulates, social behavior in prokaryotes and “basal eukaryotes” holds the key to understand the evolutionary rationale of sociality. The natural lifestyle of microbes is characterized by inherent “feast and famine” cycles, limiting amounts of nutrients being rather the rule than the exception, long periods of nutritional deprivation being punctuated by short periods that allow fast growth. The feast-to-famine transition is not merely a response to a drop in nutrient availability; this transition also involves cooperative cell-to-cell signaling pathways and social aggregation, the results of which range from sporulation to fruiting body and complex pattern formation. Both the bacteria *Myxococcus xanthus* and amoeba *Dictyostelium discoideum* are single-celled under abundant resources but socialize under metabolic stress. Largely, stochastic processes route clonal cells into different cell fates. Cells destined to become metabolically dormant, resilient, spores coerce other cells into death by means of toxins. The resources that thereby become available fuel the metamorphosis to spores in an otherwise resource-depleted environment.

Cooperative assembly of unicellular organisms into multicellular aggregates, mounds and fruiting bodies has evolved many times in evolution and is common in nature. When exposed to harsh environmental conditions such as starvation, hard surfaces, heat, and hazardous chemicals, bacteria show cooperative behavior with the formation of complex colonies with different spatiotemporal patterns that represent efficient strategies for adaptation and survival. Biofilms are large, three-dimensional aggregates of bacteria with several properties that require differentiation and division of labor. Microbial cooperation is often associated with public goods that can increase the local carrying capacity, automatically creating a social trait-group structure. Bacteriocins have been found in all major lineages of Bacteria and Archaea and play a major role in communication and cooperation of cells. Almost all bacteriocins are synthesized during postlogarithmic growth when both food and space are exhausted. Under metabolic stress, *Bacillus subtilis*, *Streptococcus pneumoniae* and a host of other bacterial species commit siblicide/fratricide and cannibalism, using the remains of their kin as resource for sporulation, competence for genetic transformation or biofilm formation. Siblicide and the extracellular DNA it

provides appear to have an important role in biofilm and matrix formation. The latter functions as a permeability barrier to limit both the diffusion of beneficial nutrients away from the biofilm and prevent or slow the diffusion of harmful substances. Biased by kin selection theory these siblicides, although clearly enforced, are interpreted as altruistic sacrifice.

In the “veil of ignorance” thought experiment, individuals choose between alternative social arrangements in a society. Ignorant of the position they will occupy in that forthcoming society individuals establish rules that they regard as fair from behind a veil of ignorance. As a measure of risk or inequity aversion, equal allocations of resources are chosen. Individuals consistently dislike unfair social outcomes but rather prefer playing risky but fair social lotteries. When it comes to distributing non-divisible, scarce goods in social competitions, a fair lottery excludes unjust influences. In evolutionary biology, the veil-of-ignorance concept has been used to explain the randomization of alleles in fair meiosis where each gene has a 50% chance to make it into any gamete.

In colonies of clonal cells that are metabolically stressed the competition for scarce resources is decided by a fair lottery. Behind the “veil of ignorance”, the competitors are not “aware” of their relative position in the competitive hierarchy. This hierarchy is determined stochastically through a variety of cellular processes with inherent noise that renders the cells heterogeneous and the lotteries fair.

According to Mayr (1961) evolutionary biology differs from functional biology because it also asks about the “why” of behavior: “It is obvious that the evolutionist has in mind the historical ‘how come?’ when he asks ‘why?’ Every organism, whether an individual or a species, is the product of a long history, a history that dates back more than 2000 million years.” Since the evolutionary past holds the key to understand the evolutionary present, this chapter is intended to trace the ecological conditions and genetic “fossil record” (Runnegar, 1986; Buss, 1987 p. 90; Heininger, 2012, 2013) of social behavior in prokaryotes and “basal eukaryotes”. Aggregation and the formation of stalks for dispersal of resistant and metabolically quiescent spores allow social bacteria and cellular slime molds to escape deteriorating local conditions (Bonner, 1982; Velicer et al., 2000). Importantly, experiments with bacteria (Travisano & Velicer, 2004) and social amoeba (Strassmann et al., 2000a) suggest that the ‘decision’ to cooperate or defect (in a general sense) is

stochastic, and moreover that these 'decisions' are controlled by genetically-encoded probabilities that are evolvable (Khare et al., 2009). (When speaking of 'decisions', use of the term is in an evolutionary sense, not implying any conscious rationalization on the part of individual organisms.) Molecular biological processes underlying these 'decisions' are exemplarily illustrated with reference to the social bacteria *Myxococcus xanthus* and amoeba *Dictyostelium discoideum*.

The social interactions of *Myxobacteria* and *D. discoideum* highlight that

- (i) Both cooperation and competition phenomena are shaped by ecological conditions and are context-dependent
- (ii) Interactions are dynamic
- (iii) Winners and losers of social interactions are largely determined by stochastic processes.

### 5.1 *Myxococcus xanthus*

Myxobacterial cells are single-celled but social; they swarm by gliding on surfaces as they feed cooperatively. Upon nutrient deprivation, populations of the bacterium *M. xanthus* migrate towards high-density focal points and cluster into aggregates of approx. 100,000 rod-shaped individuals (Shimkets, 1999). These aggregates form a multicellular fruiting body in which a fraction of the cells develop into myxospores. During the process of aggregation, early mound and fruiting body formation, approximately 80% of the cells undergo cell lysis, while the remaining 20% are converted into myxospores. Depending on the particular conditions of development, however, the proportion of dying cells may also range from 20 to 90%. Spore development includes the differentiation from the rod-shaped vegetative cell to a spherical, nonmotile, environmentally resistant and metabolically quiescent myxospore. Both sporogenesis and programmed cell death in the cells building the fruiting body are effected by a toxin-antitoxin system (Nariya & Inouye, 2008). One pathway governs aggregation and sporulation of some cells in the starving population and requires the so-called C-signaling. The levels of the bifunctional transcription factor/antitoxin MrpC and its related proteolytic fragment MrpC2 are increased, inhibiting the cell death pathway in the spores via direct interaction of MrpC with the MazF toxin (Nariya & Inouye, 2008). Another pathway causes programmed cell death that requires the MazF toxin (Mittal & Kroos, 2009a, 2009b) whose endoribonuclease activity ultimately results in cell death (Nariya & Inouye, 2008; Mittal & Kroos, 2009a). In cells destined to undergo programmed cell death, binding of MrpC to the mazF promoter region would

activate transcription, leading to increased MazF toxin levels. Accordingly, MrpC is a key determinant of cell fate (Mittal & Kroos, 2009b). Stochastic cell fate appears to be determined by developmental heterogeneity and feedback loop-based bistability (Russo-Marie et al., 1993; Lee, 2009; Bhardwaj, 2013, see chapter 5.4.1) involving the Spo0A transcriptional regulator (González-Pastor et al., 2003; Ellermeier et al., 2006). This bistable switch, cued initially by stochastic variations in gene expression at the single-cell level, divides a population of genetically identical cells into alternate cell fates (Søgaard-Andersen & Yang, 2008). Cannibalism is considered to provide essential nutrients for the conversion of rod-shaped cells to mature spores (Wireman & Dworkin, 1977; Dworkin, 1996). Deletion of the toxin results in elimination of the obligatory cell death during fruiting body development causing dramatic reduction in developmental progression and spore formation (Nariya & Inouye, 2008; Søgaard-Andersen & Yang, 2008) suggesting that cell death is a necessary component to complete sporogenesis that depends on energy and building blocks provided by the apoptotic cells. Interestingly, the toxin-antitoxin system is also linked to persisters (Moyed & Bertrand, 1983). Persisters are cells that neither grow nor die in the presence of bactericidal antibiotics (Lewis, 2010). These cells are not mutants but phenotypic variants of regular cells that form stochastically in microbial populations (Lewis, 2010), representing a type of microbial bet-hedging (Heininger, 2015).

There are two developmental strategies for myxobacteria. One is a complicated social behavior: fruiting body structures form from numerous cells, and the cellular development is dependent on cell density. A fruiting body ensures that a new life cycle is able to start in a terrestrial environment (Kraemer et al., 2010). The other is simple: the social behavior is an evolutionary burden in asocial habitats like seawater. In asocial habitats myxospores form directly from vegetative cells, and the cells grow independent of the cell density (Zhang et al., 2005). It seems that the adaptation of the halotolerant myxobacteria to a marine environment is a degenerative procedure (Zhang et al., 2005). There could be a shift between the two developmental patterns if the cells migrate between the two environments (Li et al., 2011).

### 5.2 *Dictyostelium discoideum*

The social amoeba or cellular slime mould *Dictyostelium discoideum* is at the transition of uni- and multicellularity and a valuable model organism for a variety of biomedical phenomena including social

interactions (Annesley & Fisher, 2009; Heininger, 2012). *D. discoideum* is single-celled under conditions of nutritional abundance. When their bacterial food source is exhausted, as many as 100,000 cells aggregate to form a multicellular migrating slug, which moves toward a region suitable for culmination. This eventually becomes a fruiting body in which some amoebae in the group differentiate to form hardy spores and other microbes die to form a stalk structure. Most of the prestalk cells are located in the front one-fifth of the slug, whereas all of the prespore cells are located in the rear four-fifths. One apparent difference between the prespore and prestalk populations is in their degree of heterogeneity: there are several prestalk-cell subtypes, whereas, apart from an anteroposterior gradient in their utilization efficiency of certain prespore-promoter constructs (Haberstroh & Firtel, 1990), the prespore cells seem to be a homogeneous population (Williams, 2006). Importantly, the multicellular structure is able to pass through soil barriers that solitary amoeba cannot cross and lifts the spores above the soil where spores can be picked up for long-distance dispersal (Kuzdzal-Fick et al., 2007). Both stochastic and deterministic processes regulate migration and cell fate decisions (Miyanaga et al., 2007; Gregor et al., 2010; Prindle & Hasty, 2010; Chattwood & Thompson, 2011; Chattwood et al., 2013). A lottery system decides who becomes a spore and who does not (Gadagkar & Bonner, 1994). There is a manipulation of the aggregated cells so that the fertile spores become the reproductives and they literally suppress, by producing an inhibitor, some of the cells from following suit; they force those cells to become sterile stalk cells (Inouye, 1989). As in developmental programs of multicellular organisms (Heininger, 2001, 2013), prespore cells coerce prestalk cells into an apoptotic death program and the death of stalk cells fuels the energetically costly metamorphosis of the spore cells (Heininger, 2001, 2012). A closer look at the molecular biological events that regulate the social interactions elucidates the underlying exploitation in clonal populations. Prespore cells determine the fate of apoptosing prestalk cells by differentiation-inducing factors (DIFs), chlorinated alkylphenones, and other factors (Early & Williams, 1988; Maruo et al., 2004). *D. discoideum* amoebae are induced to differentiate into prestalk cells by the signalling molecule DIF-1 (Thompson & Kay, 2000a). The DIFs are synthesized in and released by prespore cells (Kay & Thompson, 2001) and are inactivated in prestalk cells (Brookman et al. 1987, Kay et al., 1999; Thompson & Kay, 2000a; b; Kay & Thompson, 2001), establishing a feedback loop that controls DIF-1 levels (Insall et al., 1992). The

inactivation, however, is inhibited by cyclic AMP (cAMP) (Insall et al., 1992) that plays a pivotal role in chemotaxis, differentiation and response to stress (Saran et al., 2002). DIF-1 is rather a poison than a signal (Atzmony et al., 1997; Parkinson et al., 2011; Strassmann & Queller, 2011) and acts antagonistically to cAMP by repressing prespore differentiation and directing a proportion of the cell population to differentiate as prestalk cells (Kay & Jermyn, 1983; Early & Williams, 1988; Kawata et al., 1996; Strassmann & Queller, 2011b). At low levels DIFs may induce prespore differentiation (Oohata, 1996) but at higher doses are requisite for prestalk cell development (Kopachik et al., 1983; Sobolewski & Weeks, 1988; Maruo et al., 2004). Mitochondrial malate dehydrogenase (mMDH) may be one of the target molecules of DIF-1: DIF-1 inhibits the enzymatic activity of mMDH and cell energy production, probably leading to the inhibition of proliferation (Matsuda et al., 2010) and cell death (Luciani et al., 2009). Prespore-produced DIF-1 inhibits redifferentiation of prestalk cells into prespores, i.e. transition into the dispersing and perennial germline (Firtel, 1995; Hudson et al., 2002). Thus, prespore cells inhibit the conversion of prestalk to prespore cells (Inouye, 1989, Shaulsky & Loomis, 1993; Kawata et al., 1996; Söderbom & Loomis, 1998; Maruo et al., 2004; Yamada et al., 2010) and ensure the supply of nutrients and building blocks by apoptotic stalk cells. The need to procure these resources in a resource-depleted environment regulates the dynamic and context-dependent relative proportion of prespore and prestalk cells. The balance is dynamic and responds to the loss of the respective other cell type. Cells that are initially destined to become prespore cells become apoptotic stalk cells when prestalk cells are removed from the equilibrium (Nadin et al., 2000; Råfols et al., 2001) and prestalk cells become prespore cells when prespore cells are removed (Shaulsky & Loomis, 1993; Råfols et al., 2001; Maruo et al., 2004). It can be inferred that survival and death of cells depends on environmental cues, the proportion of dying cells being regulated by the metabolic needs of the developing germ cells and the spore-dispersing role of fruiting bodies.

The conceptual framework of kin selection theory biased the interpretation of *D. discoideum* developmental skew. Despite the robust evidence that during clonal development prespore cells coerce prestalk cells into cell death, stalk cell death has consistently been regarded as being altruistic (Atzmony et al., 1997; Strassmann et al., 2000a; Hudson et al., 2002; Brännström & Dieckmann, 2005; Li & Purugganan, 2011). On the other hand, unequal

representation of genotypes within the sporehead of *D. discoideum* chimera has been taken as evidence for social exploitation (Strassmann et al., 2000a; Fortunato et al., 2003). One interpretation of these results is that there are widespread fixed cheating strategies (Hudson et al., 2002). In fact, however, both *D. discoideum* clonal and chimeric development deploys a substantial element of cell competition (see chapter 4.1.1). Importantly, during clonal development all *D. discoideum* genotypes examined differ significantly from one another in their constitutional proportion of developmental spore and stalk cell formation (Buttery et al., 2009). Intriguingly, culture conditions may give rise to differences in DIF sensitivity of genetically identical amoebae (Leach et al., 1973; Thompson & Kay, 2000b; Castillo et al., 2011). Cells with lowered DIF sensitivity, resulting from growth with glucose (see chapter 10.3), “cheat” and are overrepresented in the sporeheads when mixed with microbes grown without glucose (Leach et al., 1973; Thompson & Kay, 2000b). Similarly, in chimeras between cells that were weakened by growing them in media lacking glucose, or more acid media than normal, and normally cultured cells that were genetically identical, weakened cells were outcompeted by healthy cells in becoming spores (Castillo et al., 2011). A gene, *dimA*, in *D. discoideum* has two contrasting effects. It is required to receive the signalling molecule DIF-1 that causes differentiation into prestalk cells. Ignoring DIF-1 and not becoming prestalk should allow cells to “cheat” by avoiding the stalk. However, in aggregations containing the wild-type cells, lack of the *dimA* gene results in exclusion from spores (Foster et al., 2004). This pleiotropic linkage of stalk and spore formation limits the potential for cheating in *D. discoideum* because defecting on prestalk cell production results in an even greater reduction in spores.

In realistic starvation conditions, up to 15% of cells do not aggregate. In short-term starvation, non-aggregating cells have an advantage over cells in aggregates since they resume growth earlier upon arrival of new nutrients, but have a shorter lifespan under prolonged starvation. The partitioning of cells into aggregating and non-aggregating fractions is optimal in fluctuating environments with an unpredictable duration of starvation periods. *D. discoideum* thus constitutes a model system lying at the intersection of microbial cooperation and solitary bet-hedging (Dubravcic et al., 2014).

### 5.3 Microbial cooperation and competition

The natural lifestyle of microbes is characterized by inherent “feast and famine” cycles, limiting amounts of

nutrients being rather the rule than the exception, long periods of nutritional deprivation being punctuated by short periods that allow fast growth (Kolter et al., 1993; Msadek, 1999; Navarro Llorens et al., 2010; Heininger, 2012). The feast-to-famine transition is not merely a response to a drop in nutrient availability; this transition also involves cell-to-cell signaling pathways, the results of which range from sporulation to fruiting body and complex pattern formation (Shapiro & Dworkin, 1997; Shimkets, 1999). These transitions are characterized by key events in shedding light on the dynamics and patterns of microbial sociobiology.

Cells alter their gene expression in response to each other and to the local microenvironment (Thiery & Chopin, 1999; Eichenberger et al., 2004; Waters & Bassler, 2005; Battesti et al., 2011), and cell groups can evolve rapidly (Kreft, 2004a; West et al., 2006; Merlo et al., 2006; Nadell et al., 2009, 2013; Xavier, 2011, Le Gac et al., 2012). Arguably the most complex social behaviors occur in two spore-forming species: *Bacillus subtilis* and *Myxococcus xanthus* (Nadell et al., 2009, see chapter 5.1). Developmental processes display features of both cell cooperation and competition. Aggregation by these species comes closest to multicellular development: sporulation in both results from a series of temporally separated checkpoints that produce a predictable, directional sequence of differentiation events (Monds & O’Toole, 2008). *B. subtilis* provides a dramatic example of bacterial differentiation; populations of a single strain display bimodal distributions for multiple phenotypes, including competence, chaining (Losick & Desplan, 2008), motility (Kearns et al., 2004), production of extracellular polymeric substances (Vlamakis et al., 2008), and spore formation (Branda et al., 2001). A subpopulation of cells in wild *B. subtilis* biofilms produces spores in small fruiting body structures that develop at the tips of biofilm surface irregularities. Larger groups of spores are formed by *M. xanthus*, in which starving cells aggregate to form a fruiting body whose cell density approaches that of many biofilms (Julien et al., 2000). It is also striking that in both species spore-destined cells kill other members of the population during fruiting body formation (Wireman & Dworkin, 1977; González-Pastor et al., 2003; Nadell et al., 2009). In *B. subtilis*, cell death releases nutrients that increase the viability of the remaining population, allowing it to delay commitment to sporulation (González-Pastor et al., 2003).

#### 5.3.1 Cooperation

Cooperative assembly of unicellular organisms into multicellular aggregates such as biofilms, mounds and fruiting bodies has evolved many times in evolution

and is common in nature (Bonner, 2000; Claessen et al., 2014). The structural complexity and degree of organization of microbial multicellular structures vary from a simple single-layer biofilm and simple aggregates to complicated structures like the fruiting bodies of myxobacteria and slime molds, complex natural biofilms and the colonies of various microbes (Watnick & Kolter, 2000; Crespi, 2001; Palková & Váchová, 2006; Annesley & Fisher, 2009; Velicer & Vos, 2009; Cáp et al., 2012; Elias & Banin, 2012). O'Toole et al. (2000) describe biofilm development as a process of microbial development, not unlike that observed in fruiting-body formation by *M. xanthus* and sporulation in *B. subtilis*. Biofilms are large, three-dimensional aggregates of bacteria—usually comprised of several metabolically diverse species but sometimes hundreds of them—which adhere to surfaces in moist or watery environments. These include soils, teeth, living tissue, medical implants, air conditioning systems, pipelines, sewage treatment plants, and marine equipment—just about any sort of surface in an aqueous environment (Costerton et al., 1987; Kroes et al., 1999; Ram et al., 2005; Ley et al., 2006b; Lyon, 2007). When exposed to harsh environmental conditions such as starvation, hard surfaces, extreme heat, and hazardous chemicals, bacteria show cooperative behavior with the formation of complex colonies with different spatiotemporal patterns that represent efficient strategies for adaptation and survival (Shapiro, 1988; 1998; Budrene & Berg, 1991; Ben-Jacob E, et al., 1994; 2000; Harshey, 1994; Heininger, 2001; Ben-Jacob, 2003) and that are coordinated by cell-to-cell signaling (Kaiser & Losick, 1993; Kaiser, 1996; Wirth et al., 1996; Watnick & Kolter, 2000; Ben-Jacob et al., 2004; Bassler & Losick, 2006; Ben-Jacob, 2009). Cooperative biofilm formation tends to peak at intermediate frequencies of disturbance but the peak shifts toward progressively higher frequencies of disturbance as resource supply increases (Brockhurst et al., 2010). *Saccharomyces cerevisiae* is also able to agglomerate cells into organized structures such as flocs, biofilm, and pseudohyphae. These non-sexual clumps create protective shields for cells in inner parts to escape from abiotic/biotic attacks (Smukalla et al., 2008), and to respond to nutrient starvation (Gimeno et al., 1992; Cullen & Sprague, 2000). Biofilm maturation is controlled by the availability of nutrients and quorum sensing (i.e. the ability of cells to sense a high population density) (Stanley & Lazazzera, 2004). Biofilms can be thick, homogeneous mats of cells, or they can be complex structures composed of pillars with water channels that have been proposed to allow for nutrient influx, oxygen flow and waste efflux (Davey

& O'Toole, 2000). Biofilm communities exhibit several properties that are thought to require differentiation and division of labor among cells to produce highly resilient biofilm structures (Stoodley et al., 2002). Mature biofilms of *Pseudomonas aeruginosa* were shown to have a radically different protein profile from planktonic bacteria grown in chemostats (Sauer et al., 2002). As much as 50% of the detectable proteome (over 800 proteins) was shown to have a sixfold or greater difference in expression. Of these, more than 300 proteins were detectable in mature biofilm samples that were undetectable in planktonic bacteria.

Microbial cooperation is often associated with public goods that can increase the local carrying capacity (West et al., 2007b; Platt & Bever, 2009). Public goods are those produced by an individual and shared with other group members (Driscoll & Pepper, 2010), automatically creating a social trait-group structure (Wilson 1975, 1980). They typically increase the fitness of all group members, but at a unilateral cost to the producer. Examples include the production of siderophores (West & Buckling, 2003), viral replication enzymes (Turner & Chao, 1999), specialized resources (Guyon et al., 1993; Gordon et al., 1996) and secreted exoenzymes (Hillesland et al., 2007; Koschwanez et al., 2011). The depth of the mature biofilm appears to be regulated to allow for maximal nutrient acquisition. Far from being a case of pure Darwinian competition, interactions among these species and with eukaryotic hosts may be mutually beneficial (Wingreen & Levin, 2006). A recent case in point is the discovery of a mutualistic interaction of four bacterial species with the tomato plant (Botta et al., 2013). Rather than competing, the four species coexist and strongly promote plant growth by fixing nitrogen, providing growth hormones, and preventing hostile bacterial species from growing.

Several stress conditions induce microcolony formation (Webb et al., 2003a; Jefferson, 2004). The most ubiquitous environmental trigger appears to be nutrient stress, suggesting that aggregation and formation of multicellular structures is an adaptive response that mediates survival under unfavorable conditions. As final common pathway of cellular stress responses (see chapter 9.3), oxidative stress triggers biofilm and fruiting body formation (Schembri et al., 2003; Murphy et al., 2005; Wen et al., 2005; Sampathkumar et al., 2006; Boles & Singh, 2008; Geier et al., 2008; Cáp et al., 2012). *Escherichia coli* and *Salmonella typhimurium* for example, when exposed to oxidative stress, attract neighboring cells that allows the cooperative degradation of toxic materials (Budrene & Berg, 1991; Blat & Eisenbach,

1995). The extracellular polymer matrix of biofilms provides protection from desiccation, toxins and antibiotics, and it might also serve to bind and hold nutrients and enhance physiological stability (Decho, 1994). Biofilm-associated cells are more resistant to many toxic substances such as antibiotics, chlorine, and detergents (Costerton, 1987; Costerton et al., 1999; Hogan & Kolter, 2002). There is evidence that decreased diffusion into the biofilm (De Beer et al., 1994; Suci et al., 1994), decreased bacterial growth rate in a biofilm (Evans et al., 1990), biofilm-specific substances such as exopolysaccharide (Yildiz & Schoolnik, 1999), and the quorum-sensing specific effects (Davies et al., 1998, Hassett et al., 1999) may be reasons for this resistance. In addition, a strong advantage to polymer production arises as an emergent property (see chapter 16). Secretion of extracellular polymers by a cell allows it to push descendants into a more oxygen-rich environment. At the same time, it provides a strong competitive advantage at the scale of the cell lineage by suffocating neighboring nonproducers (Xavier & Foster, 2007). This pleiotropic linkage of competitive advantage and polymer production limits the potential for cheating in biofilms. The effect of polymer production, therefore, has a strong analogy in plants competing for light, where vertical growth and increased foliage area selfishly increase access to light at the expense of competitors (Goodnight et al., 1992).

The human oral cavity is one of the most densely populated sites of the human body, consisting of as many as 600 to 800 bacterial species (Paster et al., 2006; Dewhirst et al., 2010). Tooth biofilms have been shown to consist of stable consortia of hundreds of distinct species, and bacterial mats are believed to consist of even larger numbers of species, in dynamic equilibrium among themselves, and with multiple bacterial viruses (Wingreen & Levin, 2006). These microbial inhabitants have co-evolved not only with their host, but also with each other, leading to extensive intercellular communications across species. There is evidence that oral microbes participate in intercellular communications with co-inhabitants through cell contact-dependent physical interactions, metabolic interdependencies, as well as coordinative signaling systems to establish and maintain balanced microbial communities (Bamford et al., 2009; Guo et al., 2014; Sztajer et al., 2014). Cooperative metabolic interactions either via cross-feeding or through cooperatively metabolizing substrate maximize co-residents' potential to extract energy from limited substrates. In addition to synergistic interactions, oral bacterial species are also engaged in intense

competition for limited space and nutritional resources using compounds such as bacteriocin and  $H_2O_2$ , which plays a crucial role in defining the structure and activity of oral microbial communities (Guo et al., 2014).

### 5.3.2 Competition and siblicide

In search of food and space to multiply, bacteria secrete ribosomally synthesized polypeptides that cause the selective killing of competing microorganisms. The antimicrobial compounds are called bacteriocins, and usually have a narrow spectrum of activity as they kill only closely related bacteria, which compete for the same resources (Heininger, 2001; González-Pastor et al., 2003; Guiral et al., 2005; Ellermeier et al., 2006; Håvarstein et al., 2006; Claverys and Håvarstein, 2007; Be'er et al., 2009, 2010). Also bacteria competing with unrelated or distantly related strains for limited resources in the same niche cooperate to secrete antibacterial compounds as "chemical weapons" to attack the competing strains (Czárán et al., 2002; Eijsink et al., 2002). Bacteriocins have been found in all major lineages of Bacteria and Archaea (Torreblanca et al., 1994; Riley & Wertz, 2002). Within a species tens or even hundreds of different kinds of bacteriocins are produced (James et al., 1991). According to Klaenhammer (1988), 99% of all bacteria make at least one bacteriocin and the only reason more have not been found is that few researchers have looked for them. Several studies have shown the involvement of bacteriocins and bacteriocin-like peptides in, for example, quorum sensing (Diep et al., 1995; Kuipers et al., 1995; Kleerebezem et al., 1999; Kleerebezem & Quadri, 2001; Eijsink et al., 2002; Kleerebezem, 2004; Gobbetti et al., 2007) and remodelling of sugar metabolism in lactic acid bacteria (Opsata et al., 2010), suggesting that these peptides also play a role in communication and cooperation of cells. Bacteriocins may also act as communication signals in bacterial consortia, e.g., biofilms (Gillor, 2007). Almost all bacteriocins are synthesized during postlogarithmic growth when both food and space for bacterial multiplication are exhausted (Baba & Schneewind, 1998) or during stress (Gillor et al., 2008). Bacteriocins and antibiotics are frequently upregulated by stress responses to nutrient limitation and cell damage but very rarely upregulated by stress responses to heat or osmotic stress, which typically are not competition related (Cornforth & Foster, 2013). Further growth can then only occur at the expense of bacterial competitors, and the fight for survival employs some exquisitely designed compounds that are toxic for specific microbial target cells. Stress-related genes were found to be upregulated in biofilm settings. For instance,

genes regulated by the SOS system (involved in repairing DNA damage), such as *recA*, *dinI* and *sulA*, were upregulated by twofold or more in *E. coli* biofilms compared with their respective expression in stationary-phase planktonic cultures (Beloin & Ghigo, 2005; Beloin et al., 2008). Antibiotic activities can be obtained from many different peptide sequences and structures, but bacteriocins generally share the fate of extensive posttranslational modification (Kolter & Moreno, 1992; Bierbaum et al., 1996). Such processing confers specific chemical properties and toxic activities that could not be otherwise achieved with a repertoire of 20 proteinogenic amino acids (Bierbaum et al., 1996). When combined with secretion into the extracellular medium, post-translational processing can also prevent the premature activation of the toxic properties of a bacteriocin, thereby protecting host cells from committing suicide (Garrido et al., 1988; Kolter & Moreno, 1992; Kupke & Götz, 1996; Peschei & Götz, 1996; Thumm & Götz, 1997). In *E. coli*, production of an antibacterial toxin (colicin) is controlled by the SOS system and stochastic factors resulting in colicin production by only a small fraction (0.5–3%) of their respective *E. coli* populations during stationary growth phase (Mulec et al., 2003; Cascales et al., 2007; Mrak et al., 2007; Kamenšek et al., 2010; Majeed et al., 2014). Once activated in the medium, bacteriocins have the remarkable property of finding and killing specific bacterial competitors while causing little or no harm to the host cell (Baba & Schneewind, 1996). In many strains, bacteriocin production is controlled in a cell-density dependent manner, using a secreted peptide-pheromone for quorum-sensing. The sensing of its own growth, which is likely to be comparable to that of related species, enables the producing organism to switch on bacteriocin production at times when competition for nutrients is likely to become more severe. Unlike other antimicrobials, the lethal activity of bacteriocins is often limited to members of the same species as the producer, suggesting a major role in competition with conspecifics (Riley et al., 2003; Be'er et al., 2009, 2010). Such “chemical weapons” are even used to attack sibling cells within the same colony (Heininger, 2001; González-Pastor et al., 2003; Ellermeier et al., 2006; Claverys & Håvarstein, 2007). In liquid cultures, the outcome of competition between *E. coli* that produce colicin and sensitive *E. coli* is frequency dependent (Chao & Levin, 1981); the colicinogenic bacteria are at an advantage only when fairly common (frequencies in excess of  $2 \times 10^{-2}$ ). However, in a soft agar matrix, a structured habitat, the colicinogenic bacteria have an advantage even when initially rare (frequencies as low as  $10^{-6}$ ). In a

liquid culture, bacteria exist as randomly distributed individuals and the killing of sensitive bacteria by the colicin augments the amount of resource available to the colicinogenic bacteria to an extent identical to that experienced by the surviving sensitive bacteria. On the other hand, the bacteria in a soft agar matrix exist as single-clone colonies. As the colicinogenic colonies release colicin, they kill neighboring sensitive bacteria and form an inhibition zone around themselves. By this action, they increase the concentration of resources around themselves and overcome their growth rate disadvantage. Based on these findings, Chao and Levin (1981) suggested that structured habitats are more favorable for the evolution of colicinogenic bacteria.

Another example of siblicide is “cannibalism” in *Bacillus subtilis*, where bacteria during the early stages of sporulation produce chemicals that kill some siblings, which become food for the surviving bacteria (González-Pastor et al., 2003; Ellermeier et al., 2006). Spore formation by *Bacillus subtilis*, which is triggered by nutrient limitation, is an elaborate developmental process that takes place over the course of 7 to 10 hours and involves the conversion of a growing cell into a dormant cell type (a spore) that can remain inert for many years. The decision to form a spore is a life-or-death one (Bassler & Losick, 2006). A *B. subtilis* cell could be at a considerable disadvantage if it commits to spore formation in response to what turns out to be a brief fluctuation in nutrient availability. To guard against this possibility, the bacterium deploys a system of cannibalism in which cells that have entered the sporulation pathway forestall the absolute commitment to spore formation (González-Pastor et al., 2003; González-Pastor, 2011). At the heart of the cannibalism system is the master regulator for sporulation, Spo0A, which is activated by phosphorylation via a phosphorelay that is subject to three positive feedback loops. In response to nutrient limitation, about half of the *B. subtilis* cells activate Spo0A and enter the pathway leading stochastically to competence or sporulation (Mirouze et al., 2011), and the other (Spo0A-inactive) cells do not. The ultimate decision to sporulate is, however, stochastic in that only a portion of the population sporulates even under optimal conditions (Chastanet et al., 2010; Chastanet & Losick, 2011; Narula et al., 2012). Cells that have activated Spo0A produce and export a killing factor and a protein toxin that together kill nonsporulating siblings. Their deaths result in the release of nutrients that, in turn, delay or reverse progression into sporulation by the cells that have activated Spo0A. When no siblings remain to be cannibalized and no other sources of nutrients become available,

development progresses to the point that spore formation becomes irreversible. The response to the cannibalism toxin involves an intercellular chemical signaling system of unusual simplicity (Ellermeier et al., 2006). To avoid suicide, toxin-producing cells (i.e., Spo0A-expressing cells) simultaneously produce a membrane bound immunity protein that neutralizes the toxin in the membrane. It is likely that cells become cannibalistic after the commitment to sporulation. If cells, however, become cannibalistic for lower levels of phosphorylated Spo0A (that corresponds to the competence window), they can decide between competence and cannibalism (Schultz et al., 2009).

Another example of fratricide is the allolysis behavior of the pathogen *Streptococcus pneumoniae* (during the transition to competence) (Steinmoen et al., 2002, 2003; Guiral et al., 2005; Håvarstein et al., 2006; Claverys & Håvarstein, 2007; Eldholm et al., 2009; Trappetti et al., 2011). *S. pneumoniae* is known for its ability to enter into a state of genetic competence under conditions of high cell population density in response to a secreted signaling peptide. Analogous to the case of *B. subtilis* sporulation, only a fraction of the *S. pneumoniae* cells in the population become competent in response to the peptide autoinducer. Those that do so elaborate a bacteriocin that causes the lysis of noncompetent cells in the population. Claverys and coworkers (Guiral et al., 2005; Håvarstein et al., 2006) report that the lysed cells release not only transforming DNA and nutrients but also pneumolysin and other factors important for virulence. Thus, rather than relying on self for secretion of virulence factors, *S. pneumoniae* kills some its relatives for this purpose which facilitates invasion of its host.

After the pioneering work in *B. subtilis* and *S. pneumoniae*, siblicide has been demonstrated in various other bacterial species (Sedgley et al., 2009; Thomas et al., 2009; Hwang et al., 2011), suggesting that this may be a frequent phenomenon. Exopolymeric substances (EPS) form the extracellular matrix of biofilms (Lawrence et al., 1991) and comprise a wide variety of polysaccharides, proteins, glycoproteins, glycolipids and, in some cases, large amounts of extracellular DNA (eDNA). eDNA was first shown to be present in the extracellular matrix of biofilms formed by *Pseudomonas aeruginosa* and necessary for biofilm formation (Whitchurch et al., 2002), and is now widely recognized as a major constituent of the matrix (Flemming et al., 2007). The matrix functions as a permeability barrier to limit both the diffusion of beneficial nutrients away from the biofilm and prevent or slow the diffusion of harmful

substances such as antibiotics and predatory cells of the immune system from accessing matrix-embedded cells (Costerton et al., 1999). Fratricide and the eDNA it provides may also have an important role in biofilm formation (Webb et al., 2003b; Thomas et al., 2009; Trappetti et al., 2011; Berg et al., 2012; Wei & Håvarstein, 2012) and is essential for efficient gene transfer between *Pneumococci* in biofilms (Wei & Håvarstein, 2012).

#### 5.4 Excursion: "Veil of ignorance" and fair lotteries

John Harsanyi (1953, 1955) and John Rawls (1971) both used the veil of ignorance thought experiment to study the problem of choosing between alternative social arrangements and the problem of social justice (Okasha, 2012). Parties to an original agreement to establish a society and laws to govern are assumed to be completely ignorant of the position they will occupy in that forthcoming society. The purpose of this ignorance is to ensure that any decisions how to distribute resources across different positions are not motivated by a desire to tailor society to benefit one's own specific circumstances. A just society establishes rules that individuals regard as fair from behind a veil of ignorance about their position within society (Frank, 2013).

When it comes to distributing non-divisible, scarce goods in social competitions, three distributive mechanisms seem particularly prominent: (i) Selection, i.e. allocation according to some relevant criterion; (ii) Auction, i.e. bestowing the good on the highest bidder; or (iii) Lottery, i.e. a random allocation (Saunders, 2008). Given appropriate selection is impossible when parties have equal claims (e.g. in clonal populations), a lottery is preferable to an auction because it excludes unjust influences. The fairness of lotteries (Sher, 1980) gives each individual an equal chance of obtaining the good in question, as a surrogate for their equal claim to the good (Saunders, 2008). Of course, not all goods can be literally cut in half, as illustrated by the Biblical story of Solomon – half a baby is no use to anyone, and the real mother would rather surrender her claim than have her child cut in half. Thus, there are indivisible goods that cannot be shared in any sense and for which any allocation is necessarily 'winner takes all' (Saunders, 2008).

Individuals consistently have a strong betrayal aversion (Bohnet et al., 2008) and strongly dislike unfair social outcomes (Saito, 2012; Gaudeul, 2013), but rather prefer playing risky but fair social lotteries (Gaudeul, 2013; López-Vargas, 2014). A biased outcome is more readily accepted when chosen by an unbiased random draw than by one that is biased (Bolton et al., 2005). As a measure of risk or inequity

aversion, equal allocations are chosen either for insurance purposes or are due to impartial social preferences that value equality per se (Carlsson et al., 2005; Frignani & Ponti, 2008; Schildberg-Hörisch, 2010). In the inequity aversion model, individuals enforce social norms of fairness, thereby stabilizing cooperation and social cohesion (Fehr & Schmidt, 1999; Fehr & Fischbacher, 2004). Animals are risk-averse (Heininger, 2015) and individuals from cooperative species appear also to be inequity-averse (de Waal, 1996; Brosnan & de Waal, 2003, 2014; de Waal & Davis, 2003; Range et al., 2009; Brosnan et al., 2010a; Massen et al., 2012; Wascher & Bugnyar, 2013; but see Henrich, 2004; Bräuer et al., 2009; Silberberg et al., 2009; Horowitz, 2012). Brosnan (2011) argued that inequity aversion is a mechanism to promote successful long-term cooperative relationships amongst nonkin, a hypothesis that is supported by model simulations (Ahmed & Karlapalem, 2014).

The veil-of-ignorance concept has also surfaced in biology, in the context of meiosis, the cell division process by which sexually reproducing organisms halve their chromosome number: only one of each chromosome pair is passed to each gamete. Most of the time meiosis is 'fair', so that any particular gene has a 50% chance of making it into any gamete – a fact known as Mendel's law of segregation. When meiosis is fair, randomization puts each allele behind a veil of ignorance with regard to its direct transmission (interests) in each progeny. Behind the veil, each part of the genome can increase its own success only by enhancing the total number of progeny and thus increasing the success of the group (Frank, 2013). Randomization of position levels individual opportunity and promotes group cohesion. Given randomization of individual success within the group, an individual increases success only by increasing the success of the group as a whole (Frank, 2013). Probably any fair process can be corrupted by selfish individuals that try to "corriger la fortune". For example in many species, rogue genes can cheat Mendel's law and get into more than their fair share of gametes. This is known as 'meiotic drive' or 'segregation distortion'; the genes in question are called segregation-distorters (Zimmering et al., 1970; Okasha, 2012).

In addition to meiosis, various fair lottery processes determine the random allocation of the reproductive position in the forthcoming society of a multicellular organism or in a termite colony. Mammalian germline determination is a stochastic process. Cell populations in the embryo are not comprised of a single cellular entity, but instead display significant heterogeneity at

the molecular level, heterogeneity that is associated with an apparent probabilistic element of fate determination (Enver et al., 2009; Hough et al., 2009). Phenotypic fluctuations may be a general feature of any non-terminally differentiated cell (Stockholm et al., 2007, 2010; Chang et al., 2008; Hayashi et al., 2008; Kalmar et al., 2009). The cells fluctuate slowly but continuously between different phenotypic states that leads to a dynamic equilibrium with relatively constant proportions of various phenotypic variants in the population. The cellular microenvironment created by the cells themselves contributes actively and continuously to the generation of fluctuations depending on their phenotype. As a result, the cell phenotype is determined by the joint action of the cell-intrinsic fluctuations and by collective cell-to-cell interactions (Stockholm et al., 2010). Pluripotency is the capacity of a single cell to generate in a flexible manner all cell lineages of the developing and adult organism. The master pluripotent regulator Nanog has a key role in safeguarding stem cell pluripotency against differentiation and mediates germline development (Chambers et al., 2007; Silva et al., 2009; Zhang & Wolynes, 2014). Nanog is expressed in pluripotent embryo cells, derivative embryonic stem cells, and the developing germline of mammals and birds (Chambers et al., 2003; Mitsui et al., 2003; Yamaguchi et al., 2005; Laval et al., 2007). Murine embryonic stem cells display heterogeneity characterized by fluctuations between two clearly different phenotypic states of embryonic stem cells; one is stable ("high Nanog"; HN) and the other is unstable ("low Nanog"; LN). The transition between the HN to LN phenotype is stochastic and rare, whereas those from LN to HN are frequent. The observations are consistent with a model with excitable dynamics where the first change is rapid and noise-triggered followed by slow relaxation to the initial state (Kalmar et al., 2009). Likewise, in mouse embryonic stem cell cultures, a subset of cells is positive for both the pluripotency marker gene Oct-4, the undifferentiated state marker of embryonic stem cells Rex1, and a definitive marker of the germ cell lineage Stella, and these cell types and the marker-negative cells can interconvert (Hayashi et al., 2008; Toyooka et al., 2008).

Among the workers of a termite colony, only individuals in the sensitive period (a short period during the moulting interval when the developmental fate of an organism at the next moult is determined) are able to respond to orphaning of the colony and become neotenic replacement reproductives. As all workers pass through this period, they all have a fair chance of becoming neotenic, while at the same time

the number of actually competing individuals (that fight to death to take over the colony) is reduced. Thus, the sensitive period, besides honest signalling (via cuticular hydrocarbon profiles and trophallaxis), functions as a 'fair lottery' mechanism (Hoffmann, 2011; Hoffmann & Korb, 2011).

Evolution has no foresight. The "veil of ignorance" thought experiment also applies to a reproducing organism concerning the evolutionary scenarios that its offspring will experience. In uncertain, unpredictable environments bet-hedging is the evolutionarily stable strategy (Heininger, 2015). Risk spreading in unpredictable environments confers equality of opportunity and thus *ex-ante* fairness of lottery (Saito, 2012). It is an intriguing aspect of lotteries that individuals that can gain more from lotteries (low-income people or cells/animals under vital stress) are more willing to participate in lotteries (Spiro, 1974; Brinner & Clotfelter, 1975; Suits, 1977; Clotfelter & Cook, 1987, 1989; Livernois, 1987; Hansen, 1995; Clotfelter et al., 1999; Hansen et al., 2000; Blalock et al., 2007; Haisley et al., 2008; Beckert & Lutter, 2013; Leach, 2013). In fact, at the transition of unicellularity to multicellularity, vitally endangered, starving, microbes are ready to try their luck in life-death lotteries. If they would not cooperate and gamble, the chances that all of them die are substantial. The curtain of ignorance appears to affect the behavior from vitally endangered cells to social decisions in humans. In the Prisoner's Dilemma game, a paradigmatic example for studying the dilemmas between individual interests and collective welfare, many subjects compete when they know that the opponent has competed and when they know that the opponent has cooperated, but behind the curtain of ignorance they cooperate significantly more often (Shafir & Tversky, 1992). In the disjunctive case, when the other player's strategy is not known, 65% of the subjects exhibited cooperation on at least one of the six Prisoner's Dilemma triads that they played (Shafir & Tversky, 1992). Unpredictable environments shaped a multitude of evolutionary processes that engage fair randomization processes and downstream selection (either by a selective environment or internal milieu) such as RNA quasispecies (Eigen, 1996), somatic generation of antibody diversity (Jerne, 1955; Burnet, 1957; Tonegawa, 1976, 1983), sexual reproduction, cell differentiation, and cancerogenesis (Heininger, 2001, 2013, chapter 4.1.1).

#### **5.4.1 Apoptosis as fair lottery with unequal outcome**

*If a number of persons engage in a series of fair bets, the distribution of cash after the last bet is fair, or at*

*least not unfair, whatever this distribution is.*

John Rawls (1971, p. 75 of revised edition 1999)

As noted in chapter 5.4, in the case of indivisible goods, the winner of a fair lottery "takes it all". When resources are too scarce to ensure the survival of all members of a clonal society (particularly if the survivors have to undergo the energetically demanding metamorphosis from vegetative cells into metabolically dormant, resilient spores), the outcome of the competition for resources is decided by a fair lottery. Behind the "veil of ignorance", cells competing for the indivisible good "life" are not "aware" of their relative position in the "commonwealth" of cells (Leigh, 1977).

The phenomenon that clonal cells display stochastic bistability has been attributed to cellular noise (Korobkova et al., 2004; Maamar et al., 2007; Leisner et al. 2008; Veening et al., 2008; Lopez et al., 2009). Connections between gene expression noise and cell state transitions have been demonstrated in many biological processes (Eldar & Elowitz, 2010). Bistability and the binary decision making it imparts have been widely observed and hypothesized as one of the possible mechanisms for cell fate determination (Biggar & Crabtree, 2001; Ferrell, 2002; Xiong & Ferrell, 2003; Wu et al., 2013). For example, competence/fratricide bistability is the result of stochastic cell fate determination (Leisner et al., 2008; Veening et al., 2008; Johnston et al., 2014, see chapter 5.3.2). In a gene network model, different levels of noise, designed to mimic degrees of "noisy" transcriptional activity in cellular systems, were found to either promote or disrupt state transitions, with some transitions requiring layovers at one or more intermediate states (Faucon et al., 2014). Cell-to-cell variation in genetically identical cells of multicellular organisms is often regulated by active non-genetic mechanisms (Kimble & Hirsh, 1979; Kimble, 1981; Doe & Goodman, 1985; Sternberg & Horvitz, 1986; Priess & Thomson, 1987; Jan & Jan, 1995; Karp & Greenwald, 2003; Hoang, 2004; Colman-Lerner et al., 2005). The two pathways resulting in death or survival may be mechanistically independent, and cell fate is determined by a stochastic kinetic competition between them that results in cell-to-cell variation (Huang et al., 2010). The specific molecular interactions and/or chemical conversions depicted as links in the conventional diagrams of cellular signal transduction and metabolic pathways are inherently probabilistic, ambiguous, and context-dependent (Kurakin, 2007). Regulatory systems or decisions, in which the outcome of a cellular event is at least partially the result of intrinsic noise, are said to be

stochastic (Theise & Harris, 2006; Losick & Desplan, 2008; Eldar & Elowitz, 2010). Cell fate decisions are often controlled by both stochastic and deterministic features (Losick & Desplan, 2008; MacArthur et al., 2009; Snijder & Pelkmans, 2011). For instance, bacteria determine their fate by “playing dice with controlled odds” (Ben-Jacob & Schultz, 2010). Constrained randomness, intermediate between rigid determinism and complete disorder is what is usually seen (Theise & Harris, 2006). Specific environmental or genetic cues may bias the process, causing certain cellular fates to be more frequently chosen (as when tossing identically biased coins). Still, the outcome of cellular decision making for individual cells is a priori unknown (Balázsi et al., 2011).

Stochastic models of apoptosis make it possible to represent reactions as processes that are discrete and random, rather than continuous and deterministic. Stochastic models are advantageous when the number of individual reactants of any type is small (typically fewer than ~100) or reaction rates very slow (Zheng & Ross, 1991). In these cases, a Monte Carlo procedure is used to represent the probabilistic nature of collisions and reactions among individual molecules (Gillespie, 1977). Modeling and experimentation in bacteria, yeast, and mammalian cells, have provided a mechanistic framework for understanding stochastic variation (“noise”) in rates of transcription and translation (Raj & van Oudenaarden, 2008). The number of transcriptional initiation complexes on any single gene is small (potentially as small as 1–2), and the probability that a transcript will be created in any time interval is therefore highly stochastic. Fluctuations in mRNA levels result in fluctuating rates of protein synthesis. With short-lived or low-copy-number proteins, this can cause large fluctuations in protein levels, whereas with relatively abundant proteins, such as those controlling apoptosis, the most significant effect is that different cells contain different concentrations of each protein, and thus unique proteomes. Model-based simulation suggested that natural variation in the levels of apoptotic regulators is responsible for variability in the time and probability of cell death (Spencer et al., 2009; Spencer & Sorger, 2011). Stochastic behavior-dependent bistability results in different individual cells responding at somewhat different concentrations and time. When observed at a population level, the response is thus graded. Such contrast between population level and single cell level has been illustrated experimentally in a number of systems, including *Xenopus levis* oocytes (Bagowski et al., 2001, 2003; Pomerening, 2008; Ferrell et al., 2009), and oxidative stress induced apoptosis mediated by ERK pathway and p53 pathway

(Nair et al., 2004).

Individual cells differ widely in their responses to apoptotic stimuli (Spencer & Sorger, 2011). Correlation in the probability of death and death time among sister cells has been observed in a variety of cell types following exposure to a variety of apoptosis-inducing agents. In contrast, randomly selected cells were found to be uncorrelated, and no obvious correlation with cell-cycle phase or with position in the dish could be detected (Bhola & Simon, 2009; Spencer et al., 2009). Importantly, the degree of similarity between sisters fell as the time since cell division increased so that within one to two generations, sisters were no more correlated than randomly chosen pairs of cells. This transient heritability in timing of death argues against a genetic or epigenetic explanation for cell-to-cell variability in apoptosis, as genetic and epigenetic differences tend to be stable over much longer timescales (Spencer & Sorger, 2011).

#### **5.4.2 Are “self-destructive” acts the phenotype of fair lotteries?**

Within the kin selection paradigm, apoptosis of unicellular and within multicellular organisms is often interpreted as altruistic suicide or self-sacrifice (Kondo, 1988; Alison & Sarraf, 1992; Allsopp & Fazakerley, 2000; Gardner & Kümmerli, 2008; Ackermann et al., 2008; Nedelcu et al., 2011). In *D. discoideum* cells killed by nonkin are called victims (Ho et al., 2013), but cells killed by kin are considered altruists that sacrifice themselves (Strassmann et al., 2000a). Ackermann et al. (2008) provided several examples of behavior of unicellular pathogens that was interpreted as self-destructive cooperation (Avery, 2006). Some bacterial toxins that are instrumental in pathogenesis can only be released if the cell producing the toxin lyses (Paton, 1996; Wagner et al., 2002; Voth & Ballard, 2005). Some of these toxins induce inflammation in the host, and there is now growing evidence that pathogens can decrease competition by co-inhabitants of the same niche through manipulation of the host’s immune system (Lysenko et al., 2005; Raberg et al., 2006; Brown SP et al., 2007; Stecher & Hardt, 2008). One example is pneumolysin from *Streptococcus pneumoniae*. This toxin is released by “self-destructive” bursting which promotes the invasion of the lung by cells that refrain from this extreme behavior (Paton, 1996; Ogunniyi et al., 2007). In the *S. typhimurium* enterocolitis model, most of the bacteria that invade the gut tissue and thereby contribute to the public good (inflammation as a proxy for the public good) seem to be killed by the intestinal innate immune defenses. Thus, “cooperation through

invasion of the gut tissue is a largely self-destructive act" (Ackermann et al., 2008). Another example is TcdA, a key virulence factor of *Clostridium difficile* (Voth & Ballard, 2005). TcdA lacks a standard secretion signal and is released by bacterial lysis. Purified TcdA toxin alone can trigger gut inflammation (Lima et al., 1988), and gut inflammation enhances intestinal *C. difficile* colonization (Rodemann et al., 2007). In this case, TcdA released by "self-destructive" acts seems to provide the pathogen with a competitive advantage, presumably by decreasing competition from commensal bacteria. It has been noticed that from a genetic-determinism point of view, such self-destructive cooperation is very puzzling (Gardner & Kümmerli, 2008): a gene that leads all its carriers to make the ultimate sacrifice should become extinct in a single generation. However, these processes are the result of gene expression noise (Fraser & Kærn, 2009) that may lead to random cell fates (see chapter 5.4.1 and Heininger, 2015). Randomization of fate levels individual opportunity and promotes group cohesion. Given randomization of individual success within the group, an individual increases success only by increasing the success of the group as a whole (Frank, 2013). These random fates have been termed "coin-flipping altruism" by Cooper and Kaplan (1982). According to this logic every participant of a lottery, by buying a lottery ticket, would commit an act of altruism towards the eventual winner(s) of the lottery.

## 6. The ecological context-dependency of social interactions

*The key remaining questions of evolutionary biology are more ecological than genetic in nature.*

Edward O. Wilson, 1987

### Summary

**Ecological conditions play a major role in the evolution of sociality. Harsh or unpredictable environments, intense predator pressure, constraints on independent breeding, strong intra- or inter-specific competition, or resources that are difficult to acquire except as a group have been suggested to select for social living. Cooperative breeding is chiefly viewed as a 'best-of-a-bad-job' strategy, undertaken when constraints prevent independent reproduction, forcing some individuals to pursue the alternative strategy of helping others. Current theory suggests that mutualisms are best viewed as reciprocal exploitations that nonetheless provide net benefits**

**to each partner This view stresses the disruptive potential of conflicts of interests among the erstwhile partners resulting in a dynamic and flexible balance between cooperation and competition. Cooperation is never here to stay.**

Ecological conditions play a major role in the evolution of sociality (Rubenstein & Wrangham, 1986; Slobodchikoff, 1988; Krebs & Davies, 1993; Arnold & Owens, 1999; Foster & Xavier, 2007; Korb & Heinze, 2008; Westneat & Fox, 2010; Davies et al., 2012; Gordon, 2014; McAuliffe & Thornton, 2015). For instance, several ecological hypotheses, not mutually exclusive, have been proposed to explain the evolution of cooperative breeding. The most influential hypotheses can be classified according to the following scheme (Pen & Weissing, 2000):

(i) Ecological constraints hypothesis (Brown, 1974; Emlen, 1982a, 1997; Koenig et al., 1992).

(ii) Life-history hypothesis (Russell, 1989; Cockburn, 1996; Arnold & Owens, 1998).

(iii) Benefits-of-philopatry hypothesis (Stacey & Ligon, 1987, 1991).

The ecological constraints and life-history hypotheses both stress that the direct fitness benefits of seeking independent breeding opportunities are too small to outweigh the indirect inclusive fitness benefits of helping relatives. In contrast, the benefits-of-philopatry hypothesis emphasizes the long-term direct benefits of staying near the natal nest: short-term losses incurred by not dispersing are compensated by greater long-term direct benefits, in the form of inheritance of the natal territory (Pen & Weissing, 2000).

The life history strategies of cooperative breeders appear to be biased towards the K-selected end of the r-K continuum, being characterized by delayed maturity, high adult survival, and low reproductive and dispersal rates (Brown, 1974, 1987; Gaston, 1978; Russell, 1989; Rowley & Russell, 1990; Poiani & Jermiin, 1994; Arnold & Owens, 1998, 1999). Cooperative breeding seems to have a secondary role for the maintenance of delayed dispersal, although 96% of bird species where the offspring remain with their parents into adulthood to form family groups also breed cooperatively (Emlen, 1995). Cooperative breeding can be seen as an independent decision, and as such it is a consequence rather than a cause of delayed dispersal (Brown, 1987; Stacey & Ligon, 1987; Koenig et al., 1992; Emlen, 1994; Hatchwell & Komdeur, 2000), which is consistent with the observation that dispersal can be delayed without the retained offspring engaging in reproduction (Ekman et al., 2001a). Even if some of the retained offspring in a species participate in cooperatively breeding units,

there are usually a substantial fraction of them that do not engage in help-at-the-nest (Ekman et al., 2001a). It has been hypothesized that several species that delay dispersal and associate in family groups but do not practise alloparenting, exercise prolonged brood care to raise offspring fitness (Ekman et al., 1994; Ekman, 2006). Phylogenetic analyses revealed two important characteristics of family living (Covas & Griesser, 2007). First, family living has a strong phylogenetic component, being unevenly distributed between families (or between genera in families that present both cooperative and pair breeders), and is the ancestral state in several lineages (Cockburn, 1996, 2003; Arnold & Owens, 1998). Second, family living occurs more frequently among long-lived bird species (Arnold & Owens, 1998; Covas & Griesser, 2007; Griesser & Barnaby, 2010). Life-history theory predicts that long-lived species should benefit from a delayed onset of reproduction (Goodman, 1974; Stearns, 1992; Charlesworth, 1994), and this has been supported by studies that demonstrated a positive effect of delayed onset of reproduction on lifetime reproductive success in long-lived bird species (Stacey & Ligon, 1987; Ekman et al., 1999; Krüger, 2005). Furthermore, longevity not only gives the option to offspring of delaying the onset of reproduction, but it also reduces the cost to parents of a prolonged investment in offspring (Ekman & Rosander, 1992). Extended parental investment is an important factor that has been suggested to facilitate family formation (Brown, 1987; Ekman et al., 2001a; Ekman, 2006). Clearly, extended brood care does increase the reproductive success of parents and survival of offspring, both direct fitness benefits. Australian brown thornbill (*Acanthiza pusilla*) juveniles that delayed dispersal were four times more likely to recruit than juveniles that dispersed early (Green & Cockburn, 2001). Philopatric Siberian jay (*Perisoreus infaustus*) offspring have an odds ratio of being killed by predators 62% lower than offspring that dispersed promptly after independence to join groups of unrelated individuals (20.6% versus 33.3% winter mortality). The higher survival rate among philopatric offspring was associated with parents providing nepotistic predator protection that was withheld from unrelated group members (Griesser et al., 2006). Ekman (2006) argued that a variety of family groups maintained in the absence of alloparental care underlines the capacity of general group living enhancing survival as a primary agent selecting for family cohesion. These seasonal constraints on fitness components selecting for family cohesion may contribute to the large scale geographical pattern with a relative paucity of family cohesions among bird

species in the northern hemisphere. On the basis of an extensive literature survey, Russell (2000) and Russell et al. (2004) found that juveniles of tropical and southern temperate species stay on natal territories significantly longer than juveniles of northern temperate species. Juveniles in an estimated 40% of tropical-southern temperate species (excluding flocking and cooperatively breeding species) remain on natal territories for 3–10 months after fledging which means that in these species a significant proportion of the offspring's first year of life is spent with its parents on natal territories (Gill & Stutchbury, 2010). Green and Cockburn (2001) concluded that delayed dispersal is not a strategy confined to species that breed cooperatively and suggested that prolonged philopatry in cooperative species in the Corvida are more likely to be driven by direct fitness benefits to offspring rather than indirect benefits accrued by raising non-descendent kin. It has been suggested that rather than regarding life history traits as predisposing and ecological factors as facilitating cooperation, they are more likely to act in concert (Hatchwell & Komdeur, 2000).

The fact that cooperative breeding should not be essential for delayed dispersal is consistent with the view that the behavior of remaining in the natal territory is maintained as a product of ecological constraints on dispersal options (Ekman et al., 2001a). A variety of conditions have been suggested to select for social-living (Avilés, 1999), including high risks involved with dispersal (Emlen, 1982a), lack of mates (Rowley, 1981, Pruett-Jones & Lewis, 1990), constraints on independent breeding (Emlen, 1991), intense predator pressure (Alexander, 1974; Wilson EO, 1975; Caraco & Pulliam, 1984; Stern & Foster, 1996), strong intra- or inter-specific competition (Wilson EO, 1975; Buss, 1981; Hogendoorn & Velthuis, 1993), harsh or unpredictable environments (e.g. Reyer, 1980; Emlen & Wrege, 1991; Jarvis et al., 1994; Covas et al., 2008), or resources that are difficult to acquire except as a group (Slobodchikoff, 1984; Raffa & Berryman, 1987; Wyatt, 2003; Whitehouse & Lubin, 2005; Platt et al., 2012). In theoretical models, harsher environments led to higher long-term frequencies of cooperators (Smaldino et al., 2013a, b), lending support to Kropotkin's (1902) proposal that harsh environments should select for cooperation. In a comparative study of reproduction among southern sea lions (*Otaria byronia*) during a single breeding season, it was documented that only one of 143 pups born to gregarious group-living females died before the end of the season, compared to a 60 percent mortality rate among solitary mating pairs. The main reasons were that pups in colonies were protected

from harassment and infanticide by subordinate males and were far less likely to become separated from their mothers and die of starvation (Campagna et al., 1992). Diverse selective pressures have contributed to the evolution of the varied social groups of carnivores: the benefits of strength of numbers for defense of kills and territory, and in the hunting and killing of large prey; the ability to intimidate predators and to be vigilant against their approaches; the potential for information transfer and social learning (Dukas, 1998), and a suite of alloparental behavior patterns (Macdonald, 1983). The various conditions, which have been collectively referred to as the 'ecological constraints hypothesis' (Brown, 1974; Emlen, 1982a, 1991; 1997; Brockmann, 1997) would result in deaths outpacing births and, thus, in unsustainable rates of growth for populations of solitary individuals attempting to colonize such environments.

Cooperative breeding is chiefly viewed as a 'best-of-a-bad-job' strategy, undertaken when constraints prevent independent reproduction, forcing some individuals to pursue the alternative strategy of helping others (Arnold & Owens, 1999; Dickinson & Hatchwell, 2004; Russell, 2004). The fitness benefits of helping are most apparent in harsh conditions (Reyer, 1980; Covas et al., 2008). Numerous studies have demonstrated the importance of territory quality, access to breeding sites, resource availability, and other ecological factors in influencing reproductive and dispersal decisions in cooperatively breeding species (e.g., Pruett-Jones & Lewis, 1990; Walters, 1990; Komdeur, 1992; Walters et al., 1992). In the cooperatively breeding Seychelles warbler, *Acrocephalus sechellensis*, transfers of warblers to unoccupied islands showed that both habitat saturation and variation in territory quality dramatically affected the frequency of delayed dispersal. At first there was no cooperative breeding, but as all high-quality areas became occupied, young birds hatched on them began to stay as helpers, rather than occupy breeding vacancies on lower quality territories. However, as the number of helpers on high-quality territories increased, it paid some helpers to leave, even to poor territories. Thereafter, young reared on poor territories did better to leave to breed on poor territories, rather than stay at home (Komdeur, 1992; Komdeur et al., 1995). Among 20 species of sponge-dwelling shrimp (*Synalpheus*), eusocial species, consistent with hypotheses that cooperative groups enjoy an advantage in challenging habitats, are more abundant, occupy more sponges and have broader host ranges than nonsocial sister species (Duffy & Macdonald, 2009). In addition to ecological and demographic constraints, the energetic costs of

reproduction, specifically costly gestation and costly postnatal investment in litter growth limit the benefits of attempting to breed as a subordinate in communally breeding carnivores (Creel & Creel, 1991). In mole-rats, the degree of sociality increases as resource abundance decreases and variability in rainfall increases (Faulkes et al., 1997; O'Riain & Faulkes, 2008).

Environmental uncertainty and harshness play a key role in explaining the incidence and distribution of avian cooperative breeding behavior (Emlen, 1982a, 1991; du Plessis et al., 1995; Hatchwell & Komdeur, 2000; Hatchwell, 2007; Rubenstein & Lovette, 2007; Cockburn & Russell, 2011; Jetz & Rubenstein, 2011). Experimental studies in which constraints on independent breeding were relaxed resulted in helpers moving to adopt the vacant breeding opportunities (Pruett-Jones & Lewis, 1990; Komdeur, 1992; Walters et al., 1992). Seychelles warblers became independent breeders once they had been released into an unoccupied island containing many good breeding territories. However, as the new population increased and all the high-quality habitat became occupied, the young again began to remain at home where they acted as helpers, as they usually do in their native habitat in which breeding vacancies are rare (Komdeur, 1992). The highly eusocial allodapine bee species *Exoneurella tridentata*, appears to have evolved sociality in very harsh, xeric conditions (Dew et al., 2012), and in years with harsh weather conditions colonies of primitively eusocial sweat bee, *Halictus ligatus*, showed an increase in sociality, i.e. higher levels of queen-worker dimorphism and decreased worker cheating (Richards & Packer, 1996). In a similar vein, communality among the bees may also be associated with more arid environments (Australia, Southwest USA) possibly because of restricted opportunities for fossorial nesting (Wcislo & Tierney, 2009). In some ant, termite, and social spider species, rainfall is positively correlated with sociality (Riechert et al., 1986; Murphy & Breed, 2007; Picker et al., 2007; Purcell, 2011).

Several authors argue that humans can be considered cooperative breeders because, although parenting behavior is highly culturally variable, in no culture do mothers raise their children without help from others (Hrdy, 1999, 2009; Mace, 2000; Sear & Mace, 2008; Hill & Hurtado, 2009; Smaldino et al., 2013b). Hill and Hurtado (2009), in their studies of contemporary South American hunter-gatherer societies, found not only that cooperative breeding behavior was ubiquitous, but also, crucially, that husband-wife pairs were physically incapable of procuring sufficient food for their offspring

and themselves without help from others (Smaldino et al., 2013b). Moreover, they found that meat acquisition of Ache hunters over a given 90-day period was often highly variable for any given individual, as a result of illness, injury, or luck. Sharing food resources between nuclear families was therefore necessary to ensure the survival of young children (Smaldino et al., 2013b). It is likely that hominins have been raising their children cooperatively for some time (Hrdy, 2009). The large brains of humans inevitably make our offspring costly to raise because the growth and development of brain tissue requires high levels of energy and nutrients (Charnov & Berrigan, 1993). Isler and van Schaik (2009) have argued that the increased encephalization of the hominin line would not have been possible unless females were receiving help provisioning their young, particularly during the heightened habitat instability in the East African Rift System at the beginning of the Pleistocene (Trauth et al., 2005; Bobe & Leakey, 2009; Potts, 2013). Cooperative breeding has been suggested as a potentially crucial factor in the evolution of human prosociality and our tremendous cognitive advantage over our nearest relatives, the great apes (Burkhart et al., 2009; Hrdy, 2009).

### 6.1 The dynamics of cooperation and competition

As self-organized systems (see chapter 16), social units are dynamic. The production of structures as well as their persistence requires permanent interactions between the members of the colony and with their environment. These interactions promote the positive feedbacks that create the collective structures and act for their subsistence against negative feedbacks that tend to eliminate them (Garnier et al., 2007). Ongoing interactions in social systems may be a real-life manifestation of cooperative coaction that in models evolves more readily than reciprocal cooperation (van Doorn et al., 2014). Current theory suggests that mutualisms are best viewed as reciprocal exploitations that nonetheless provide net benefits to each partner (Nowak et al., 1994; Leigh & Rowell, 1995; Maynard Smith & Szathmáry, 1995; Herre & West, 1997; Doebeli & Knowlton, 1998; Herre et al., 1999; Sachs et al., 2004; Foster & Wenseleers, 2006; Sachs, 2006, 2013; Leigh, 2010; Jones et al., 2012). This view stresses the disruptive potential of conflicts of interests among the erstwhile partners. There is a dynamic and flexible balance between cooperation and competition (Nonacs & Reeve, 1995). In models, the unstable balance results in the oscillatory nature of cooperation (Nowak & Sigmund, 1989, 1993a; Imhof et al., 2005, van Doorn et al., 2014). Cooperation is never here to stay. Instead, there are endless cycles between all-out

defectors, harsh retaliators, careful forgivers and unconditional cooperators (Imhof et al., 2005; Imhof & Nowak, 2010). Even eusociality can be lost or suppressed under appropriate ecological circumstances (Wcislo & Danforth, 1997; Danforth et al., 2003). Competition for resources is a common feature of mutualisms (Holland et al., 2005; Holland & DeAngelis, 2010; Jones et al., 2012). Simple models of consumer–resource interactions revealed multiple equilibria, including one for species coexistence and others for extinction of one or both species, indicating that species' densities alone can determine the fate of interactions (Holland & DeAngelis, 2009, 2010). Across a dozen genera, queens able to found a colony alone often join unrelated queens, thereby enhancing worker production and colony survivorship. The benefits of joining other queens vary with group size and ecological conditions. However, after the first workers mature, the queens fight until only one survives (Bernasconi & Strassmann, 1999).

Phylogenies reveal that parasites as well as autonomous (non-mutualist) taxa are nested within ancestrally mutualistic clades. Close scrutiny of mutualistic interactions reveals that heterogeneous selection pressures (e.g. adaptation to local habitats, drift and low gene flow) can alter the strength and net fitness effect, causing these interactions to become antagonistic or parasitic under certain conditions (Johnson et al., 1997; Hochberg et al., 2000; Hochberg & van Baalen, 2000; Bever, 2002; Thompson & Cunningham, 2002; Sachs & Wilcox, 2006; Thrall et al., 2006; Palmer et al., 2008). Although models have focused on the propensity of mutualism to become parasitic, such shifts appear relatively rarely (Sachs & Simms, 2006; Sachs et al., 2011a). By contrast, diverse systems exhibit reversions to autonomy, and this might be a common endpoint to mutualism (Nishiguchi & Nair, 2003; O'Brien et al., 2005; Sachs & Simms, 2006; Mueller et al., 2010; Sachs et al., 2010, 2011b; Kikuchi et al., 2011; Sachs, 2013). Mutualisms and commensalisms dissolve when one party ceases to benefit from, or becomes less dependent on, the other. The potential for conflicts of interest to shape or destabilize mutualistic associations will depend on the extent to which the survival and reproductive interests of the symbiont align with those of the host (Herre et al., 1999; Jones et al., 2012). Leigh and Rowell (1995) and Leigh (1999, 2010) pointed out that the crucial aspect of the evolution of mutualism is whether partners have a sufficient common interest. As long as partners have a sufficient common interest, they should continue to cooperate, but as soon as conditions change to boost selfish interests, one (or

both) of the partners may defect and a struggle rather than a harmonious relationship ensues (van Baalen & Jansen, 2001; Jones et al., 2012). Changing resource supply rates influence mutualistic interactions (Schwartz & Hoeksema, 1998). The energy flow through an ecosystem (or productivity) varies across landscapes (Rosenzweig, 1995) and is believed to play a major role in determining coevolutionary dynamics (Rosenzweig, 1995; Hochberg & van Baalen, 1998, 2000; Thompson, 2005; Lopez-Pascua & Buckling, 2008). The benefits derived from resource-trading depend strongly on the nature of the trade-off between the acquisition of one resource and the acquisition of another, described by the shape (linear, convex or concave) of the resource acquisition constraints of the individuals involved. The benefit derived from resource exchange depends on three factors: (i) relative differences between the partners in their resource acquisition abilities; (ii) relative differences between the partners in their resource requirements; and (iii) variation in the shape of resource acquisition trade-offs (Hoeksema & Schwartz, 2003). These models provide a suite of predictions about whether or not resource exchange is beneficial for two heterospecific individuals relative to a strategy of non-interaction (Schwartz & Hoeksema, 1998; Hoeksema & Schwartz, 2003). Long-term mutualisms dissolve if one party ceases to need, or to benefit from, the other's services (Leigh, 2010). Corals expel zooxanthellae when they can no longer provide carbohydrates (Trench, 1997; Baker, 2001). The saxifrage herb *Lithophragma* preferentially aborts flowers full of eggs of the flower-parasitizing pollinator moth *Greya* when cheaper pollinators are available (Thompson & Cunningham, 2002). Interactions between African acacias and their ant defenders become more aggressively antagonistic if large herbivores, whom the ants deter, are removed (Palmer et al., 2008). Live-in nematodes compromise the fitness of their fig-wasp host if the fig fruit their host enters is likely to harbour other fig wasps whose young can be colonized by these nematodes' young (Herre, 1993).

## 7. Cooperation and competition: threshold traits on a continuum of ecological variables

### Summary

**In complex nonlinear relationships changes in effects can be disproportionate to the changes in**

**the causal element(s). Many traits are phenotypically discrete but may be polygenically or polyetiologically determined. Such traits can be understood using the threshold model of quantitative genetics that posits a continuously distributed underlying trait, called the liability, and a threshold of response: individuals above the threshold display one morph and individuals below the threshold display the alternate morph. Theoretical work found that kin competition can strongly antagonize the benefits of kin cooperation and inhibit the evolution of cooperation in viscous populations.**

**Conflicts may have both beneficial and disastrous consequences. Conflict is likely to be a major driver of evolutionary change within and between species. Cheater's payoff is frequency-dependent. Cheating or defecting strategies may do very well as long as they are rare in a population of cooperative individuals but fare worse or even perish when surrounded only by other cheaters. The anthropocentric and moralizing concepts of kin selection theory may bias the interpretation of behavior deviant to expectation. Phenotypes of dominance hierarchies, division of labor or bet-hedging strategies may be mistaken as "cheating".**

Typically, animals first respond behaviorally to changes and challenges in their environment (Tregenza, 1995; Kappeler et al., 2013), whereas adaptations of their morphology, physiology and life history take much longer (Releya, 2002). In fact, maximal behavioral flexibility might be generally advantageous in various natural situations (de Witt et al., 1998; Wright et al., 2010), including adaptations to climate change (Parmesan, 2006). Thus, evolution places a premium on behavioral plasticity or flexibility (Thorpe, 1974; Wilson, 1978; Kappeler et al., 2013). Variation in social systems occurs in many species, either between or within populations (Lott, 1984, 1991; Schradin, 2013). Interactions between organisms exist along a continuum from mutualism and commensalism to parasitism (Starr, 1975; Lewis, 1985; Ewald, 1987; Hochberg et al., 2000; Moran & Wernegreen, 2000; Thompson & Cunningham, 2002; Neuhauser & Fargione, 2004; McCreadie et al., 2005; Moran, 2007; Leung & Poulin, 2008; Pérez-Brocal et al., 2013; Heath & Stinchcombe, 2014). Variation in environmental conditions or the nature of density-dependent interactions along environmental gradients may be important in generating dynamic patterns of competition and cooperation in many natural populations (Buss, 1981; Branch & Barkai, 1988; Bertness, 1989; Bertness & Yeh, 1994;

Holmgren et al., 1997; Tielbörger & Kadmon, 2000; Amar et al., 2008; Hudson & Trillmich, 2008; Roulin & Dreiss, 2012; Wong et al., 2013, 2014). Many traits are phenotypically discrete but may be polygenically or polyetiologically determined. Such traits can be understood using the threshold model of quantitative genetics that posits a continuously distributed underlying trait, called the liability, and a threshold of response: individuals above the threshold display one morph and individuals below the threshold display the alternate morph. In complex nonlinear relationships (see chapter 16) changes in effects can be disproportionate to the changes in the causal element(s). This may be a threshold effect so that change in the effect is proportionate to change in causal element(s) until a particular point is reached when the change becomes disproportionate (Byrne & Callaghan, 2014). The exploration of such effects is the domain of catastrophe theory. Semelparity and iteroparity (Roff, 1996, 1998; Lesica & Young, 2005; Heininger, 2012), and sexual and asexual reproduction (Heininger, 2013) are threshold traits. The discontinuous variation depends on both the genotype and the environment. The plasticity of morphs suggests that they are opposite ends of a continuum of variation rather than representing a simple dichotomy. Likewise, empirical data suggest that "altruism" and selfishness are rather plastic phenotypic expressions of a single genotype (Yakubu, 2012, 2013).

Intra- and interspecific competition has the inherent potential to reduce diversity via exclusion of inferior competitors (Grime, 1973; Armstrong & McGehee, 1980; Passarge et al., 2006). Full symmetry of competition may be evolutionarily unstable in populations of related individuals as it may increase the probability of extinction due to demographic stochasticity (Aikio & Pakkasmaa, 2003). The theory of heterogeneous advantage predicts that competition intensifies when genetic diversity is low and, therefore, diametrically opposes the predictions of kin association (Griffiths & Armstrong, 2001). Several mechanisms may lead to heterogeneous advantage (Griffiths & Armstrong, 2001): (i) If different genotypes have different ecological needs they may use a homogeneous resource in different ways (Young, 1981). (ii) Mixtures may exploit a spatially heterogeneous environment more fully than homogeneous groups (Bell, 1985). (iii) In temporally heterogeneous habitats, mixtures may be more likely than homogeneous groups to produce genotypes that are better suited to the environment (Williams, 1975). (iv) Mixtures may be more resistant to pathogens because there should be a greater chance of there

being a resistant genotype present (Wolfe, 1985). Evidence for heterogeneous advantage has come from laboratory studies in animals and plants (Kearsey, 1965; Caligari, 1980; Pérez-Tomé & Toro, 1982; Ellstrand & Antonovics, 1985; Fowler & Partridge, 1986; Martin et al., 1988; Jasienski et al., 1988; Kelley, 1989; López-Suárez et al., 1993). Heterogeneous advantage outweighed the benefits of kin association for juvenile salmon in a natural habitat both at an individual level, as shown by the differences in the condition indices, and at a population level as shown by the differences in density (Griffiths & Armstrong, 2001). Studies of the effects of kinship on larval amphibian growth found no significant differences between sibling and mixed treatments with respect to mass or variation in mass, suggesting that the effects of kin selection and genetic similarity between competitors may in some cases cancel each other out (Twomey et al., 2008). On the other hand, when siblings are likely to interact, genetic variation among individuals can decrease competition for resources and generate substantial fitness benefits within a single generation (Aguirre & Marshall, 2012). In ecological communities and theoretical models, mutualism/facilitation mediates competition and increases biodiversity and stability in ecosystems (Hacker & Gaines, 1997; Pachepsky et al., 2002; Schmitt & Holbrook, 2003; Bascompte et al., 2006; Guimarães et al., 2007; Bastolla et al., 2009; Thébault & Fontaine, 2010; Cain et al., 2011; Mittelbach, 2012; McIntire & Fajardo, 2014).

By helping kin/neighbors to produce more offspring, the intensity of competition experienced by the focal individual's offspring and that of its neighbors is increased. Helping relatives/neighbors thus leads to local crowding and an increase in local competition, here understood as the extent to which an actor and a recipient (or their offspring) are more likely to compete against each other for the same resources than are two adult individuals (or offspring) sampled at random from the population (Grafen, 1984; Wade, 1985; Kelly, 1992, 1994a; Taylor, 1992; Wilson et al., 1992; Queller, 1994a; West et al., 2002a; El Mouden & Gardner, 2008; Grafen & Archetti, 2008; Lehmann & Rousset, 2010; Van Dyken, 2010). Evidence that resource-based helping creates negative ecological feedback already exists for survival or fecundity restraint (Wilson et al., 1992; van Baalen & Rand, 1998; Mitteldorf & Wilson, 2000; Le Galliard et al., 2003; Werfel & Bar-Yam, 2004; Hauert et al., 2006; Alizon & Taylor, 2008; Lion & Gandon, 2009, 2010; Van Dyken & Wade, 2012). For example, the level of fighting between males of fig wasp taxa shows no correlation with the estimated relatedness of

interacting males, but is negatively correlated with the number of females (future mating opportunities) (West et al., 2001). Thus, the benefits of kin-cooperation can potentially be negated by kin-competition (Grafen, 1984; Murray & Gerrard, 1984; Wilson et al., 1992; Taylor, 1992a, b; Queller, 1992, 1994; Kelly, 1994; Frank, 1998; West et al., 2001, 2002a; Gardner et al., 2004; Queller, 2004; El Mouden & Gardner, 2008; Grafen & Archetti, 2008; Platt & Bever, 2009; Lehmann & Rousset, 2010; Van Dyken & Wade, 2012). This tends to inhibit the evolution of helping. The cooperation-negating threat of kin competition has heightened the sense that true “altruism” in nature poses a serious conceptual dilemma. In particular, a number of models have shown that increased kinship “altruism” is exactly balanced by increased kin competition, making it impossible for true “altruism” to evolve (Charlesworth, 1979; Taylor, 1992; Wilson et al., 1992; Gardner & West, 2006). As stated by Kümmerli et al. (2009a), “relatedness and the scale of competition ... will not usually be independent”.

Competition among relatives often emerges because kin are in close spatial proximity and depend upon the same limited resources (Stockley & Bro-Jorgensen, 2011). This problem was pointed out by Alexander (1974) and West-Eberhard (1975) many years ago, suggesting that an individual's closest relatives, and by extension his/her closest associates and/or social allies, are often also his/her closest competitors (Smith, 2014). Competition among kin can reduce, or even negate, the kin-selected indirect benefits of altruism directed towards relatives. Interestingly, in such contexts, the direct benefits gained from outcompeting relatives through forces such as sibling rivalry and parent conflict generally appear to overwhelm the indirect benefits of social tolerance among kin (Trivers, 1974; Mock & Forbes, 1992; Johnstone, 2000; Cant, 2006). In some species, rates of conflict actually increase with levels of genetic relatedness. This is the case for rhesus macaques (Bernstein & Ehardt, 1986), ringtailed lemurs (Kappeler, 1993), African elephants, *Loxodonta africana* (Archie et al., 2006a), and yellow-bellied marmots, *Marmota flaviventris* (Smith et al., 2013). For example, as predicted by kin selection, rates of affiliation are positively correlated with genetic relatedness in yellow-bellied marmots as pups, yearlings and adults, but rates of conflict are also highest among the closest relatives at all three stages (Smith et al., 2013).

In an apparently wide class of models the cooperation-enhancing effect of limited dispersal is balanced by the competition-enhancing effect of limited dispersal (Taylor, 1992a, b; Wilson et al., 1992;

Queller, 1994a; West et al., 2002a; El Mouden & Gardner, 2008; Grafen & Archetti, 2008). Whereas cooperative individuals are more likely to benefit kin in viscous populations, they also compete for limiting resources with these same kin (Platt & Bever, 2009). Early theoretical work found that such kin competition can strongly antagonize the benefits of kin cooperation and inhibit the evolution of cooperation in viscous populations (Grafen, 1984; Queller, 1992a, 1994a; Taylor, 1992a, b; Wilson et al., 1992). Consistent with this, empirical studies have failed to find a relationship between relatedness and aggressiveness in colonies of the multiple-queen wasp, *Parachartergus colobopterus* (Strassmann et al., 1997), fig wasps (West et al., 2001), and bruchid beetle larvae (Smallegange & Tregenza, 2008), suggesting that the effects of kin competition might negate any kin-selected benefits associated with being less aggressive toward kin.

In plants, competitive interactions may occur among the siblings that germinate from the seeds produced by a maternal parent (Willson et al., 1987; Cheplick, 1992, 1993a, 1993b; Kelly, 1996; Cheplick & Kane, 2004). Whenever the dispersal system results in relatives that are spatially aggregated, local competition becomes kin (sibling) competition (Lambin et al., 2001). Evolutionary consequences of such neighbor interactions will depend on whether there is variation among genetically related groups (i.e., families) as well as the relatedness of competing individuals (Nakamura, 1980; Wilson, 1987; Donohue, 2003). Sibling competition has been proposed as a selective force that could account for the evolutionary advantages of sexual reproduction—the hypothesis is that the genetically variable offspring produced will experience less severe competition than genetically similar or identical offspring (Maynard Smith, 1978; Bulmer, 1980; Barton & Post, 1986; Cheplick, 1992). This is because more diverse offspring are predicted to show greater ability to partition limiting resources (Young, 1981; Argyres & Schmitt, 1992). By analogous reasoning, outcrossing breeding systems may be selected for as a way to minimize the negative fitness consequences of sibling competition (Schmitt & Ehrhardt, 1987; McCall et al., 1989). In species with self-fertilizing or cleistogamous breeding systems, individuals are especially likely to be competing with close relatives (Cheplick, 1993b, 1996; Stevens et al., 1995; Cheplick & Kane, 2004). Data exist for agronomically important species and the cleistogamous summer annual *Triplasis purpurea* that reveal greater overall yield whenever different (as opposed to identical) genotypes are grown in competition (Allard & Adams, 1969; Harper, 1977;

Price & Waser, 1982; Turkington, 1996; Cheplick & Kane, 2004). On the other hand, there have been a few reports showing greater growth or reproduction of individuals when competing with genetic relatives (compared with unrelated plants) in some species (Willson et al., 1987; Tonsor, 1989; Andalo et al., 2001; Donohue, 2003). The balance between negative and positive interactions (see chapter 10.4) has been shown to shift along environmental gradients (Tielbörger & Kadmon, 2000), with competition prevailing under environmentally benign conditions and positive interactions dominating under more harsh conditions (Bertness & Callaway, 1994; Bertness & Hacker, 1994; Bertness & Leonard, 1997; Callaway & Walker, 1997; Brooker & Callaghan, 1998; Callaway et al., 2002).

### 7.1 Conflict as a driver of evolutionary innovation

More than 40 years ago, Van Valen's Red Queen hypothesis (1973) emphasized the primacy of biotic conflict over abiotic forces in driving selection. According to the Red Queen hypothesis, each adaptation by a species is matched by counteracting adaptations in another interacting species, such that perpetual evolutionary change is required for existence. Despite continued evolution, average relative fitness remains constant: evolution is a zero-sum game (Brockhurst et al., 2014). Thus, for a vast number of biological situations, the salient aspects of the selective environment are biotic conflicts (Venditti et al., 2010; Ezard et al., 2011; Liow et al., 2011; Brockhurst et al., 2014). Conflicts may have both beneficial and disastrous consequences. Conflicts can have a variety of outcomes including co-existence, cooperation, specialization, diversification, niche shifts, speciation, and extinction (MacArthur & Levins, 1964; Tilman, 1982; Helling et al., 1987; Schluter, 1994, 2000, 2001, 2010; Grover, 1997; Rainey & Travisano, 1998; Dieckmann & Doebeli, 1999; Bolnick, 2001, 2004; Pfennig & Pfennig, 2005; Hall & Colegrave, 2007; Svanbäck & Bolnick, 2007; M'Gonigle et al., 2009; Heininger, 2012). The fitness-boosting effects of conflict in coevolutionary systems has been demonstrated at various levels of biological organization (Spitze, 1991; Spitze et al., 1991; Clarke et al., 1994; Lynch & Spitze, 1994; Reznick et al., 2004; Fisk et al., 2007; Pal et al., 2007; Paterson et al., 2010). A growing body of work directly identified parasites and other natural enemies as key contributing factors in driving host/prey diversification (Bohannan & Lenski, 2000; Schluter, 2000; Buckling & Rainey, 2002; Brockhurst et al., 2004, 2005; Morgan & Buckling, 2004; Vamosi, 2005; Nosil & Crespi, 2006; Meyer & Kassen, 2007; Benmayor et al., 2008).

Conflicts of interest between cooperators and cheaters maximize population fitness under co-existence (MacLean et al., 2010a). Likewise, the conflict between more or less cooperative partners is central to the maintenance of partner choice and cooperation itself in mutualisms (Foster & Kokko, 2006).

Antagonistic coevolution is a cause of rapid and divergent evolution, and is likely to be a major driver of evolutionary change within and between species. There have been several studies suggesting that intraspecific competition (Pacala & Roughgarden, 1985; Taper & Case, 1992; Schluter, 1996, 2000, 2010), predation (Naisbit et al., 2001; Vamosi & Schluter, 2002; Nosil, 2004; Nosil & Crespi, 2006), or infectious agents (Buckling & Rainey, 2002; MacColl, 2009; MacColl & Chapman, 2010; Schluter, 2010; Karvonen & Seehausen, 2012; Loker, 2012) lead to divergent selection. Mathematical theory has also indicated that, given the right conditions, divergence is expected to occur readily between competing species by a coevolutionary sequence of reciprocal changes in the traits used to consume resources (Taper & Case, 1985; Abrams, 1986; Doebeli, 1996).

Mutualism is characterized by competition for resources between the partners (Holland et al., 2005; Holland & DeAngelis, 2010; Jones et al., 2012) and increases biodiversity and stability in ecosystems (Pachepsky et al., 2002; Bastolla et al., 2009). Mutualism promotes coexistences of two species. Moreover, mutualism often can increase the carrying capacities of both species, and then promotes their competitive abilities (Zhang, 2003). An inferior competitor, if cooperative to a superior competitor, is also able to survive (Zhang, 2003). On the other hand, parasitic exploitation can generate substantial genetic and phenotypic polymorphism within species and may also be an important factor causing reproductive isolation and promoting speciation (Summers et al., 2003). When the bacterium *Pseudomonas fluorescens* and its viral parasite, phage  $\phi 2$  coevolved with each other, the rate of molecular evolution in the phage was much higher than when the phage evolved against a constant host genotype (Paterson et al., 2010). Guppies collected from stream environments lacking predators were found to be inferior in every aspect of their life history profile to those evolved in other, nearby sites with predators present (Reznick et al., 2004). Fitness gains appear to accelerate under the challenge of moderate conflicts. Differences in the evolutionary interests of males and females, a well studied conflict of interest, may provide an important route to speciation (Chapman et al., 1995; Arnqvist & Rowe, 1995, 2005; Chapman & Partridge, 1996; Rice,

1996, 1998a, b; Alexander et al., 1997; Parker & Partridge, 1998; Holland & Rice, 1999; Arnqvist et al., 2000; Gavrillets, 2000, 2004; Martin & Hosken, 2003; Chapman, 2006) and, indeed, sexual conflict seems to be a key “engine of speciation” (Arnqvist et al., 2000; Martin & Hosken, 2003; Gavrillets, 2004). On the other hand, when selection differs between the e.g. sexual conflict partners, a mutation beneficial to the one may be harmful to the other (sexually antagonistic) and can interfere with the other's adaptive evolution (Rice, 1984, 1992, 1998b; Chapman et al., 1995). Thus, conflicts may even result in extinction following disruptive selection (Rice, 1984, 1998b; Tanaka, 1996; Parker & Partridge, 1998; Arnqvist et al., 2000; Kisdi et al., 2001; Johansson, 2008; Heininger, 2012, 2013).

## 7.2 The ecology of "cheaters"

Sociobiology seeks to explain social behavior as a product of natural selection (Wilson EO, 1975). Natural selection acts on both cooperative and competitive phenotypes, across multiple scales of biological organization. In the Darwinian tradition it has not been challenging to explain behaviors that are competitive, but it is regarded as a conundrum how cooperation can be stable in the face of selfishness and cheating (Wilson EO, 1975; Keller, 1999; Foster, 2004; Travisano & Velicer, 2004; West et al., 2006; Foster et al., 2007). “Cheaters” may be selected for (Porter & Simms, 2014). By its nature, cooperation can be exploited by selfish individuals, meaning, firstly, that selfish individuals derive an advantage from exploitation which is greater than the average advantage that accrues to unselfish individuals. Secondly, exploitation has no intrinsic fitness value except in the presence of the “cooperative behavior” (Koeslag & Terblanche, 2003). Exploiting the behavioral efforts of others is particularly widespread. It is known as “freeloading” in economics, “tolerated theft,” and “food-sharing” in anthropology and under various names such as “joining,” “kleptoparasitism,” and “scrounging” (Barnard & Sibly, 1981; Brockmann & Barnard, 1979; Giraldeau & Caraco, 2000) in behavioral ecology.

Exploiters save the time and energy that mutualists spend on reciprocating. “Cheaters” are widespread in unicellular and facultatively multicellular organisms (Hilson et al., 1994; Dao et al., 2000; Pál & Papp, 2000; Strassmann et al., 2000a; Velicer et al., 2000, 2002; Ennis et al., 2003; Fiegna & Velicer, 2003; Rainey & Rainey, 2003; Castillo et al., 2005; Rankin et al., 2007; Kuzdzal-Fick et al., 2011). “Cheating” is also rampant in most mutualisms (Poulin & Grutter, 1996; Johnson et al., 1997; Foster & Delay, 1998; Irwin & Brody, 1998; Addicott & Bao, 1999; Currie et al., 1999;

Ferriere et al., 2002); in some cases, “cheaters” have been associated with mutualisms over long spans of evolutionary time (Addicott, 1985, 1996; Machado et al., 1996; Pellmyr et al., 1996; Després & Jaeger, 1999; Pellmyr & Leebens-Mack, 1999; Bronstein, 2001). Exploiters can evolve from former mutualists that cease service provisioning and then represent “cheaters”, or they can invade the mutualism starting from an originally independent lifestyle and then represent parasites of the mutualism (Bronstein, 2001; Segraves et al., 2005, Kautz et al., 2009; Orón-Tamayo & Heil, 2013). Exploitation has been reported for a wide range of mutualisms, including nectar robbing (e.g., bees and birds) (Roubik, 1982; Maloof & Inouye, 2000), domatia exploiters (Gaume et al., 2006, Shenoy & Borges, 2008), mycorrhizal fungi that uptake the plant carbon but transfer no nutrients to the plant (Smith et al., 1996), and strains of *Rhizobium* and *Bradyrhizobium* that transfer less or no nitrogen to the host than mutualistic strains (Wilkinson et al., 1996). On the other hand, non-photosynthetic orchids may be “cheaters” because they obtain nutrients from mycorrhizal fungi without providing carbon in return (Taylor & Bruns, 1997). Within the conceptual framework of a continuous gradation between mutualism, commensalism, and parasitism, host resistance and immunological responses against parasitic exploiters can be viewed as analogous to the “policing” of mutualists/symbionts (Leung & Poulin, 2008).

Public goods are those produced by an individual and shared with other group members (Driscoll & Pepper, 2010; Powers et al., 2011). They typically increase the fitness of all group members, but at a unilateral cost to the producer. Examples of such public goods production are widespread in nature and include the production of extra-cellular substances by microbes (Griffin et al., 2004; Gore et al., 2009), the sharing of information by an individual with the rest of its group, as occurs during predator inspection by guppies (Dugatkin, 1990), and alarm calls in birds and mammals (Charnov & Krebs, 1975; Hollén & Radford, 2009). The production of such goods is a type of cooperative behavior (West et al., 2007c) that is vulnerable to exploitation by “cheating” nonproducers, which reap the benefits of the public goods without contributing to them. The exploitation of hosts by opportunistic pathogenic bacteria, such as *Bacillus thuringiensis*, involves sharing the exploits of toxin production from multiple individuals as single individuals are incapable of overcoming host defenses. The exploitation of toxin producers by cheats (non-toxin producing strains) has consequences for pathogen virulence (Raymond et al., 2007, 2009), and

host-pathogen epidemiology (Bonsall, 2010). This can lead to a “Tragedy of the Commons” (Hardin, 1968; Rankin et al., 2007), in which cheating nonproducers increase in frequency, even though this leads to a decline in mean fitness (Powers et al., 2011).

Despite exploitation of common goods by naturally arising cheaters, however, cooperation persists (Naumov et al., 1996; Strassmann et al., 2000a; Schaber et al., 2004; Dobata & Tsuji, 2009; Vos & Velicer, 2009; Wilder et al., 2009). Cooperators have evolved various processes to curb cheaters (Waite & Shou, 2012): direct and indirect reciprocity, sanctions, partner choice and fidelity (Weyl et al., 2010; Archetti et al., 2011; Nowak & Highfield, 2011; Frederickson, 2013), pleiotropy, privatization of common goods, diminishing returns, positive assortment, adaptive race. In the following, I adhere to the categorization of anti-cheater mechanisms presented by Waite and Shou (2012):

(i) Genes required for cooperation can have pleiotropic effects, such that a cell defective in paying the cost of cooperation is also incapable of enjoying the cooperative benefit (Foster et al., 2004; Banin et al., 2005; Xavier & Foster, 2007; Harrison & Buckling, 2009; Dandekar et al., 2012). For example, in the social amoeba *Dictyostelium discoideum*, a gene encoding the receptor necessary for differentiation into stalk cells is also necessary for proper spore formation; thus, cheaters trying to avoid the stalk fate cannot become spores (Foster et al., 2004).

(ii) The budding yeast *Saccharomyces cerevisiae* secretes invertase to hydrolyze the disaccharide sucrose into glucose and fructose, which can be metabolized more efficiently. These monosaccharides were initially thought to be strictly common goods (Greig & Travisano, 2004), although it was later found that ~1% are retained by the producing cell (Gore et al., 2009). Even such a seemingly insignificant level of privatization can allow cooperators to invade a population of cheaters (Doebeli & Hauert, 2005; Gore et al., 2009). This could explain the coexistence of invertase-producing cooperative cells with nonproducing cheating cells in wild populations (Naumov et al., 1996).

(iii) When individuals interact through the production and/or consumption of inexpensive common goods in randomly formed groups that assemble and disassemble cyclically, as long as an increase in the availability of the common good leads to a less than proportional increase in the fitness of its consumers, a stable equilibrium between cooperators and cheaters is expected (Foster, 2004; Archetti & Scheuring, 2011). This “diminishing return” of the common good (Foster, 2004; Gore et al., 2009) can account for the

surprising observation that in the yeast invertase system, maximum group size is attained with a mixture of cheaters and cooperators: Cooperators produce more invertase than they can use, and cheaters convert this excess benefit into additional biomass (MacLean et al., 2010a). The cost-to-benefit ratio can be kept low if the common good is produced facultatively (i.e., only when needed), which is the case for most organisms, or if the durability of common goods is high, as found in siderophore production in *Pseudomonas aeruginosa* (Kümmerli et al., 2009c; Kümmerli & Brown, 2010).

(iv) For cooperation based on scarce common goods, mechanisms of “positive assortment” that increase the frequency of interactions between cooperators (Fletcher & Doebeli, 2009) can facilitate the persistence of cooperation. Positive assortment can involve specifically directing benefits to other cooperators and excluding or punishing cheaters based on recognition or previous experience (Hamilton, 1964; Trivers, 1971; Axelrod & Hamilton, 1981). This can occur even in organisms lacking nervous systems. For instance, microbes can achieve “recognition” through cell adhesion and chemical communication (Strassmann et al., 2011b), and legumes “reward” and “punish” beneficial and cheating rhizobia, respectively (Kiers et al., 2003; Heath & Tiffin, 2009). Another mechanism of positive assortment is “population viscosity,” brought about by limited dispersal in spatially structured environments, which keeps cooperators clustered with their relatives in homotypic cooperation (Hamilton, 1964; Maynard Smith, 1964; Chao & Levin, 1981; Nowak & May, 1992), or with their partners in heterotypic cooperation (Harcombe, 2010). Thus, natural cooperative systems, whether homotypic or heterotypic, use many different mechanisms to mitigate the tragedy of the commons, allowing cooperation via common goods to be a successful evolutionary strategy (Waite & Shou, 2012).

(v) The “adaptive race” model: If during adaptation to an environment, the fitness gain of cooperators exceeds that of cheaters by at least the fitness cost of cooperation, the tragedy of the commons can be averted. Although cooperators and cheaters sample from the same pool of adaptive mutations, this symmetry is soon broken: The best cooperators purge cheaters and continue to grow, whereas the best cheaters cause rapid self-extinction (Waite & Shou, 2012).

(vi) Direct and indirect reciprocity, sanctions, partner choice and fidelity are discussed in chapter 15.3.

Taking into account that cooperation may take place at a multitude of levels of communal life, “cheater”

identification may not be trivial. Cheating, as noted by Lekberg and Koide (2014), must be defined in relation to an expectation. If the expectation is cooperation/mutualism, then anything less is parasitism. In that case, parasitism and cheating are synonymous, as suggested by Smith and Smith (2012). Obviously if the expectation were parasitism, not reciprocating could hardly be considered cheating. What in sociobiological parlance is rated as “cheater” phenotype may often only reflect dominance hierarchies (Fiegna & Velicer, 2005; Fiegna et al., 2006; Santorelli et al., 2008; Buttery et al., 2009; Vos & Velicer, 2009) that may be fixed or plastic depending on the ecological conditions in which the competitions take place. Such dominance hierarchies already take place within clonal communities where cell fate decisions (i.e. spore or stalk cell) are the result of stochastic and deterministic factors (see chapter 5). Intriguingly, within the conceptual framework of the kin selection theory the interpretation of these coercion-characterized dominance hierarchies are biased: when they occur within clonal populations they are interpreted as “altruism” (e.g. Strassmann et al., 2000), but when they occur between less related strains as “cheating”. Phenotypically, queens and dominants of eusocial colonies are social parasites, at least from the perspective of suppressed workers and helpers (see chapter 9), but I am not aware of any publication in which this has been noted explicitly.

Studies of helping in birds in particular tend to focus on a single aspect of helping behavior, usually nestling provisioning. Chick provisioning alone may not, however, be a representative measure of an individual’s overall contribution to the group’s reproductive success (Arnold et al., 2005). For example, a helper may contribute little in the form of chick feeding behavior, but by participating in sentinel or mobbing behaviors, that helper may reduce the risk of a group losing young to predators (Austad & Rabenold, 1985; Schaub et al., 1992; Hailman et al., 1994; Maklakov, 2002). Such a scenario could also explain why seemingly non-cooperative individuals (Heinsohn & Packer, 1995; Boland et al., 1997; Pusey & Packer, 1997) are tolerated in some communally breeding species. Heinsohn & Packer (1995), for example, found that female lions showed persistent individual differences in the degree to which they contributed to inter-group conflicts over territory. Intriguingly, other group members clearly recognised ‘cowardly lions’ but failed to punish them suggesting that cooperation was not maintained by simple reciprocity. Instead poor defenders might be too costly to eject from the group or they may be good at other activities. Within large complex social groups, it is

possible that individuals might appear to defect only with respect to one form of helping, but contribute to other forms of communal behavior.

Lekberg and Koide (2014) further outlined the multiple levels of mutualistic relationships: “If cheating is simply defined as being less beneficial than others, mycorrhizal fungi that cheat plants almost certainly exist. Indeed, results from controlled greenhouse experiments show drastic differences in the effects on plant growth among fungal taxa (e.g., Bever, 2002; Munkvold et al., 2004; Smith et al., 2004; Pringle & Bever, 2008) and in the ratio of phosphate delivered to plant and carbohydrate transferred to fungus (Pearson & Jakobsen, 1993; Lendenmann et al., 2011). Because experiments are frequently performed under conditions that differ markedly from those in nature, labeling an arbuscular mycorrhizal fungus a cheat should be done with caution. In the greenhouse, for example, pathogen pressure may be low. But in the field, pathogens may be very important and the fungus that is poor at transferring phosphate may be superior in providing pathogen protection (Newsham et al., 1995). Also, while short-term greenhouse experiments may suggest the potential for cheating under very specific conditions, the real laboratory is the natural community in which time and space are very much expanded and in which plant populations struggle for survival over multiple generations during which environmental conditions are changing constantly. The importance of adopting a lifetime fitness view of symbiotic functioning was recently shown in an ant–Acacia symbiosis in which symbionts that appeared to be cheats at one life-stage were mutualistic at a different life-stage and contributed to increased lifetime fitness (Palmer et al., 2010). The same issue continues to be discussed and researched in regards to orchid mycorrhiza, which provide carbohydrate to germinating seedlings and may (Cameron et al., 2006) or may not (Rasmussen & Rasmussen, 2009) be repaid by adult plants.”

### 7.2.1 Frequency-dependence of cheater's payoff

Conflicts of interest exist between cooperators and “cheaters”. After competition between “cheat” and “co-operator” strains of yeast, population fitness is maximized under co-existence. The conditions necessary to recover the anti-intuitive result are 3-fold: (i) that resources are used inefficiently when they are abundant, (ii) that the amount of cooperation needed cannot be accurately assessed, and (iii) the population is structured, such that cooperators receive more of the resource than the “cheats” (MacLean et al., 2010a). Both experimental and theoretical work has shown that cooperative systems are highly tolerant to

“cheater” exploitation (Marco et al., 2009). Frequency-dependent effects can even promote the maintenance of cooperative behavior in microbes and animal societies. Frequency-dependent selection on “cheating” phenotypes has recently been demonstrated in a number of studies (e.g., Velicer et al., 2000; Dugatkin et al., 2003, 2005; Fiegna & Velicer, 2003; Harrison et al., 2006; MacLean & Gudelj, 2006; Ross-Gillespie et al., 2007; Sandoz et al., 2007). Cheating or defecting strategies may do very well as long as they are rare in a population of cooperative individuals but fare worse or even perish when surrounded only by other cheaters (Nowak et al., 1994; Turner & Chao, 1999; Hauert et al., 2002; Sigmund, 2002; Le Galliard et al., 2003; MacLean & Gudelj, 2006; Diggle et al., 2007b; Ross-Gillespie et al., 2007; Smith et al., 2010). Dugatkin et al. (2005) demonstrated that negative frequency-dependent mechanisms can act in *Escherichia coli* colonies: antibiotic-sensitive “cheaters” can persist at low concentrations (5–12%) on antibiotic-laced medium when associated with cooperative colonies of antibiotic-resistant individuals. “Cheaters” then enjoyed the benefit of antibiotic resistance without the cost of producing the resisting agent. However, “cheater” *E. coli* were prevented from reaching higher concentrations because they become more sensitive to the antibiotic substrate with increasing frequency. This is a case of negative frequency-dependent selection, where the fitness of a phenotype (e.g., “cheaters”) increases as it becomes rarer. As “cheaters” become more abundant either (i) they lose the benefit of associating with the group as “cheaters” reach numerical prevalence or (ii) colonies that harbor the highest concentrations of “cheaters” perform more poorly in interdemetic (i.e., group-level) competition (Avilés 1986, 1993, 1997, 2002; Wilson & Wilson, 2007). In stationary phase cultures of *E. coli* mutants do not enter, or exit early, the nondividing stationary-phase state, cooperatively maintained by the wild type. Thus they end up overrepresented as compared to their initial frequency at the onset of the stationary phase, and subsequently they increase disproportionately their contribution in terms of progeny to the succeeding generation in the next growth cycle, which is a case of evolutionary “cheating”. However, the survival advantage of the mutant at any given time during a takeover is inversely dependent on its frequency in the population, its growth adversely affects the survival of the wild type, and its ability to survive in stationary phase at fixation is lower than that of its ancestor (Vulic & Kolter, 2001). Simulation of the evolution of cooperation among nonrelatives revealed that cheaters increase in

frequency when rare, but are selected against when common due to the reduced productivity of the groups they overburden with their presence. Freeloader frequencies thus periodically rise and fall around a dynamic equilibrium (Avilés, 2002). The spider *Anelosimus studiosus* shows a within-population social polymorphism with social (cooperative) and asocial (cheater) phenotypes. Asocial individuals experience negative frequency-dependent foraging success in staged foraging contests. Asocial individuals outperform social individuals when their representation is low, but lose this competitive advantage as their relative numbers increase (Pruitt & Riechert, 2009). In groups of foraging animals, individuals often have the choice between two behavioral roles: actively search for hidden food sources (‘producer’) or exploit food sources discovered by others (‘scrounger’) (Barnard & Sibly, 1981; Barnard, 1984; Beauchamp, 2013). In some bird species individuals readily switch between producer and scrounger strategies (Coolen et al., 2001). The effectiveness of scrounging decreases linearly as the frequency of scroungers increases, whereas the effectiveness of the producer strategy remains relatively constant (Mottley & Giraldeau, 2000; Morand-Ferron et al., 2007). Morand-Ferron et al. (2007) showed that the payoffs to kleptoparasites were frequency dependent; the more scroungers that were present in a group, the lower their payoffs (estimated in latency to a successful kleptoparasitic act). When they experimentally manipulated the costs of scrounging, they found that the frequency of scrounging was high when its costs were low, and the frequency was low when its costs were high. Experimental manipulation of the costs of producing (circuitous vs direct route) had the expected effect on the frequency of scrounging: when producing was cheap there were fewer scroungers, but the reverse was true when producing was costly. It has been suggested that scrounging could affect demographic parameters and predator–prey population dynamics (Coolen, 2002). By comparing the dynamics of groups where scrounging was either absent or present, Coolen et al. (2007) found that the presence of scrounging contributes to the regulation of both predator and prey populations. Moreover, their model predicted that prey persist at higher densities when scrounging is present because the exploitation pressure is then reduced. Predators therefore can exploit a higher density of resources when scrounging is present and consequently they can also maintain a higher abundance under this condition. Thus, although scrounging negatively affects the growth rate of a population, the presence of nonsearching individuals would also contribute to maintaining higher numbers of

both prey and predators (Giraldeau & Dubois, 2008).

Producer-scrounger games have been found to apply to a potentially wide range of resource exploitation problems (Barnard, 1984). Scroungers can benefit from stealing not only food but also mating opportunities or parental care. Obligate and conditional reproductive “cheater” strategies, each with its own distinct genetic basis, do exist collaterally in numerous animal species as evolutionarily stable strategies (Alcock, 2005). The costs of courting and mating include mainly a decreased foraging efficiency and an increased mortality rate due to predation. Females’ preferences for exaggerated traits favor the use of alternative tactics, in which males steal fertilizations and hence parasitize the efforts of others while avoiding the cost of courting (Giraldeau & Dubois, 2008). Scrounging payoffs are negatively frequency-dependent and scrounger does worse than producer when scrounger is common but better than producer when scrounger is rare. There is empirical support that the proportion of males adopting alternative tactics may depend on social and ecological conditions, and that males are capable of adjusting their behavior in response to changes in the benefits associated with each tactic. For instance, the proportion of pupfish (*Cyprinodon pecosensis*) males adopting territorial, sneaker, and satellite breeding tactics depends on population density: as population density decreases, so does the benefit of maintaining a territory, leading to an increase in the proportion of sneakers and satellites (Kodric-Brown, 1986). The cost of calling, however, especially in terms of increased predation danger, will also play an important role. As the cost increases, it should erode the caller’s advantage and hence increase the proportion of satellite males. Tungara frogs, for instance, curtail conspicuous activities and reduce the intensity of their mating calls in response to simulated attacks by model bats (Ryan, 1985). Experimental manipulation of the risk of predation resulted in the expected change in tactics use in guppies (Godin, 1995): males performed a lower proportion of displays and increased their sneaky mating attempts when the risk of predation was increased.

A frequency-dependent behavioral evolutionary game concerns the parental investment decision of the great golden digger wasp (*Sphex ichneumoneus*) (Brockmann et al., 1979). The females of this species lay their egg in a burrow. They can either dig the burrow themselves; a strategy called “digging,” or use the burrow of another female, called “entering.” Digging is for all intents and purposes the producer strategy while entering corresponds to scrounger.

Research with these insects has established that the frequency- dependence of payoffs contributes to maintaining these alternative parental strategies (Brockmann et al., 1979). Conspecific brood parasitism is a taxonomically widespread alternative reproductive tactic, particularly in birds, in which a female lays eggs in the nest or egg group of a conspecific that provides all subsequent parental care (de Valpine & Eadie, 2008). Because conspecifics provide the only hosts for brood parasites, obligate parasitism cannot become fixed in a population. Further, the advantages of parasitic laying are likely to be greatest when the frequency of parasitism is low and many host nests are available containing few parasitic eggs; the advantages will decrease as frequency of parasitism increases and more host nests contain many parasitic eggs (de Valpine & Eadie, 2008). In the treehopper insect (*Publilia concava*), Zink (2003) found that the time to find hosts increased as the frequency of the parasitic tactic increases. The hatching success of such parasitic eggs may be low when hosts can detect them and adopt countermeasures. In American coots (*Fulica americana*), for instance, parasitic eggs suffer a high mortality rate, mainly because of egg rejection by their hosts (Lyon, 1993).

Cheater resistance may be an important mechanism of social parasite/cheater control and might provoke coevolutionary arms races (Foitzik et al., 2003; Travisano & Velicer, 2004; Khare et al., 2009; Martin et al., 2010) similar to those seen in victim-exploiter/host–pathogen interactions (Gavrilets, 1997; Marques & Carthew, 2007). Possible examples of such coevolution include: (i) the conflict between brood parasitic cuckoos and their hosts, where the hosts are selected to reject cuckoo eggs, and the cuckoos are selected to circumvent this (Davies, 2000; Spottiswoode & Stevens, 2010; Langmore et al., 2011; Stoddard & Stevens, 2011); (ii) in the obligate mutualism between yuccas and yucca moths, selective abortion of flowers with heavy egg loads selects against moths that lay many eggs per flower or provide low-quality pollinations (Pellmyr & Huth, 1994); (iii) both “cheats” and cooperators performing better against their opponents from the past, but less well against future phenotypes, considering a laboratory selection experiment on biofilm production in *Pseudomonas fluorescens* (Zhang et al., 2009). Asymmetrical competition for commodities can explain the long-term persistence of mutualistic partnerships in spite of the evolution or incorporation of cheaters (Ferriere et al., 2002). Paradoxically, the presence of cheaters/parasites and cheater/parasite species in many mutualisms may be central to the maintenance

of cooperation itself (Foster & Kokko, 2006; Holland et al., 2013). Consequently, mutualism–parasitism food web modules are common in nature (Ferriere et al., 2002; Genini et al. 2010; Holland et al., 2013). A mixture of “cheaters” and cooperators may even enable maximal group benefit (MacLean et al., 2010a). *S. cerevisiae* secrete invertase as a “public good” when the medium involves sucrose (and no glucose), which is digested by this enzyme. The resulting glucose is then taken up by the yeast cells. The growth rate is actually a concave function of the available glucose because there are diminishing returns to increased glucose. Thus, when the local glucose concentration is low, the increased glucose due to invertase production outweighs the cost of cooperation, but as there is more glucose in the environment from other cooperators, the additional growth rate per glucose molecule reduces below the cost of invertase production. Since production and secretion of invertase are costly, a “cheating” strategy is to take up glucose without making a contribution to the common pool of invertase. Defectors have a higher growth rate when the density of secreting cells is high but are less fit when the density of secreting cells is low (Greig & Travisano, 2004; Gore et al., 2009; MacLean et al., 2010a; Damore & Gore, 2012).

Like frequency dependence in classical population genetics, nonlinear social interactions can lead to coexistence of cooperators and defectors (Doebeli et al., 2004; smith et al., 2010; Damore & Gore, 2012). Archetti and Scheuring (2013) have shown that if benefits are nonlinear, mutualism can be maintained in well-mixed population without punishing the free riders. Examples of nonlinear benefit functions have been reported for cooperative hunting (Bednarz, 1988; Packer et al., 1990; Stander, 1991; Creel, 1997; Yip et al., 2008) and cooperative nesting (Rabenold, 1984) in vertebrates and for the production of diffusible enzymes in microbes, for example adhesive polymers (Rainey & Rainey, 2003) and antibiotic resistance in bacteria (Lee HH et al., 2010). This is likely to be a common feature of public goods in microbes, as the effect of enzyme production is generally a saturating function of its concentration (Hemker & Hemker, 1969), more specifically, a sigmoid function (Ricard & Noat, 1986). In certain cases, if a metabolic pathway is controlled by signal metabolites through an enzyme cascade, the final product follows a highly nonlinear switch-on switch-off behavior that resembles a step function (Mendes, 1997; Eungdamrong & Iyengar, 2004). Saturating benefits, and in particular sigmoid benefits, therefore are probably the rule in nature (Archetti & Scheuring, 2013). Nonadditivity makes cooperative sporulation remarkably resistant to

exploitation by “cheater” strains showing how nonlinear interactions among cells insulate bacteria against cheaters (smith et al., 2010). Selection is driven by higher-order moments of population structure, not relatedness.

Under adverse environmental conditions defectors have an elevated mortality (Harms, 2001). The mere presence of a mortality risk gradient can create a kind of stochastic segregation between cooperators and defectors. Because the distribution of cooperators is patchy in the boundary region, eventually defectors run out of cooperators to free-ride on, and perish, making the distribution of cooperators even more uneven increasing the effective barriers against the spread of future invasions (Harms, 2001). Generally, coexistence is favored in an oscillating environment (such as feast and famine cycles) and periodicity increases the number of niches in the sense of the principle of competitive exclusion (Cushing, 1986; MacLean & Gudelj, 2006). Clonal amoebae and bacterial colonies with an asocial “cheater” phenotype (and no cooperators to parasitize) have a high risk to go extinct under conditions of feast and famine cycles (Hilson et al., 1994; Pál & Papp, 2000; Ennis et al., 2003; Fiegna & Velicer, 2003; Rainey & Rainey, 2003; Castillo et al., 2005; Kuzdzal-Fick et al., 2011; Waite & Shou, 2012; Waite, 2013). In chimera of wild-type and cheater mutants of *D. discoideum*, Gilbert et al. (2007) have calculated that, when the proportion of cheater cells exceeds 25%, the advantage of the cheater relative to wild type is lost. Due to abnormal stalk morphogenesis, some social cheaters would be doomed if their spores were dispersed to grow by themselves. Gilbert et al. (2007) have also sampled 95 independent fruiting bodies isolated in the wild and tested 3,316 spores without finding a colony with defective morphology, which indicates that, at least in a limited sample, morphologically recognizable *D. discoideum* cheaters are not common (Shauly & Kessin, 2007).

### 7.2.2 Social parasitism as bet-hedging strategy?

The biological default setting of individuals is neither selfish nor cooperative but ecologically context-dependent and dynamic. Competition and cooperation are threshold traits on a continuum of ecological variables. The traditional concepts of group and individual selection appear to be two extremes of a continuum, with systems in nature operating in the interval in between (Wilson DS, 1975). What appears to be cheating could actually be a strategy to associate with many partners, even those that may temporarily be poor mutualists, to maximize lifetime fitness in uncertain and stochastic environments. This

has been referred to as bet-hedging (Lekberg & Koide, 2014, Heininger, 2015). Cues during child-hood (such as childhood exposure to family neglect, conflict and violence, and to neighborhood crime) that life will be harsh, unstable and short—these cues may probabilistically indicate that it is in one's fitness interests to exploit co-operators and to retaliate quickly against defectors (McCullough et al., 2012). Individual differences in mutual benefit cooperation are not merely due to genetic noise, random developmental variation or the operation of domain-general cultural learning mechanisms, but rather, might reflect the adaptive calibration of social strategies to local social-ecological conditions and their dynamics. Manipulation of neurohormonal signaling pathways of stress responses is able to affect the balance between cooperation and cheating in the coral reef cleaner-client fish mutualism (Bshary et al., 2011; Soares et al., 2012, 2014; Cardoso et al., 2015), arguing for the dynamic context-dependency of selfish and cooperative behaviors.

Conspecific brood parasitism (CBP) is a taxonomically widespread alternative reproductive tactic in which a female lays eggs in the nest or egg group of a conspecific that provides all subsequent parental care (de Valpine & Eadie, 2008). Spreading eggs among nests, parasites can increase the likelihood that at least some offspring will escape predation and survive to independence, also known as the "risk spreading" hypothesis (e.g., Rubenstein, 1982; Pöysä & Pesonen, 2007). In a well-studied model species of CBP, the common goldeneye (*Bucephala clangula*) Pöysä and coworkers (Pöysä 1999, 2003, 2006; Pöysä et al., 2001, 2014) found that nests are not predated at random and that parasites use public information in locating and selecting nests that have high prospects of success and preferentially lay in safe nests. By taking these findings into account, model simulations revealed that the selective advantage of parasitic egg laying related to nest predation is much higher than previously thought (Pöysä & Pesonen, 2007).

Division of labor is a routine behavior in cooperative communities (Arnold et al., 2005; see chapter 16.2), even in microbial biofilms (Crespi, 2001; Kearns, 2008; Nadell et al., 2009). Inter-individual heterogeneity in producing or responding to microbial quorum sensing signals may be interpreted as a sort of division of labor that confers group level benefits (e.g. Anetzberger et al., 2009, 2012). On the other hand, it may be considered as cheating or coercion, whereby individuals chemically manipulate quorum sensing-based collective decisions to their own advantage, and benefit at the expense of the group

(Keller & Surette, 2006; Diggle et al., 2007a; Stacy et al., 2012). In fact, signal-blind quorum sensing mutants are known to arise in natural settings (e.g. the cystic fibrosis lung; Köhler et al., 2010), and in vitro experiments suggest that these mutants may be acting as cheats (Diggle et al., 2007b). Both scenarios, although plausible (Ross-Gillespie & Kümmerli, 2014), should exclude each other as division of labor should benefit the group while cheating should harm its fitness. An alternative interpretation could be that in some cases cheating may be part of a bet-hedging strategy: behavior that is harmful under some conditions may be beneficial under other ones.

In nature, soil moisture, nutrient availability, pathogen and herbivore pressure, local plant density, the amount of light available to the plant, etc., are in constant flux. Different fungal species and families differ in their growth patterns (Hart & Reader, 2002), which may result in different abilities to provide benefits. For example, the extensive extraradical mycelium of many members of the Gigasporaceae may be advantageous for phosphate acquisition, whereas the greater intraradical colonization by members of the Glomeraceae may help provide pathogen protection (Maherali & Klironomos, 2007; Sikes et al., 2009). From the fungal perspective, the phenology of root production varies with plant species, as do a number of other traits that may influence their quality as hosts. Given this variation, and because the degree of benefit both partners experience is context-dependent (Koide, 1991; Hoeksema et al., 2010), bet-hedging may be advantageous (Lekberg & Koide, 2014). For the arbuscular mycorrhizal symbiosis, this may mean that plants and fungi support multiple partners despite some of the partners being significantly less beneficial than others under the current circumstances (Lekberg & Koide, 2014). Lekberg et al. (2010) found that while the fungus allocated more phosphate to the host that provided more carbohydrate, arbuscular mycorrhizal colonization did not differ between the good and poor hosts (although the abundance of arbuscules was higher in the good host). One interpretation of these results is that selection has favored fungi that optimize their likelihood of acquiring carbohydrate across space and time by colonizing multiple plants. Also, perhaps the biggest surprise in the research of Kiers et al. (2011b) was not that the better phosphate-transferring fungus received more carbohydrate than the worse phosphate-transferring fungus, but that the latter received as much carbohydrate as it did. From a bet-hedging perspective, it is possible that selection has favored plants that associate with fungi that range in the benefits they provide (Lekberg & Koide, 2014).

For example, the worse phosphate-transferring fungus may provide other benefits that become more important under different conditions (as carefully pointed out by Kiers et al., 2011b). For example, the behavior of the fungus they termed a “hoarder” may serve to store phosphate during winter months when plants are inactive (Merryweather & Fitter, 1998), thus preventing loss of important resources from the system (Lekberg & Koide, 2014).

The carbon that rhizobia in root nodules receive from their host fuels both reproduction and the synthesis of the storage polyester poly-3-hydroxybutyrate (PHB), as well as N<sub>2</sub> fixation, which mainly benefits the host. Rhizobia escaping nodules can use stored PHB to survive starvation and reproduce up to 3-fold, but PHB synthesis is energetically expensive and trades-off with N<sub>2</sub> fixation (Anderson & Dawes, 1990; Ratcliff et al., 2008). Some rhizobia have evolved sophisticated mechanisms to increase PHB accumulation, such as the production of rhizobitoxine, a chemical inhibitor of legume ethylene synthesis (Sugawara et al., 2006). Rhizobitoxine reduces host growth, decreasing rhizobia per nodule for all strains on a plant, but substantially increases PHB accumulation for rhizobitoxine-producing rhizobia (Ratcliff & Denison, 2009) and can be considered a tool for cheating (Ratcliff, 2010). In addition to enhancing reproduction, PHB has a role in bet-hedging: when starved, free-living high-PHB rhizobia divide asymmetrically, forming dormant, high-PHB “persisters” that survive long-term starvation and antibiotic treatment, and low-PHB “growers” that are sensitive to these stresses (Ratcliff, 2010). *Sinorhizobium meliloti* integrates bet hedging and phenotypic plasticity, forming fewer high-PHB persister cells when low competitor density predicts shorter-term starvation (Ratcliff, 2010). Since rhizobitoxine and PHB production is a marker of both cheating propensity and bet-hedging strategy, a synopsis of these phenomena identifies rhizobial cheating as potential bet-hedging strategy.

Pyoverdine defective mutants which have been isolated in natural populations, are potential cheats (De Vos et al., 2001; Visca et al., 2007). However, the status of a cheater is often determined unidimensionally, e.g. whether organisms contribute to a single commodity, e.g. in *Pseudomonas aeruginosa* siderophore production in iron-limited conditions (Griffin et al., 2004), ignoring the possibility that the organisms may contribute to another commodity of communal life (Kiers et al., 2011b). Iron is essential for, yet toxic to, bacteria. For most pathogens, including *P. aeruginosa*, there is intense competition for iron with the host (Braun, 1997; Ratledge & Dover, 2000; Skaar,

2010). Pyoverdine-deficient mutants have a greatly reduced ability to cause infection (Meyer et al., 1996; Takase et al., 2000). Therefore, it is surprising that in a detailed study of pyoverdine synthesized by *P. aeruginosa* obtained from cystic fibrosis patients, over one-quarter of the isolates were unable to synthesize pyoverdine (De Vos et al., 2001). By sequestering iron, subgrowth inhibitory concentrations of the mammalian iron chelator lactoferrin block the ability of *P. aeruginosa* biofilms to mature from thin layers of cells attached to a surface into large multicellular biofilm structures (Singh et al., 2002). On the other hand, pyoverdine defective mutants can form biofilms with the wild-type mushroom-like structures under provision of chelated forms of environmental iron. In fact, biofilms of the *pvdA* mutant grown in the presence of 1 μM ferric dicitrate show the mushroom-like appearance of the parent strain whereas the parent forms only the expected flat, thin biofilms (Banin et al., 2005). Intriguingly, mutants with a “cheater” phenotype in iron-limited conditions may achieve the maturation of biofilms when iron is only available in chelated forms. Thus, the “defectors” in iron-limited conditions turn out to provide another commodity for communal life and may be yet another example of bacterial bet-hedging. Likewise, bet-hedging strategies with regard to social competence in microbial populations resulting in superior competitors under conditions favoring antisocial behavior may be misidentified as cheating in more prosocial conditions (Brock et al., 2013; Kraemer & Velicer, 2014).

## 8. Eusociality

*..ecological, demographic and physiological factors can be more important in promoting the evolution of eusociality.*

Gadagkar, 2001

### Summary

**Eusociality is the Holy Grail of kin selection/inclusive fitness theory. Though eusociality is taxonomically rare, eusocial organisms frequently meet great ecological success and high persistence through geological time, with eusocial species representing approximately 50% of the world’s insect biomass. Each colony can be viewed as a superorganism, with a reproductive queen and non-reproductive workers as her extended phenotype. Natural selection in eusocial insects acts at the level of the colony; what benefits the queen will become heritable.**

**The haplodiploidy hypothesis of eusociality**

suggested that the high relatedness between colony members, resulting in indirect fitness gains of helpers, favored the evolution of eusociality and its associated reproductive skew. However, neither haplodiploidy nor split sex ratios in haplodiploid species appear to have played an important role in facilitating the evolution of eusociality. Currently, the monogamy hypothesis of eusociality is the most favored hypothesis by the advocates of kin selection theory. The phylogenetic evidence, however, is weak. Social systems of low relatedness have often evolved (e.g., becoming polygynous or polyandrous) from high-relatedness ancestral species. Groups of low relatedness are likely to have correlated benefits arising from increased group-level genetic diversity, and it appears these benefits often exceed the evolutionary advantages of high within-group relatedness. Eusociality is an accommodated/assimilated phenotype in which a phenotype that is produced specifically in response to some environmental stimulus, such as a stressor, becomes stably expressed independently of the evoking environmental trigger.

An alternative hypothesis for the evolution of eusociality in insects is put forward that includes both genetic, physiological, behavioral and ecological factors that jointly contributed to the phenomenon. Body size/body mass predicts several fitness components, suggesting that it is a reliable proxy for fitness in many species.

The respiratory system of insects is relatively simple: gas exchange takes place through a system of tubes, the tracheae that lead directly to the cells. Diffusion of oxygen into the organism limits the maximum possible size. Due to physiological and ecological constraints, body size is limited in insects, barring them from exploiting one of the most important means to increase fitness. However, another fitness-boosting strategy, cooperation with division of labor, stood at their disposal and, in fact, was exploited to create advanced integrative units, "superorganisms". Brood care and, particularly, maternal care is the constitutional feature of any complex sociobiological behavior and is associated with neurobiological agents that mediate social behavior ranging from mother-offspring bonding to prosociality.

### 8.1 Ecological success

Eusociality (from Greek eu- meaning 'well' or 'good'), is regarded the apex of animal social organization

(Wilson, 1971; Queller & Strassmann, 2003). Eusociality has arisen independently at least 11 times in the insects (Cameron & Mardulyn, 2001; Brady et al., 2006; Hines et al., 2007; Cardinal et al., 2010), and eusocial insects have all converged on the following three characteristics: reproductive division of labor, cooperative brood care, and overlapping generations (Michener, 1969, 1974; Wilson, 1971; Fischman et al., 2011). Though eusociality is taxonomically rare (ca. 2% of the nearly 1 million known insect species are eusocial, Wilson, 1990; Hölldobler & Wilson, 2009), organisms that have achieved this higher level of organization frequently meet great ecological success, with eusocial species representing approximately 50% of the world's insect biomass (Wilson, 1971, 1987; Strassmann & Queller, 2007). In the Amazonian rain forest near Manaus, for example, the eusocial ants, termites, bees and wasps constitute an astonishing 75% of the entire insect biomass (Fittkau & Klinge, 1973). Ants alone have more than 12,000 species and are found in every terrestrial habitat, using every resource. Their biomass exceeds that of all terrestrial non-human vertebrates combined (Hölldobler & Wilson, 1990). Humans, which can be loosely characterized as eusocial (Foster & Ratnieks, 2005), are dominant among the land vertebrates. Sherman et al. (1995) argued that cooperative breeding and eusociality are not discrete phenomena but rather form a continuum of fundamentally similar social systems and proposed to array invertebrate and vertebrate cooperative breeders along a common axis representing a standardized measure of reproductive variance.

Taking persistence of a phyletic line through geological time as the key measure of ecological success, eusocial ants have a much higher long-term success (and fitness, *sensu* Thoday, 1953; Cooper, 1984) than their extinct solitary counterparts (Wilson, 1987). Although there are exceptions (Danforth, 1990), low fecundity is a common feature in solitary aculeate Hymenoptera (Michener & Rettenmeyer, 1956; Danks, 1971; Else et al., 1978; Minckley et al., 1994; O'Neil, 2000), where females often produce a total of only 6–12 eggs in their lifetime. For example, females of the solitary specialist bee *Dieunomia triangulifera* produce a total of 2–6 eggs during their lifetime (Minckley et al., 1994), and those of *Andrena erythronii* produce a total of 8 eggs (Michener & Rettenmeyer, 1956). Similarly, in a survey based on 12 species of solitary nest-provisioning wasps, females produced an average of 9.8 eggs during their lifetime (O'Neil, 2000). Usually high preadult mortality rates (up to ~50–60%; Danks, 1971), common entire nest failure (Richards & Packer, 1995), and potentially

high adult predation rates (Dukas, 2001) further combine to reduce net fecundities of solitary aculeate Hymenopterans to levels where the extinction vortex can be initiated (Zayed & Packer, 2005). In *Ropalidia marginata*, a solitary foundress produces on the average no more than one or two offspring whereas a queen of a multi-female colony produces on the average 76 offspring (Gadagkar, 1990a).

Most Hymenoptera are not social, although all non-social bee and wasp females have the same probability as the honeybees of being more closely related to sibs than to progeny (Slobodchikoff & Shields, 1988). For example, the vast majority of the ~18,000 described species of bees are solitary or cleptoparasitic, with only approximately 6% displaying eusociality (Danforth, 2007; Michener, 2007). Eusociality occurs in three halictid taxa: *Augochlorini*, *Halictus*, and *Lasioglossum*. These groups have experienced several evolutionary reversals back to a solitary state, as many as 4–6 times both in *Halictus* and *Lasioglossum* (Wcislo & Danforth, 1997; Danforth, 2002; Danforth et al., 2003; Rehan et al., 2012). At least in these taxa evidence indicates extremely high barriers to the evolution of eusociality. Its origins are likely to have required very unusual life-history and ecological circumstances, rather than the amount of time that selection can operate on more simple forms of sociality (Rehan et al., 2012).

## 8.2 Superorganism

In eusocial insects, each colony can be viewed as a superorganism, with a reproductive queen and non-reproductive workers as her extended phenotype (Seeley, 1989; Wilson & Sober, 1989; Queller & Strassmann, 2002; Hölldobler & Wilson, 2009; Wilson & Nowak, 2014). Already Weismann (1893) was struck by the similarity between germ-soma specialization in multicellular organisms and the existence of reproductive and worker castes in ants: “The whole colony behaves as a single animal; the state is selected, not the single individual; and the various forms behave exactly like the parts of one individual in the course of ordinary selection” (p. 309). Weismann argued that the colony—not the individual ant—is the unit of selection by analogy to his view that it is germ-soma specialization in animals that defines them as individual units of selection. The term “superorganism” was first coined by Wheeler (1911), who focused on functional similarities such as metabolism, reproduction, and homeostasis, but who also stressed reproductive division of labor as analogous to germ-soma specialization: “One of the most general structural peculiarities of the [organism] is the duality of its composition, as expressed in the

germ-plasm on the one hand and the soma on the other, and the same is true of the ant colony.” (Folse, 2011) Recently, an article in PNAS reported that Apoidea- and *Apis*-specific genes are enriched for signatures of positive selection, indicating that novel genes play a disproportionately large role in adaptive evolution of eusocial insects. Worker-biased proteins have higher signatures of adaptive evolution relative to queen-biased proteins, supporting the view that worker traits are key to adaptation. Moreover, genes regulating worker division of labor were found to be enriched for signs of positive selection (Harpur et al., 2014). In honeybees, in addition to the low viability of worker-laid eggs (Pirk et al., 2004), there are strong policing mechanisms which allow only fewer than 1 in 100 worker-laid eggs to develop (Ratnieks & Visscher, 1989) so that only about 1 in 1000 males reared to adulthood derives from a worker (Page & Erickson, 1988; Visscher, 1989). In addition, theory suggests that, all other factors being equal, indirect selection on workers will be effectively weaker than direct selection on queens (Linksvayer & Wade, 2009), especially when queens are polyandrous, as in *A. mellifera* (Hall & Goodisman, 2012). Yet, although direct worker contribution to the genes of the next generation is negligible the authors of the PNAS paper concluded that “it is reasonable to assume that indirect kin-selection is mostly responsible for the adaptive evolution of worker traits” (Harpur et al., 2014).

Reflecting Weismann’s argument, it has been stressed that natural selection in social insects acts at the level of the colony (Seeley, 1997; Korb & Heinze, 2004). What benefits the queen will become heritable. Darwin (1859) already suggested that worker traits could be favored by natural selection when they provide a benefit to reproductive family members within the colony. I would like to cite Nowak et al. (2010): “... descent is from queen to queen, with the worker force generated as an extension of the queen (or cooperating queens) in each generation. Selection acts on the traits of the queen and the extrasomatic projection of her personal genome and not the workers.... The interaction between queen and workers is not a standard cooperative dilemma, because the latter are not independent agents. Their properties depend on the genotype of the queen and the sperm she has stored.... Inclusive fitness theory always claims to be a ‘gene-centred’ approach, but instead it is ‘worker-centred’: it puts the worker into the centre of attention and asks why does the worker behave altruistically and raise the offspring of another individual? The claim is that the answer to this question requires a theory that goes beyond the standard fitness concept of natural selection. But here

we show that this is not the case.”

### 8.3 Kin selection and eusociality

Eusociality is the Holy Grail of kin selection/inclusive fitness theory (Queller & Strassmann, 1998; Hughes et al., 2008; Boomsma et al., 2010; Strassmann et al., 2010). Masterminded by the kin selection/inclusive fitness theory, various theories have been put forward that suggested that the high relatedness between colony members, resulting in indirect fitness gains of helpers, favored the evolution of eusociality and its associated reproductive skew.

#### 8.3.1 Haplodiploidy hypothesis of eusociality

Hamilton suggested that due to the haplodiploid genetics of the Hymenoptera, females are relatively more related to their siblings than to their own offspring which promotes altruistic sib rearing and, consequently, the evolution of eusociality (Hamilton, 1972). Hamilton (1964, 1972) suggested that the inflated genetic relatedness of full sisters under haplodiploidy (life-for-life  $r = 3/4$ ) explains why females, and not males, engage in altruistic sib-rearing in hymenopteran societies. This haplodiploidy hypothesis has fallen out of favor with the realization that the average value of siblings of both sexes is exactly the same ( $r = 1/2$ ) for females and males, irrespective of the sex ratio (Charlesworth, 1978; Charnov, 1978; Craig, 1979; Bourke & Franks, 1995; Ross et al., 2013). Moreover, the haplodiploid hypothesis of eusociality (Hamilton, 1964; Trivers & Hare, 1976; Andersson, 1984) lost favor (e.g. Smith SM et al., 2009; Nowak et al., 2010; Gardner et al., 2012) since it is not compatible with the discovery of eusociality in diploid animals such as termites (Thorne, 1997; Smith SM et al., 2009), aphids (Aoki, 1977; Stern & Foster, 1996), platypodid ambrosia beetles (Kent & Simpson, 1992), *Synalpheus* sponge-dwelling shrimp (Duffy, 1996), and naked mole rats (Alexander et al., 1991) that do not have skewed degrees of genetic relatedness within families. Moreover, diploid meerkats (*Suricata suricatta*), dwarf mongoose (*Helogale parvula*), African wild dogs (*Lycaon pictus*) and silver backed jackals (*Canis mesomelas*) are all examples of mammalian species characterized by a reproductive division of labor, an overlap of generations and the co-operative care of offspring born to the group, thus satisfying the original criteria of eusociality (Batra 1966; Michener 1969; Wilson 1971; O’Riain & Faulkes, 2008). On the other hand, several large taxonomic groups are haplodiploid but do not have eusocial members (e.g., some mites, scale insects, whiteflies, and beetles). The parasitic Hymenoptera constitute an extremely large number of species yet they are all non-social (Askew, 1971). Two

major differences between the solitary parasitic Hymenoptera and the social Hymenoptera are the abundance and distribution of food resources available to the larvae of each group (Slobodchikoff & Schulz, 1988). The association between haplodiploidy and eusociality is below statistical significance (Nowak et al., 2010), all of which suggests that haplodiploidy alone is neither necessary nor sufficient for eusociality to emerge.

##### 8.3.1.1 Split sex ratios

In eusocial species, the sex ratio of helpers varies from female-only, in taxa such as the social Hymenoptera (ants, bees, and wasps) (Wilson EO, 1975), to an unbiased mixture of males and females, as in most termites (Thorne, 1997). One possibility for rescuing the haplodiploidy hypothesis involves split sex ratios, whereby there is a greater female bias among a potential altruist’s siblings than in the population as a whole (Trivers & Hare, 1976; Seger, 1983; Grafen, 1986; Grafen et al., 2012). It is thought that this allows the potential altruist to enjoy the benefit of close genetic similarity to her siblings (because they are primarily sisters) without the concomitant reduction in the reproductive value of females (because the population sex ratio need not be as biased; Boomsma & Grafen, 1990, 1991; Boomsma, 1991). However, it has been argued that Hamilton’s hypothesis does not work (Trivers & Hare, 1976; Charlesworth, 1978; Charnov, 1978; Craig R, 1982; Pamilo, 1991a; Bourke & Franks, 1995; Davies & Gardner, 2014) and that the sex of helpers could instead be explained by variation in the ecological factors that favor eusociality (Queller & Strassmann, 1998).

While most articles have examined whether the haplodiploidy hypothesis can be made to work with split sex ratios (e.g., Trivers & Hare, 1976; Seger, 1983; Grafen, 1986; Godfray & Grafen, 1988), Gardner et al. (2012) focused on those scenarios that are biologically most plausible and found that the extent to which haplodiploidy favors eusociality will be either:

- (i) small (unmated females); in an empirically plausible range of unmatedness rates (0%–6%, with a mode of 0%), the potential for helping is boosted by only 0%–3% when considering the origin of helping and only 0%–7% when considering the subsequent elaboration of helping; or
- (ii) small to medium but not widespread (queen replacement). Under the empirically supported range of probabilities of queen survival (60%–80%), haplodiploidy always promotes helping, with the potential for facultative helping boosted by up to 50% and the potential for obligate helping boosted to up to

7%. The overall importance of this mechanism will depend on how frequently queen replacement leads to split sex ratios: to date, it has been found only in some cooperative bees, suggesting it is not a general factor on the route to eusociality (Boomsma, 1991; Mueller, 1991; Packer & Owen, 1994).

In the absence of split sex ratios, haplodiploidy neither promotes nor inhibits the origin of facultative helping, irrespective of the population sex ratio, because the increased relatedness to siblings is exactly balanced by the decreased reproductive value of daughters (Craig, 1979; Gardner et al., 2012). When parameterized with empirical data, results of two recent studies suggest that split sex ratios in haplodiploid species have not played an important role in facilitating the evolution of eusociality (Gardner et al., 2012; Alpedrinha et al., 2013). Ross et al. (2013) have provided clear support for the hypothesis that the sex of the helping caste in eusocial species is driven by ecology and not the genetics of sex determination. It appears that the sex bias in "altruistic" sib-rearing within this group of insects owes to a sex bias in the provision of parental care among their solitary ancestors, a pattern which holds across other eusocial species in which the original function of workers was nursing (Lin & Michener, 1972; Alexander, 1974; West-Eberhard, 1975; Evans, 1977; Charlesworth, 1978; Eickwort, 1981; Craig R, 1982; Andersson, 1984; Starr, 1985; Bourke & Franks, 1995; Queller & Strassmann, 1998; Ross et al., 2013; Davies & Gardner, 2014). Gardner et al. (2012) concluded "that: (1) many of the proposed consequences of haplodiploidy are unlikely to have been important for the evolution of eusociality, because they rely on biological assumptions that the comparative data suggest did not occur en route to eusociality, such as multiple mating or associations between same-generation breeders (the "semisocial route"); (2) the most plausible route by which the haplodiploidy hypothesis could work is with split sex ratios, building on Trivers and Hare (1976); (3) although split sex ratios can be favored for many reasons, there are only two mechanisms that have both been observed empirically and are consistent with the biology of primitively social hymenopterans—virginity and queen replacement; and (4) while these two mechanisms can lead to haplodiploidy favoring eusociality, the overall effect is likely to be small and can even be negative".

### 8.3.2 Monogamy hypothesis of eusociality

The monogamy hypothesis is the currently most favored hypothesis for the evolution of eusociality (Boomsma, 2007, 2009, 2013; Hughes et al., 2008b; Cornwallis et al., 2010; Davies et al., 2012; Gardner et

al., 2012; Wilson & Hölldobler, 2014). All currently available evidence indicates that obligatory sterile eusocial castes arose only via the lifetime association with monogamous mothers (Wilson & Nowak, 2014). Wilson and Hölldobler (2014) noted: "At least in ants and other social Hymenoptera, the reason for the monogamy window principle is open to several alternative explanations that are relevant to the origin of eusociality. The first explanation is based on direct observation of natural history. A single mating, with the sperm stored in the mother's spermatheca, provides the same amount of genetic variation as matings by individual solitary (noneusocial) species. Because the earliest eusocial colonies consist of a relatively small number of individuals, the number of sperm from a single mating (paid out through the spermathecal valve) is adequate to last for the founding female's usually brief lifetime as queen. Another selection pressure favoring this explanation of monogamy was seldom invoked by previous authors but also is confirmed by direct observation: The mortality of the eusocial foundresses is very high from the moment they leave the mother nest and mate until they finish constructing a nest. Time is of the essence in the interval between leaving the relative safety of the mother nest and entering the relative safety of the new one. [...] ...there is little relative advantage to a foundress to mate more than once. The advantage of acquiring greater genetic diversity in the small cohort of first offspring is outweighed by the protection afforded by a constructed nest." The monogamy hypothesis was challenged (Nowak et al., 2010; Nonacs, 2011). Two recent papers have modeled the effects of the number of matings for the evolution of cooperation, and have found that monogamy often is not intrinsically advantageous. Indeed, polygamy often spreads cooperation faster through populations (Nonacs, 2011; Leggett et al., 2012). In contrast to the predictions of the kin selection theory, worker egg-laying and killing the queen is a much more common event in *Bombus terrestris* colonies (van Honk et al., 1981) than in genetically more diverse *Apis mellifera* colonies where workers are related by only 0.3 (Strassmann, 2001). Nowak et al. (2010) consider the phylogenetic evidence as weak because the ancestral state of the majority of solitary Hymenoptera species is likely to be monogamy. Because there are hundreds of extant related solitary species and only six known hymenopteran eusocial lines, the kinship-based monogamy hypothesis of Hughes et al. (2008) does not explain why only a few of the monogamous lines evolved eusociality (Wilson & Hölldobler, 2014). Hence, monogamy as an evolutionary preadaptation is indistinguishable from

ecological factors favoring cooperation, such as defending nests or sequentially provisioning offspring.

### 8.3.3 Low relatedness due to polygyny and polyandry

Due to the haplodiploidy of Hymenoptera, mothers and daughters have a relatedness of 0.5 and relatedness for two sisters is always 0.75. Thus, a female would be able to pursue her genetic interests and increase her inclusive fitness more effectively by raising her mother's daughters rather than her own. Hamilton (1964, 1972) argued that haplodiploidy makes eusociality easier to evolve, even in the absence of efficiency benefits to cooperation. In reality, however, genetic relatedness between workers in social insect colonies and the reproductive brood they rear is far below 0.75, the value expected for full sisters, often below 0.5 the value expected between mother and daughter and, not uncommonly, approaching zero. Such values are on account of queen turnover, multiple mating by queens or polygyny (Gadagkar, 1985).

An at least equally interesting message in the phylogenetic data may be how often social systems of low relatedness have evolved (e.g., becoming polygynous or polyandrous) from high-relatedness ancestral species (Nonacs, 2011). Multiple mating is prominent in eight genera, the honeybee (*Apis*: Palmer & Oldroyd, 2000), the yellow jacket wasps (*Vespula*: Goodisman et al., 2002), the seed harvester ants (*Pogonomyrmex*: Rheindt et al., 2004), the higher leaf-cutting ants (*Atta* and *Acromyrmex*: Boomsma et al., 1999; Sumner et al., 2004), the army ants (*Dorylus* and *Eciton*: Kronauer et al., 2004, 2006) and the desert ant (*Cataglyphis*: Pearcy et al., 2004). This suggests that polyandry has benefits to queen fitness (Fournier et al., 2008). Groups of low relatedness are likely to have correlated benefits arising from increased group-level genetic diversity, and it appears these benefits often exceed the evolutionary advantages of high within-group relatedness (Baer & Schmid-Hempel, 1999; Cole & Wiernasz, 1999; Rosengaus & Traniello, 2001; Tarpay, 2003; Nonacs & Kapheim, 2007, 2008). For example, the Australian desert ant *Rhytidoponera mayri* has relatedness levels of 0.1 to 0.2 among workers (Crozier et al., 1984). Similarly, multiple queen colonies of the fire ant *Solenopsis invicta* have a relatedness near zero among both the workers and the queens (Ross & Fletcher, 1985). In the neotropical multiple-queen wasp, *Parachartergus colobopterus*, average genetic relatedness among colony members overall is low (0.32 to 0.06) (Strassmann et al., 1997). In the social wasps *Polistes exclamans* the relatedness between

workers and the brood that they raise is quite small (Strassmann, 1985). In polyandrous honeybees that have been estimated to mate as often as 17.3 times (Adams et al., 1977) relatedness among workers is also greatly reduced (Page & Metcalf, 1982).

Multiple-queen (polygynous) colonies are common in social insects, especially among ants, in which polygyny may be the predominant social structure (Rissing & Pollock, 1988; Keller, 1993, 1995). Colonies containing many queens are generally characterized by low within-nest genetic relatedness. Workers thus raise brood to which they are only distantly related, presenting a potential challenge to kin selection theory (Nonacs, 1988; Pamilo, 1991b; Bourke & Franks, 1995; Helms Cahan & Helms, 2012). Helms Cahan and Helms (2012) used microsatellites to show that *Messor pergandei* ants display primary polygyny in Californian and Nevadan populations but secondary monogyny (queens become aggressive following worker emergence and reduce to a single queen) in Arizona, but that co-foundresses are unrelated in all these populations. Since co-founding with non-relatives cannot yield any indirect fitness benefits, primary polygyny must have evolved in California and Nevada but not in Arizona for unknown ecological reasons. It has been suggested that ecological constraints on independent colony founding favor polygyny in a number of ant species (Crozier, 1979; Pamilo & Rosengren, 1984; Herbers, 1986, 1993; Hölldobler & Wilson, 1990; Heinze, 1993a; Rosengren et al., 1993; Bourke & Franks, 1995). This argument is akin to ecological constraints on independent breeding favoring communal breeding in birds, vertebrates and insects (Emlen, 1982b, 1991, 1994; Vehrencamp, 1983; Pamilo & Rosengren, 1984; Reeve, 1991; Koenig et al., 1992; Reeve & Ratnieks, 1993; Keller & Reeve, 1994). In fact, the degree of polygyny and the frequency of empty nest sites are inversely correlated across populations of *Leptothorax longispinosus* (Herbers, 1986). Moreover, an experimental increase of nest sites resulted in a decrease in the mean number of queens per nest. In a comparative study of leptothoracine ants, Bourke and Heinze (1994) found that polygyny was associated with nest-site limitation, cold climate and habitat patchiness, all factors that increase dispersal costs. The differences in reproductive patterns, dispersal habits and reproductive phenotypes associated with variation in queen number support the hypothesis that ecological constraints on independent colony founding are a major factor selecting for polygyny (Keller, 1995).

Although nests of most social insects are established

independently by a single female (haplometrosis), colony founding by multiple females (pleometrosis) occurs in a number of social insect groups including ants (Hagen et al., 1988; Strassmann, 1989; Herbers, 1993; Sasaki et al., 1996; Choe & Perlman, 1997; Cahan et al., 1998; Bernasconi & Strassmann, 1999; Johnson, 2004), bees (Kukuk & Sage, 1994; Schwarz et al., 1997; Schwarz et al., 1998), wasps (Reeve, 1991; Ito, 1993), termites (Shellman-Reeve, 1997; Hacker et al., 2005), mites (Saito, 1997), aphids (Miller, 1998a, b, 2004), and thrips (Morris et al., 2002; Crespi et al., 2004; Bono & Crespi, 2006, 2008). Geographic variation in method of colony foundation (pleometrosis versus haplometrosis) without respect to relatedness occurs in desert ants *Pogonomyrmex californicus*, *Acromyrmex versicolor*, *Myrmecocystus mimicus* and *Messor pergandei* (Cahan et al., 1998; Rissing et al., 2000; Overson et al., 2013). Cofounding has been studied most extensively in the ants, bees, and wasps, and the relative importance of genetic and ecological factors vary considerably for different species. Bartz and Hölldobler (1982) found that colonies of *Myrmecocystus mimicus*, founded by a single queen, could not persist beyond a few weeks of foundation, because they could not produce sufficient workers fast enough to engage in inter-colony raiding, and subsequently had their broods stolen. A similar relationship has also been reported in *Lasius niger* (Sommer & Hölldobler, 1995). Jointly founded societies grow faster than founding colonies with a single queen and are thus believed to have an advantage in territorial contests with neighboring colonies (e.g. Bartz & Hölldobler, 1982; Tschinkel & Howard, 1983; Rissing & Pollock, 1987; Sommer & Hölldobler, 1995). Cooperating foundresses are generally unrelated in ants (Hagen et al., 1988; Strassmann, 1989; Sasaki et al., 1996; Bernasconi & Strassmann, 1999) and some bees (Kukuk & Sage, 1994; Danforth et al., 1996; Paxton et al., 1996); such cofoundress associations are usually communal in that reproduction is shared more or less equally among females, with low reproductive skew (Kukuk & Sage, 1994; Crespi & Choe, 1997; Reeve & Keller, 2001). Thus, per capita brood production either increases or remains constant with increasing numbers of foundresses (Kukuk & Sage 1994; Danforth et al., 1996; Crespi & Choe, 1997), though there are some exceptions, particularly in ants (Bernasconi & Strassmann, 1999). In other colonies of unrelated cofounders, once the first workers have eclosed, the cofoundresses typically become intolerant of each other, begin to fight and only a single queen survives per colony (Hölldobler & Wilson, 1990; Heinze, 1993b; Choe & Perlman, 1997; Bernasconi & Strassmann,

1999). In contrast, cofoundresses are typically related in eusocial wasps and bees (McCorquodale, 1988; Reeve, 1991; Kukuk & Sage, 1994; Crespi & Choe, 1997; Schwarz et al., 1997; Reeve & Keller, 2001), though cumulating evidence suggests that the presence of unrelated females may be more common than previously assumed (Queller et al., 2000; Fanelli et al., 2005; Liebert & Starks, 2006; Nonacs et al., 2006). In either case, production of workers and reproductives is often dominated by a single female (high reproductive skew) (Reeve, 1991; Reeve & Keller, 2001; Liebert & Starks, 2006) and per capita brood production declines with increasing group size (Michener, 1964; Karsai & Wenzel, 1998; Clouse, 2001; Soucy et al., 2003; Liebert & Starks, 2006), though there are some exceptions to this general pattern (Schwarz et al., 1998; Bouwma et al., 2006; Smith AR et al., 2007).

#### **8.4 Eusociality is an assimilated/accommodated phenotype**

Genetic assimilation is the evolutionary process by which a phenotype that is produced specifically in response to some environmental stimulus, such as a stressor, becomes stably expressed independently of the evoking environmental trigger (Waddington, 1942, 1953, 1956, 1957; Scharloo, 1991; Masel, 2004; Braendle & Flatt, 2006; Pigliucci et al., 2006). Genetic assimilation is a special case of a more general phenomenon, called genetic accommodation (West-Eberhard, 2003; Braendle & Flatt, 2006). This scenario of phenotypic evolution posits that (1) a mutation or environmental change triggers the expression of a novel, heritable phenotypic variant, (2) the initially rare variant phenotype starts to spread (in the case of an environmentally induced change, due to the consistent recurrence of the environmental factor), creating a subpopulation expressing the novel trait, and (3) selection on existing genetic variation for the regulation or form of the trait causes it to become (a) genetically fixed or to remain (b) phenotypically plastic (West-Eberhard, 2003). According to Braendle and Flatt (2006), only process (3) represents genetic accommodation in the strict sense as it was defined by West-Eberhard (2003) but, for the sake of conceptual simplicity, they refer to genetic accommodation as the entire sequence of steps (1) to (3). Genetic assimilation describes only scenario (3a), i.e. the fixation of the response leading to environmental insensitivity, also called "environmental canalization" (West-Eberhard, 2003), whereas genetic accommodation can describe both the evolution of environmentally insensitive (3a) and sensitive (3b) trait expression (Braendle & Flatt, 2006). Another

difference between the two concepts is that the model of genetic accommodation assumes that the trigger uncovering previously cryptic or novel phenotypes is either genetic or environmental, whereas the concept of genetic assimilation typically assumes only an environmental trigger. Thus, genetic accommodation is a generalization of genetic assimilation (Braendle & Flatt, 2006). Importantly, the ecological conditions that gave rise to the assimilated phenomenon in the first place can be traced through deep evolutionary time by the "fossil record" in the genome (Runnegar, 1986; Buss, 1987 p. 90), and in physiology and development (Heininger, 2001, 2012, 2013). There are demographic predispositions to the evolution of eusociality (Gadagkar, 1991b). In concert with assured fitness returns, delayed reproductive maturation and variation in age at reproductive maturity become more powerful in selecting for worker behavior, and mixed reproductive strategies become available to a wider range of individuals. These phenomena provide a consistently more powerful selective advantage for the worker strategy than do genetic asymmetries created by haplodiploidy.

The evolutionary road to assimilated eusociality is highlighted by each newly formed colony of primitively eusocial Hymenoptera where aggression is one of the most distinct behavioral attributes of the queen to establish dominance hierarchies in small colonies (Michener & Brothers, 1974; Breed & Gamboa, 1977; Michener, 1990; Pabalan et al., 2000). Aggression by the dominant reproductive individual limits both mating opportunities and reproduction of subordinates (Reeve, 1991; Röseler, 1991; Peeters, 1993; Premnath et al., 1996; Monnin & Peeters, 1998). However, after reproductive dominance is established, a reduction in aggression levels often is observed, which appears to be mediated by chemical cues, at least in *Ropalidia marginata*, *Polistes dominulus* (Premnath et al., 1996; Sledge & Boscaro, 2001) and *Bombus terrestris* (Fletcher & Ross, 1985; Röseler & Van Honk, 1990; Sramkova et al., 2008; Amsalem & Hefetz, 2010). Following the process of genetic assimilation, conditionally induced phenotypic variation becomes constitutively produced (i.e. no longer requires the environmental signal for expression) (Pigliucci et al., 2006). Thus, like sexual reproduction (Heininger, 2013), eusociality is an accommodated/assimilated phenotype.

With regard to the dynamic and rather gradual than distinctive aspects of accommodation and assimilation of eusociality, the current definition of eusociality appears highly artificial and not helpful to understand its evolution (O'Riain & Faulkes, 2008). Various

authors, e.g., Kukuk (1994), Gadagkar (1994a), Crespi and Yanega (1995), and Sherman et al. (1995) have argued for the redefinition of eusociality. Arguments (reviewed by Costa and Fitzgerald, 1996) range from the expanded view of Sherman et al. (1995), which attempts to classify all species with evidence of reproductive skew as eusocial, to the narrow view of Crespi and Yanega (1995) that argue for the restriction of eusociality to species characterized by irreversible behavioral or morphological castes. Gadagkar (1994a) suggested that, (i) the scope of eusociality is expanded to include semisocial species, primitively eusocial species, highly eusocial species as well as those cooperatively breeding birds and mammals where individuals give up substantial or all personal reproduction for aiding conspecifics, (ii) there should be no requirement of overlap of generations or of life-time sterility, and (iii) the distinction between primitively and highly eusocial should continue, based on the presence or absence of morphological caste differentiation.

### **8.5 A joint genetic-physiological-behavioral-ecological hypothesis of eusociality in insects**

Here I put forward an alternative hypothesis for the evolution of eusociality in insects that includes both genetic, physiological, behavioral and ecological factors that jointly contributed to the phenomenon. The various factors that bring about eusocial behavior are ordered hierarchically from genetic to ecological levels. This ordering does not reflect a weighting of the relative importance of the various levels for the evolution of eusociality. I think that for each road to eusociality a specific blend of different factors effected the phenotype.

#### **8.5.1 Genetic**

Recombination directly affects the multilocus genotypic diversity among offspring and also influences population level genetic diversity through background selection or selective sweeps that depend on linkage disequilibria. Genetic recombination has been shown to increase colony genetic diversity (Sirviö et al., 2006; Oldroyd & Fewell, 2007). Generally, eusocial taxa have a high recombination rate (Beye et al., 2006; Sirviö et al., 2006, 2011; Wilfert et al., 2007). For instance, the polyandrous social honeybee has a genome-wide recombination rate approximately ten times higher than any other higher eukaryote studied so far (Hunt & Page, 1995; Beye et al., 2006; The Honeybee Genome Sequencing Consortium, 2006). Although not as high as the honeybee recombination rate, the phylogenetically very similar primitively eusocial and predominantly monogamous bumble bee *Bombus terrestris* also has a very high

recombination rate (Stolle et al., 2011). The high genome-wide recombination rate of both bee species clearly exceeds the average recombination rate in insects or vertebrates (Wilfert et al., 2007; Lattorff & Moritz, 2008). This high recombination rate is probably not due to Red Queen host-parasite coevolution (Kidner & Moritz, 2013). In contrast, the genome-wide recombination rate for the solitary *Nasonia* parasitoid wasp (Niehuis et al., 2010) is less than one tenth of the rate reported for the honeybee. Thus, social Hymenoptera show a higher recombination rate (mean 10.27 cM/Mb,  $n = 4$ ) than nonsocial parasitoid Hymenoptera (mean 3.99 cM/Mb,  $n = 4$ ) (Wilfert et al., 2007; Lattorff & Moritz, 2008). Within species, recombination rates can also vary among individuals of the same sex (e.g. Broman et al., 1998; Kong et al., 2004), between the sexes (Lynn et al., 2004) and among different parts of the genome (Jensen-Seaman et al., 2004). These findings indicate that monogamy is the ancestral state in both solitary and eusocial Hymenoptera and thus hardly qualifies as the state facilitating the road to eusociality (see Nowak et al., 2010). Rather, an increased rate of recombination appears to differentiate already primitively eusocial from solitary Hymenoptera. Recombination rate is a genetically regulated trait that can be changed by selection without significant constraints (Otto & Lenormand, 2002), as natural populations of closely related species have been reported to differ in their crossover frequencies (True et al., 1996). Artificial selection has led to increased recombination rates in domesticated animals (Burt & Bell, 1987) and Otto & Lenormand (2002) estimated that the recombination frequency (number of chiasmata) increased by 24.6% over a median of 50 generations of artificial selection for traits unrelated to recombination. Given that recombination rate is readily selected for, it appears to have evolved in eusocial species as a secondary trait to increase genotypic diversity among offspring as a means to maintain colony fitness (see below) and eusociality.

High recombination rates (Wilfert et al., 2007), multiple mating (Boomsma & Ratnieks, 1996; Kronauer et al., 2007) and multiple queens (Hölldobler & Wilson, 1990), which have evolved many times in some social insect lineages (Hughes et al., 2008a, b; Nonacs, 2011), all lead to high levels of genetic variation among colony members. In fact, several species of social insect have among the highest reported degrees of polyandry and recombination rates of all animals (Boomsma & Ratnieks, 1996; Fuchs & Moritz, 1999; Kronauer et al., 2007; Wilfert et al., 2007; Smith et al., 2008). The resulting genetic diversity within colonies of these taxa generates low within-colony

relatedness and more than 12 hypotheses have now been advanced to explain this transition (Palmer & Oldroyd, 2000). Of these, four are generally regarded as most plausible (Crozier & Fjerdingstad, 2001). They are: (i) bet-hedging against insufficient or deficient sperm (Cole, 1983); (ii) reducing the risk of producing diploid (non-functional) males, which arise as a byproduct of the sex determination system (Page, 1980); (iii) providing disease resistance via worker genetic diversity (Sherman et al., 1988); and (iv) generating a more stable and resilient system of division of labor (Crozier & Page, 1985). High genetic diversity of workers increases colony performance by enhancing disease/parasitism resistance (Shykoff & Paul Schmid-Hempel, 1991; Liersch & Schmid-Hempel, 1998; Baer & Schmid-Hempel, 1999; Brown & Schmid-Hempel, 2003; Tarpay, 2003; Tarpay & Seeley, 2006; Seeley & Tarpay, 2007; Mattila et al., 2012), division of labor (Crozier & Page, 1985; Gove et al., 2009), and a number of other potential fitness-enhancing mechanisms (Crozier & Page, 1985; Crozier & Fjerdingstad, 2001; Jones et al., 2004; Mattila & Seeley, 2007; Oldroyd & Fewell, 2007; Mattila et al., 2008, 2012; Wiernasz et al., 2008).

### 8.5.2 Physiological

Body size/body mass predicts several fitness components, suggesting that it is a reliable proxy for fitness in many species (Mittelbach, 1981; Peters, 1983; Post & Evans, 1989; van den Berghe & Gross, 1989; Merrett, 1994; Lundvall et al., 1999; Roitberg et al., 2001; Kingsolver & Pfennig, 2004; Neff & Cargnelli, 2004; Brown C et al., 2007; Pfennig et al., 2007; Schwagmeyer & Mock, 2008). For geometrically and physiologically simple aerobic organisms, diffusion of oxygen into the organism limits the maximum possible size (Raff & Raff, 1970; Alexander, 1971). It has been suggested that the atmospheric oxygen partial pressure ( $aPO_2$ ) provides a key biophysical limitation on the maximal size of some animal groups, and specifically that elevations in  $aPO_2$  increased oxygen supply to the tissues, allowing larger body sizes (Graham et al., 1995; Dudley, 1998). According to this oxygen-limitation hypothesis, high  $aPO_2$  values reaching a maximum of 27–35 kPa in the late Carboniferous and early Permian (< 300 million years ago) led to the evolution of giant organisms in many animal groups (Graham et al., 1995; Dudley, 1998; Harrison, et al., 2010). The subsequent  $aPO_2$  decrease to 13 kPa in the Triassic (Berner, 2006) resulted in lower gas transfer rates and in substantially smaller body sizes of the surviving fauna of these groups (Dudley, 1998; Klok & Harrison, 2009).

Insects were one of the major animal groups that

experienced gigantism in the late Paleozoic (Shear & Kukalová-Peck, 1990; Grimaldi & Engel, 2005). Their respiratory system is relatively simple. Gas exchange takes place through a system of tubes, the tracheae that lead directly to the cells (Chapman, 1998). The circulatory system contributes little to oxygen transport, because the capacitance of hemolymph for oxygen is low. In contrast, most gill- and lung-breathing animals must operate respiratory and circulatory systems in series to deliver oxygen. A variety of recent empirical findings support a link between oxygen and insect size: (i) Cumulative evidence shows that oxygen levels influence body size in insects (Loudon, 1988; Dudley, 1998; Frazier et al., 2001; Harrison et al., 2006; Kaiser et al., 2007; Klok & Harrison, 2009; Harrison & Haddad, 2011; Heinrich et al., 2011). Hypoxia not only reduces body size (Harrison et al., 2006), but also constrains the evolution of increased body size by limiting the variation available to selection (Klok & Harrison, 2009). (ii) Insects developmentally and evolutionarily reduce their proportional investment in the tracheal system when living in higher  $aPO_2$ , suggesting that there are significant costs associated with tracheal system structure and function (Locke, 1958; Loudon, 1989; Jarecki et al., 1999; Henry & Harrison, 2004; Arquier et al., 2006; Klok et al., 2010). (iii) Larger insects invest more of their body in the tracheal system, potentially leading to greater effects of  $aPO_2$  on larger insects. Studies that have investigated the scaling relationship of the tracheal system to date suggest that tracheal investment is hypermetric, with greater proportional investment in larger insects (Kaiser et al., 2007; Greenlee et al., 2009). During ontogeny of the American locust, *Schistocerca americana*, tracheal investment increases in the leg muscle (Hartung et al., 2004) and at the whole-body level with tracheal volumes and ventilation scaling approximately with  $mass^{1.3}$  (Lease et al., 2006; Greenlee et al., 2009). Similarly, across four tenebrionid beetle species, tracheal volumes scale with  $mass^{1.29}$  (Kaiser et al., 2007). Such a trend appears to be general for insects: tiny stick insects have tracheal volumes of around 2 per cent (Schmitz & Perry, 1999), while giant scarabaeid beetles have tremendous air sacs (Miller, 1966). Theoretical calculations suggest that the observed hypermetry is consistent with a need to overcome reduced rates of diffusive gas exchange in longer, blind-ended tracheoles (Harrison et al., 2009). The relationship between atmospheric  $pO_2$  and maximum insect size is more complicated than implied by coincidence of late Paleozoic hyperoxia and insect gigantism. The overall correlation between  $pO_2$  and maximum wing length in each 10-Myr bin is highly significant ( $r = 0.54$ ,  $P =$

0.002), although the strength of the size-oxygen relationship is greatly diminished ( $P = 0.42$ ) after controlling for collection paleolatitude (a proxy for temperature) via multiple linear regression or for autocorrelation in body-size data using generalized least-squared regression ( $P = 0.62$ ,  $P = 0.80$  including paleolatitude) (Clapham & Karr, 2012). These results, as well as instances of decoupling, such as an Early Cretaceous decrease in insect size during a substantial increase in atmospheric oxygen, imply that atmospheric oxygen did not control maximum body size over the entire evolutionary history of insects, or that it was not the only control raising the possibility that other factors, such as competitive or predatory interactions with flying vertebrates (birds, bats, and pterosaurs), may have contributed to or even been the dominant control on evolutionary size trends (Okajima, 2008; Butterfield, 2009; Chown, 2012; Clapham & Karr, 2012).

Putative termite nest fossils have been reported as early as the Triassic (Hasiotis, 2003; Bordy et al., 2009). Molecular evidence estimated Isoptera, all with social behavior, to have diverged in the mid Triassic/Early Jurassic (Ware et al., 2010). Although it has been questioned whether the imposing nests of Triassic and Early Jurassic insects have belonged to termites (Grimaldi & Engel, 2005; Vrřanský & Aristov, 2014), the nests allow to date the evolutionary origins of insect eusociality to the Triassic. Intriguingly, the same signaling pathways, IIS and TOR that control body size in insects (Edgar, 2006), also regulate eusocial behavior including reproductive repression and division of labor (see chapter 11.2). The association of low  $aPO_2$ , small insect body size and the evolutionary innovation of eusociality in the Triassic period may suggest a relationship between these factors. Due to physiological and ecological constraints, body size is limited in insects, barring them from exploiting one of the most important means to increase fitness. However, another fitness-boosting strategy, cooperation with division of labor, stood at their disposal and, in fact, was exploited to create advanced integrative units, "superorganisms", a collection of single creatures that together possess the functional organization implicit in the formal definition of organism (Wilson & Sober, 1989).

An intriguing clue for the role of oxygen-body size limitation in the evolution of eusociality may come from the developmental interplay of oxygen and temperature (Frazier et al., 2001; Verberk & Bilton, 2011). Lower temperatures tend to cause insects to be larger, via both direct developmental effects and by evolutionary changes in mean size (Partridge &

French, 1996; Kingsolver & Huey, 2008; Chown & Gaston, 2010). Although higher temperatures strongly stimulate ectothermic metabolic rates, they only slightly increase oxygen diffusion rates and decrease oxygen solubility. Consequently, insect gas exchange systems have more difficulty meeting tissue oxygen demands at higher temperatures. Higher temperatures reduce oxygen delivery capacity relative to tissue oxygen needs, which may partially explain why ectotherms are smaller when development occurs at higher temperatures (Frazier et al., 2001; Woods & Hill, 2004). Molecular divergence dating infers recent and simultaneous origins for halictid eusociality, ~20–25 Ma in each of the three groups *Augochlorini*, *Halictus*, and *Lasioglossum* (Brady et al., 2006). This time period coincides with a global warming trend during the late Oligocene warming and mid-Miocene climatic optimum (Zachos et al., 2001). A potential correlation between eusocial evolution and climatic warming is strengthened by observations that climatic factors influence the manifestation of eusociality in some modern species that have solitary forms in colder areas and eusocial forms in warmer areas (Sakagami & Munakata, 1972; Yanega, 1988; Eickwort et al., 1996; Miyanaga et al., 1999; Richards, 2001; Soucy, 2002; Soucy & Danforth, 2002; Cronin & Hirata, 2003; Bradley et al., 2009; Soro et al., 2010). Intriguingly, polar gigantism of benthic amphipod crustaceans is dictated by oxygen availability (Chapelle & Peck, 1999).

### 8.5.3 Behavioral

Brood care and, particularly, maternal care is the constitutional feature of any complex sociobiological behavior. I am not aware of any species without brood care that was ever able to evolve a complex society. The mother-offspring affiliation can be considered the nucleus of cooperative societies. There is a continuum of neurobiological agents that mediate social behavior ranging from mother-offspring bonding to prosocial behavior in larger societies.

The formation of groups within a freely mixing population can occur in many ways (Wade, 1976; Swenson et al., 2000; Gadagkar, 2001; Pepper & Smuts, 2002; Thorne et al., 2003; Fletcher & Zwick, 2004; Hunt, 2007; Khila & Abouheif, 2010; Wade et al., 2010). A group can be pulled together when cooperation among unrelated members proves beneficial to them, whether by simple reciprocity or by mutualistic synergism or manipulation (Clutton-Brock, 2009a). A growing number of studies have documented the occasional merging of unrelated colonies in ants, wasps, and termites (Foitzik & Heinze, 1998, 2000; Fisher et al., 2004; Prezoto &

Santos-Prezoto, 2005; Johns et al., 2009; Kellner et al., 2010; Kronauer et al., 2010; Kellner & Heinze, 2011). Grouping by family can hasten the spread of eusocial alleles, but it is not a causative agent. The causative agent is the advantage of a defensible nest, especially one both expensive to make and within reach of adequate food (Nowak et al., 2010).

Aggression has been long recognized as an important component of social systems (Hall, 1964). Aggression is often considered a category of anti-social interaction that weakens the positive social consequences of cooperation and other types of affiliative interactions (e.g. Kummer, 1971; Brown, 1976, pp. 75, 253). Slobodchikoff and Schulz (1988) modelled the relationship between resources and group size as a function of aggression. Generally, cooperation decreased as aggression increased. Aggression can provide a mechanism for controlling the size of the group, for defining the distribution of resources within the group, and for defining the reproductive relationships of the group. By varying the intensity of aggression only, one may switch from egalitarian to despotic virtual societies (Hemelrijk, 1999).

Aggression could be a barrier to cooperative sociality (Cahan et al., 1998; Overson et al., 2014). Aggression serves as perhaps the most important proximate barrier to pleometrotic cooperative group formation by normally haplometrotic queens. Although queens were not immediately aggressive, haplometrotic groups showed a much higher incidence of aggression over time with associated effects on queen mortality, than did pleometrotic associations (Overson et al., 2014). Less favorable conditions such as food shortage might lead to more frequent aggression and accentuated the reproductive dominance of one queen in pleometrotic ant colonies (Sommeijer & Van Veen, 1990; Kolmer & Heinze, 2000). A dominance hierarchy may even support the beneficial competitive nature of social living as a positive selective force (West, 1967; Moosa & Ud-Dean, 2011).

### 8.5.4 Ecological

The non-social parasitic Hymenoptera (Askew, 1971) differ from the social Hymenoptera with regard to the abundance and distribution of food resources available to the larvae of each group (Slobodchikoff & Schulz, 1988). The highly eusocial allodapine bee species *Exoneurella tridentata*, appears to have evolved sociality in very harsh, xeric conditions (Dew et al., 2012), and in years with harsh weather conditions colonies of primitively eusocial sweat bee, *Halictus ligatus*, showed an increase in sociality, i.e. higher levels of queen-worker dimorphism and decreased worker cheating (Richards & Packer, 1996). In a

similar vein, communality among the bees may also be associated with more arid environments (Australia, Southwest USA) possibly because of restricted opportunities for fossorial nesting (Wcislo & Tierney, 2009). Within families and within species of arthropods, many organisms show an increasing degree of sociality at lower latitudes and altitudes. In a smaller number of cases, organisms form larger groups or found nests cooperatively at higher latitudes and altitudes (Purcell, 2011). In some ant, termite, and social spider species, rainfall is positively correlated with sociality (Riechert et al., 1986; Murphy & Breed, 2007; Picker et al., 2007; Purcell, 2011). Harsh environmental conditions may lead to a behavioral syndrome (Hemelrijk, 1999) promoting the evolution of a despotic regime (Sommeijer & Van Veen, 1990; Kolmer & Heinze, 2000).

It has been suggested that ecological constraints on independent colony founding favor polygyny in a number of ant species (Crozier, 1979; Pamilo & Rosengren, 1984; Herbers, 1986, 1993; Hölldobler & Wilson, 1990; Heinze, 1993a; Rosengren et al., 1993; Bourke & Franks, 1995). This argument is akin to ecological constraints on independent breeding favoring communal breeding in birds, vertebrates and insects (Emlen, 1982b, 1991, 1994; Vehrencamp, 1983; Pamilo & Rosengren, 1984; Reeve, 1991; Koenig et al., 1992; Reeve & Ratnieks, 1993; Keller & Reeve, 1994). In fact, the degree of polygyny and the frequency of empty nest sites are inversely correlated across populations of *Leptothorax longispinosus* (Herbers, 1986). Moreover, an experimental increase of nest sites resulted in a decrease in the mean number of queens per nest. In a comparative study of leptothoracine ants, Bourke and Heinze (1994) found that polygyny was associated with nest-site limitation, cold climate and habitat patchiness, all factors that increase dispersal costs. The differences in reproductive patterns, dispersal habits and reproductive phenotypes associated with variation in queen number support the hypothesis that ecological constraints on independent colony founding are a major factor selecting for polygyny (Keller, 1995).

## 9. Reproductive skew

*From this arises a debate: if it is better to be loved than to be feared, or the contrary. I reply that it would be nice to be both, but because they are difficult to combine together, if you cannot have both, it is much more secure to be feared than to be loved.*

Niccoló Machiavelli (1532)

### Summary

**Dominance hierarchies determine access to resources. In fact, cooperative breeding coalitions are dominant-enforced social exploitations. Subordinates in cooperative societies commonly show a degree of reproductive restraint due to factors such as a lack of access to unrelated breeding partners, targeted aggression, temporary eviction or infanticide. Generally, harsh and stochastic environmental conditions can lead to a behavioral syndrome that promotes the evolution of a despotic regime. Suppression of subordinate reproduction by dominants and high levels of reproductive skew are often found in species that have evolved in harsh conditions, where competition for resources is likely to be intense and reproduction by subordinates particularly costly to dominants. There is an interrelationship between limited dispersal (due to limited options for independent breeding) and asymmetric conflict/dominance hierarchies that underlie coerced cooperation. Beehives, wasp and ant nests are police states in which selfish and despotic queens, by means of their pheromones suppress the reproductive activity of their daughters and enforce their reproductive monopoly by murder, torture and imprisonment. Manipulative queen control leads to an evolutionary arms race between queen and workers reminiscent of parasite-host coevolutionary dynamics. When the dominant position becomes vacant previously "altruistic" subordinates may fight with their siblings until death to take over the dominant position: not exactly what can be expected from a mutually agreed-upon social contract based upon inclusive fitness gains.**

Animals that rank highly in the social hierarchy have many advantages, such as better access to food, territories, mates and offspring (Huntingford & Turner, 1987; Jones & Mensch, 1991; Collias et al., 1994; Hall & Fegigan, 1997; Lahti et al., 1998). Several models point out the evolutionary route to despotic societies (Vehrencamp, 1983; Hemelrijk, 1999; Summers, 2005). Generally, the harsh and stochastic environmental conditions that select for cooperative behavior in the first place (see chapters 6 and 15) can lead to a behavioral syndrome (Hemelrijk, 1999) that promotes the evolution of a despotic regime (Sommeijer & Van Veen, 1990; Kolmer & Heinze, 2000). Experimental studies support the notion that resource limitation results in enhanced aggression and dominance hierarchies (Machmer & Ydenberg, 1998; Cook et al., 2000; West et al., 2001; Innocent et al., 2011). In habitats where resources may not be

sufficient to sustain populations above the threshold of extinction, it may be a good strategy for dominants to “negotiate” with the subordinates to help them in the rearing of offspring. Moreover, a mutualism-competition model suggested that an inferior competitor, if cooperative to a superior competitor, is able to survive (Zhang, 2003). Given the manifold advantages of cooperation, evolution should have “found” ways to establish these cooperative alliances. However, there should have remained much conflict over the fair share of reproductive opportunities for subordinates. Models of reproductive skew were developed by Vehrencamp (1979, 1983) and Emlen (1982a). These models were inspired (Vehrencamp, 1984) by previous arguments concerning the relationship between subordinates’ options for dispersal and the ability of dominants to monopolize reproduction (Alexander, 1974). The main objective of the models was to determine the allocation of resources or fitness to dominants and subordinates that maximizes the fitness of the dominant. Skew was predicted to increase with increasing ecological constraints (a measure of the expected success of a subordinate that attempts to disperse and reproduce). The greater the difference in fitness for groups and solitary individuals, the greater the skew can be. Some reproductive skew models entailed a form of ‘social contract’ between dominants and subordinates, whereby the dominant should, in certain situations, yield reproductive concessions to the subordinate as an incentive for the subordinate to stay and help rather than leave or to dissuade them from engaging the dominant in a fight (Alexander, 1974, pp. 350-351; Reeve & Ratnieks, 1993; Reeve & Keller, 1997). For most social animals, however, reproductive concessions are unrealistic and most cooperative interactions are based instead on the direct adjustment of subordinates’ behavior by dominant individuals, i.e. manipulation. Crespi and Ragsdale (2000) assumed that dominants impose costs on subordinates which tip the behavioral decisions of subordinates towards staying and helping rather than leaving. Thus, rather than providing reproductive benefits (concessions) to subordinates in order to induce them to stay and help, dominants impose costs on subordinates which make staying and helping the subordinate’s best strategy. However, attempting to exert control over the distribution of reproduction is assumed to be itself costly, reducing the total reproductive output (Reeve et al., 1998; Johnstone, 2000; Reeve & Shen, 2006, 2013; Cant, 2012). Some forms of manipulation, such as reducing the feeding levels or rates of developing young, are cheap and easy for the dominant to perform, whereas

other forms, such as harassment (e.g. Michener & Brothers, 1974; Emlen, 1982a; Reyer et al., 1986; Abbott, 1987; Clutton-Brock & Parker, 1995; Creel & MacDonald, 1995) or disruption of independent breeding attempts (e.g. Emlen & Wrege, 1992), will demand some energy or time investment by the dominant.

Strangely, the advocates of the kin selection theory are so prejudiced with the alleged “altruism” side of the coin that they widely ignore the factual selfishness flipside of the coin (but see Michener & Brothers, 1974). In fact, Hamilton’s rule is a zero-sum game: The “altruism” from one side is exactly balanced by the selfish exploitation from the other side. This oppressive system is driven by a dynamic balance of dominance and subordination (Chapuisat & Keller, 1999; Passera et al., 2001; Tóth et al., 2002; Beekman et al., 2003; Beekman & Ratnieks, 2003; Mehdiabadi et al., 2003; Rosset & Chapuisat, 2006; Helanterä & Ratnieks, 2009). The dynamics not only applies to the queen-worker conflict but extends to the individual workers: For example, when a breeder’s position becomes available in termite colonies, a subset of workers develops into neotenic replacement reproductives that will fight with their siblings until death to take over the queen-/kingless colony (Lenz, 1985; Thorne, 1997). The higher the reproductive skew the more despotic and oppressive is the social system. Again, this dynamic balance is the result of an arms race. Victim-exploiter/host-parasite interactions with Red Queen dynamics (e.g. Gavrillets, 1997; Summers et al., 2003; Marques & Carthew, 2007; Brockhurst et al., 2014) are characterized by arms races. In fact, most societies with reproductive skew are the result of parasitic exploitation. In this regard, the reproductive skew societies are the counterparts of unitary organisms with their soma-germline dichotomy and conflict (Heininger, 2002, 2012). As discussed earlier (chapter 3) a fundamental difficulty with the evaluation of acts of fitness transfer is that the outside observer can only observe the outcome but has no knowledge of the specific motives and mechanisms. Basically, a net transfer of commodities can take place due to voluntary intent, cheating, coercion, or be the result of a lottery. For example, altruistic acts involve the actor voluntarily donating fitness to beneficiaries. Parasitic acts, on the other hand, involve the actor extracting benefit from others at net cost to the donors (Doncaster et al., 2013). Both behaviors may have the same direct net-cost transferral of fitness from donor to beneficiary; the key difference between parasitism and altruism is thus who drives the interaction.

Taking the society of the Polynesian Ifaluk Atoll as

example, Laura Betzig (2004) succinctly highlighted the interrelationship between limited dispersal and asymmetric conflict/dominance hierarchies underlying coerced cooperation in human societies: “Not so long before I first went to Ifaluk, in 1970, the American Museum of Natural History anthropologist Robert Carneiro published a paper in *Science* on the origin of the state (Carneiro, 1970). He looked at state formations in Mesopotamia, Egypt, and Peru; and he concluded that they were all “circumscribed” zones. Poor men paid Sumerian/Babylonian/Assyrian emperors, Egypt’s pharaohs, and Peru’s Incas in tribute and labor *not* because emperors/pharaohs/Incas were good to them in return, but because the costs of leaving were high. The rich land between the Tigris and Euphrates, or around the Nile Delta, or in the Andes valleys was surrounded by hostile deserts and mountains. Dissatisfied subjects had two options. They could pay overlords what they asked for, or they could vote with their feet and hope for the best.

“Skew” theories take those two options into account. Studies of animal societies have looked for “social contracts” – the equal return of social benefits for social benefits. And they’ve looked for “social controls” – the biased return of social benefits to better fighters. Evidence of the first is relatively equivocal (e.g., Emlen et al., 1998). Evidence of the second is relatively clear (e.g., Clutton-Brock, 1998). Better fighters do best where worse fighters are trapped: where the costs of running away to another good territory are high.

I think the whole of human history can be interpreted like that. The Sumerian word for “freedom,” *ama.ar.gi*, also means “freedom to move” (e.g., Lemche, 1979). Mobility makes equality; and inequality goes up where subjects can’t get away. Around 5,000 years ago, in fertile river valleys bordered by mountains and deserts, subjects started to pay overlords labor and taxes. They stopped, as soon as they found a way out. In the wide open spaces of Africa and Asia, people had voted with their feet for millions of years.

[...] sometimes they [*i.e.*, foragers, KH] give social benefits away to stay on a good territory. They give up part of the hunt/catch/crop because the hunting/fishing/gathering isn’t as good anywhere else. It’s a little ironic, to me, that so many of the new evolutionists – the “Darwinian” psychologists and anthropologists – focus so much on cooperation and so little on competition. Where’s the Darwinism? Where’s the *beef*?

In *Homo sapiens* societies, as in any other animal societies, mobility is an aid to equality. Foragers are notoriously “egalitarian,” speaking relatively. But no society lacks unfairness completely. Strong egalitarian

ethics, like “we refuse one who boasts, for someday his pride will make him kill somebody” (Lee, 1979), or “sell all you have and distribute to the poor” (Luke, 18:22), or “from each according to his ability, to each according to his needs!” (Marx, 1875/1970) aren’t repeated where cooperation is automatic. They get said, again and again, where individuals conflict, and where the winners take more than equal shares. Why do they get to take more? Sometimes, because the givers have nowhere better to go.” (Betzig, 2004)

### 9.1 Reproductive suppression in vertebrates

Social suppression of reproduction is a salient feature of cooperatively breeding species that is maintained by natural selection (Solomon & French, 1997; Koenig & Dickinson, 2004). Subordinates in cooperative societies commonly show a degree of reproductive restraint due to factors such as a lack of access to unrelated breeding partners, poor body condition, or underdeveloped foraging skills that reduce their expected payoff from attempted reproduction (Wasser & Barash, 1983; Heinsohn, 1991; Bennett et al., 1996; O’Riain et al., 2000). In other cooperatively breeding species dominants render their subordinates infertile by targeted aggression, temporary eviction or infanticide (Keverne et al., 1982; Reyer et al., 1986; Schoech et al., 1991; Wingfield et al., 1991; Solomon & French, 1997; O’Riain et al., 2000; Packard, 2003; Young et al., 2006; Cant et al., 2010). The way in which suppression is imposed at a proximate level can be direct, via interference, or harassment/aggression (e.g. Dunbar & Dunbar, 1977; Blaffer Hrdy, 1979; Silk et al., 1981a; Curry, 1988b; Rhine et al., 1988; Wasser & Starling, 1988; Faulkes & Abbott, 1997; Lacey & Sherman, 1997; Clutton-Brock et al., 1998; Clarke & Faulkes, 2001; Hackländer et al., 2003; Williams, 2004; Young et al., 2006; Stockley & Bro-Jørgensen, 2011), or indirect, via signals that communicate social dominance and can influence the reproductive and life-history decisions of young or subordinate females (e.g. Eppler & Katz, 1984; Savage et al, 1988; Barrett et al., 1993; Saltzman et al., 2009). Such stimuli induce responses at different stages of the reproductive cycle from inhibition of mating (Stockley & Bro-Jørgensen, 2011) to delayed sexual maturity, disruption of ovulation, implantation, or spontaneous abortion (e.g. Bowman et al., 1978; Huck et al., 1983, 1988; Adams et al., 1985; Harcourt, 1987; Creel et al., 1992; Faulkes & Abbott, 1997; Solomon et al., 2001; Hackländer et al., 2003; Saltzman et al., 2006, 2009).

Suppression of subordinate reproduction by dominants and high levels of reproductive skew are often found in species that have evolved in arid or semiarid conditions, where competition for resources is likely to

be intense and reproduction by subordinates is likely to be particularly costly to dominants (Clutton-Brock et al. 2006; Gilchrist, 2006). While infanticide by females has attracted less attention than infanticide by males, it is probably more widespread (Parmigiani & vom Saal, 1994; Rödel et al., 2008; Clutton-Brock & Huchard, 2013) and frequently represents a threat for group-living females (Digby, 2000). Infanticide of the offspring of other breeders has been recorded among a wide array of taxa, including many cooperative breeders (Blaffer Hrdy, 1979; Hausfater & Blaffer Hrdy, 1984; Hoogland, 1985; Pusey & Packer, 1987a; Brain, 1992; Creel et al., 1997; Clutton-Brock et al., 1998; Ebensperger, 1998; Young & Clutton-Brock, 2006; Clutton-Brock & Huchard, 2013). In cooperative breeders, like meerkats and dwarf mongooses, subordinate litters are often killed by the dominant female, and the success of subordinate litters is affected by the timing of parturition. Simultaneous breeding by more than one female reduces the ratio of helpers to pups and the growth of pups falls (Clutton-Brock et al., 2010) and evidence that infanticide is more likely in pregnant than non-pregnant females (Rasa, 1994; Creel & Waser, 1997; Clutton-Brock et al. 1998, 2001b) suggests that its function is partly to reduce resource competition for the killer's offspring (Wolff & Cicirello, 1989; Tuomi et al., 1997; Clutton-Brock et al., 1998; Rödel et al., 2008). It may have additional benefits: victims of infanticide may subsequently contribute to suckling and rearing infants subsequently produced by infanticidal females as in marmosets (Digby, 1995) and meerkats (Clutton-Brock et al., 1998). Similarly, egg tossing or eating has been observed in communal laying bird species, in which the last female to start laying usually tosses the eggs already laid from the nest (Mumme et al., 1983; Vehrencamp et al., 1988; Zahavi, 1990; Koenig et al., 1995; Macedo & Bianchi, 1997; Macedo et al., 2001).

Dominant efforts at suppression are not inevitable, instead appearing to be sensitive to variation in the payoffs of interfering with subordinate breeding: attacks are targeted at subordinates who are most likely to breed (Clutton-Brock et al., 2010); are restricted to periods when resource competition peaks and the offspring of dominants may be at a competitive disadvantage (Young & Clutton-Brock, 2006; Clutton-Brock et al., 2010); or are avoided entirely when the subordinate retaliation is likely to be effective (Packer et al., 2001). In a substantial number of social mammals, competition between resident females leads to evictions or to groups splitting (Stephens et al., 2005; Cant et al., 2010; Clutton-Brock & Huchard, 2013). For example, in

meerkats, dominant females evict (virtually) all female subordinates before they are 4 years old (Clutton-Brock et al., 2010). Increased levels of glucocorticoids are known to repress the reproductive axis (Wingfield & Sapolsky, 2003; Kalantaridou et al., 2004; Gore et al., 2006; Heining, 2013). While evicted, subordinate females suffer chronic elevation of their glucocorticoid adrenal hormone levels, reproductive downregulation (reduced pituitary sensitivity to gonadotropin-releasing hormone), reduced conception rates, and increased abortion rates (Young et al., 2006). In red howler monkeys, high-ranking females frequently evict younger and lower ranking females from their groups (Pope, 2000) while, in banded mongooses, coalitions of older dominant females intermittently evict entire cohorts of younger females from their group (Gilchrist, 2006; Cant, 2010). When subordinates are experimentally prevented from breeding using contraceptive injections, dominants in groups of wild meerkats (*Suricata suricatta*) are less aggressive towards subordinates and evict them less often, leading to a higher ratio of helpers to dependent pups, and increased provisioning of the dominant's pups by subordinate females (Bell et al., 2014). Dominants also showed improved foraging efficiency, gained more weight during pregnancy and produced heavier pups, which grew faster. These results confirmed the benefits of suppression to dominants, and help explain the evolution of singular breeding in vertebrate societies (Bell et al., 2014). The results also suggest why plural breeding is rare in cooperative vertebrates: dominants are only likely to tolerate subordinate reproduction when it has little effect on dominant reproductive success, which is only likely where social structure limits direct competition between offspring (Bell et al., 2014). Banded mongooses, a closely related social mongoose, are one of the few cooperative vertebrates where multiple females commonly breed together (Cant et al., 2010): direct competition between pups is limited because pups are cared for by a single helper who does not provision other pups (Bell, 2007).

Subordinates may try to seize the dominant position by fighting (Davies, 1992; Gust, 1995; Monnin & Peeters, 1999; Alberts et al., 2003; Cant et al., 2006a). The stability of the dominant-subordinate relationship therefore requires that subordinates prefer to queue peacefully rather than engage in escalated conflict over rank. To understand the factors influencing the subordinate's decision of whether to enter into an escalated fight over rank, three features of the conflict between dominant and subordinate have been taken into account: (i) the contestants may be relatives; (ii) subordinates may eventually obtain the resource

without fighting, i.e. they may inherit if they outlive the dominant; and (iii) subordinates may share the resource with the dominant without fighting, i.e. they may obtain a share of current reproduction. Skubic et al. (2004) showed that a male *Neolamprologus pulcher* helper cichlid should base its decision to parasitize primarily on an increase in expulsion risk resulting from reproductive parasitism (punishment), intra-group relatedness and the parasitism capacity. If expulsion risk is high then helpers should not parasitize reproduction at medium body size but should parasitize either when small or large. As far as can be judged from a limited data base, in paper wasps that do not distinguish degrees of relatedness among nestmates (Queller et al., 1990), genetic relatedness had no significant effects on the probability of escalation (Cant et al., 2006a). Since reproductively suppressed subordinates are more likely to fight for dominant status, attempts by dominants to reproductively suppress subordinates will increase the threat of escalated conflict. Overall, subordinates that stand to gain more from a reversal in the dominance roles were more likely to enter into the escalated conflict (Cant et al., 2006a). To avoid escalated conflicts, dominants may appease challengers by making reproductive concessions (Reeve & Ratnieks, 1993; Field & Cant, 2009).

In singular cooperative breeders, the death of the breeding female is often followed by intense fighting between her daughters and the death or eviction of unsuccessful competitors (Clutton-Brock et al., 2006; Sharp & Clutton-Brock, 2011). As soon as a subordinate animal rises to a dominant position in its cohort, the previous reproductive “altruist” (according to kin selection theory) turns into a selfish reproductive dictator (Faulkes & Abbott, 1997). Female subordinates in the group-living Lake Tanganyika cichlid *N. pulcher* are reproductively capable, but apparently suppressed with respect to egg laying. Nevertheless, some reproduction is tolerated, possibly to ensure continued alloparental care by subordinate females. Upon removal of the dominant female from the group, the medium females immediately seize the dominant breeding position and start to reproduce as frequently as control pairs (Heg, 2008). However, the non-reproductive worker and the reproductive queen are both products of the same genotype, and their phenotypic differences result from differences in environment rather than genotype. That previously “altruistic” subordinates become selfish dominants after the death of the breeding female can be regarded as due to pleiotropic plasticity (see chapter 9.3), the plastic phenotypic expressions of a single genotype (Yakubu, 2012, 2013). Likewise, field studies going

back to the 1830s observed that the same honeybee egg could produce a selfish queen or an “altruistic” worker depending upon what diet the larva was fed (Prete, 1990).

## 9.2 Reproductive suppression in eusocial insects

Eusociality as the Holy Grail of inclusive fitness theory lost its glorieole when it became evident that the unselfish help of the workers is enforced (Ratnieks, 1988). (To remind you, the prediction of the inclusive fitness theory is that this help should be voluntary [given a sufficient benefit to cost ratio] since helping your kin should increase the representation of your genes in future generations and this should be a strong inclusive fitness benefit selecting for the reproductive “altruism”) In fact, beehives, wasp and ant nests are police states (Foster & Ratnieks, 2001; Monnin & Ratnieks, 2001; Cuvillier-Hot et al., 2004b) in which selfish and despotic queens, by means of their pheromones suppress the reproductive activity of their daughters and enforce their reproductive monopoly by murder, torture and imprisonment (Whitfield, 2002). Workers are enslaved, made docile and submissive by force and chemicals. In addition to queen pheromones, worker sterility is thought to be enforced by mutual policing. Worker policing occurs in two forms: (i) physical policing, in which workers with activated ovaries are attacked by nestmates (Hölldobler & Carlin, 1989; Liebig et al., 1999; Dietemann et al., 2003; Hartmann et al., 2003), and (ii) egg policing, in which workers detect and destroy worker-laid eggs (Ratnieks & Visscher, 1989; Monnin & Peeters, 1997; Foster & Ratnieks, 2000; Tsuchida et al., 2003; d’Ettorre et al., 2004; Endler et al., 2004; Helanterä & Sundström, 2005). The importance of policing in maintaining worker sterility has been demonstrated repeatedly (Foster & Ratnieks, 2001; Wenseleers et al., 2004a, b; Ratnieks & Wenseleers, 2005, 2008; Ratnieks & Helanterä, 2009). Long before Machiavelli, queens of eusocial societies “discovered” the principle of “divide and rule”. (No surprise in the light of Orgel’s second rule: “Evolution is cleverer than you are”.)

Inclusive fitness theory predicts that, other things equal, worker policing occurs when workers are more closely related to queen-produced males than to worker-produced males (Starr, 1984; Woyciechowski & Lomnicki, 1987; Ratnieks, 1988). Worker policing should be a classic kin-selected trait (Hamilton, 1964) that is favored when relatedness is low (Ratnieks, 1988; Frank, 2003; Wenseleers & Ratnieks, 2006a), due to relatedness differences arising from either polyandry (multiple mating by queens) or polygyny (multiple queens per colony). However, worker

policing also occurs, according to comparative analyses, across the eusocial Hymenoptera as a whole (Wenseleers & Ratnieks, 2006a) and even in species where queen mating frequency is below 2: for example, in the ant *Camponotus floridanus* (Endler et al., 2004), the bumblebee *Bombus terrestris* (Zanette et al., 2012) and the hornet *Vespa crabro* (Foster et al., 2002), or in species that reproduce parthenogenetically, such as the ant *Platythyrea punctata* (Hartmann et al., 2003) and the Cape honeybee *Apis mellifera capensis* (Pirk et al., 2003). This has led to doubts concerning the importance of relatedness in selecting for worker policing (Foster et al., 2002; Hartmann et al., 2003; Pirk et al., 2003, 2004; Endler et al., 2004; Gadagkar, 2004a; Wilson, 2005). This doubt was supported by Hammond and Keller (2004), who used a comparative analysis of 50 species of ants, bees, and wasps to show that the proportion of males that are workers' sons is not influenced by relatedness.

Punishment allows the evolution of cooperation (or anything else) in sizable groups (Boyd & Richerson, 1992; Clutton-Brock & Parker, 1995; Frank, 2003; Ratnieks & Wenseleers, 2008; Bourke, 2011; Shutters, 2012) and also enforced cooperation in an experimental setting (Fehr & Gächter, 2002). Who would call this state of coerced helping "altruism"? Advocates of Hamilton's rule do it. George Orwell's "1984" has made a home in the heads of the kin selection community. "Worker policing is a mechanism by which a society resolves its conflicts," says Ratnieks. "I think it's the best example of conflict resolution in nature" (Whitfield, 2002). Obviously this "conflict resolution" works well for Hymenopteran societies as is demonstrated by the anarchy that is inflicted upon these societies by workers that do no longer respond adequately to queen pheromones, establishing a type of social parasitism (Oldroyd et al., 1994; Barron & Oldroyd, 2001; Barron et al., 2001; Martin et al., 2002; Wossler, 2002; Lopez-Vaamonde et al., 2004; Hoover et al., 2005a, b; Beekman & Oldroyd, 2008; Dobata & Tsuji, 2009). But on the other hand, this forceful conflict resolution undermines the argumentative power of the kin selection theory that pretends to explain the occurrence of cooperation and "altruism" solely on the basis of inclusive fitness gains of "altruists": a female would be able to pursue her genetic interests and increase her inclusive fitness more effectively by raising her mother's daughters rather than her own. In a less dogmatic and biased scientific climate the findings of "enforced altruism" (chapter 20) should have refuted the kin selection/inclusive fitness theory long ago.

Overt aggression by the queen is very rare and appears restricted to small colonies (Franks & Scovell; 1983; Kikuta & Tsuji, 1999; Wenseleers et al., 2005; Brunner & Heinze, 2009). In larger colonies the queen is unable to control a larger number of workers by agonistic acts and reproduction appears to be controlled chemically by glandular or cuticular pheromones (Monnin, 2006; Heinze & d'Ettorre, 2009). Queen pheromones have been postulated to be either a manipulation that is detrimental to workers ('queen control') or a signal to which workers are selected to respond ('queen signal'). It remains controversial whether these agents are manipulative, i.e., actively suppress worker reproduction, or honestly signal the fertility status of the queen to which workers react in their own interest by refraining from laying eggs (West Eberhard, 1981; Seeley 1985, p. 30; Woyciechowski & Lomnicki, 1987; Bourke, 1988a; Keller & Nonacs, 1993; Foster et al., 2000; Katzav-Gozansky et al., 2003, 2004; Alaux et al., 2004; Hefetz & Katzav-Gozansky, 2004; Tóth et al., 2004; Katzav-Gozansky, 2006; Conte & Hefetz, 2008; Heinze & d'Ettorre, 2009; Brunner et al., 2011; Tan et al., 2012). Manipulative queen control is thought to lead to an evolutionary arms race between queens and workers, resulting in complex queen bouquets that diverge strongly among different populations and species. In contrast, honest signals should evolve more slowly and might therefore differ less strongly within and among species. It has been argued that pheromonal manipulation of workers by the queen should not be evolutionarily stable since workers should be selected to ignore such signals (Keller & Nonacs, 1993). However, arms races would allow the queens to stay a step ahead of the workers, particularly if changing the chemical composition of pheromones is not too costly (West Eberhard, 1981; Foster et al., 2000; Hefetz & Katzav-Gozansky, 2004; Katzav-Gozansky, 2006). Katzav-Gozansky (2006) elaborated features of pheromone cocktails that argue for an arms race: (i) the evolution of multiple pheromonal sources, when theoretically one set should have sufficed; (ii) the evolution of a complex blend of pheromones in the first place (Hefetz & Katzav-Gozansky, 2004); (iii) escalation in the arms race whereby workers have become not only insensitive to the queen pheromones (Hoover et al., 2005b) but are also somehow able to camouflage their eggs in such a way that they are not recognized as worker eggs by their worker nestmates (Beekman & Oldroyd, 2003). According to Tóth et al. (2004), the high variability in worker reproduction in stingless bee species is consistent with the expectation of an evolutionary arms race in which worker and queen

control change with time. Tan et al. (2012) also provided evidence for an ongoing evolutionary arms race for reproductive dominance in *Apis cerana*. Brunner et al. (2011) found that cuticular hydrocarbons associated with fecundity evolve slightly faster than worker-specific components in the blend of cuticular hydrocarbons which might reflect an arms race between queens and workers.

The manipulation model (Crespi & Ragsdale, 2000) assumes that subordinates cannot avoid dominant-imposed costs, when subordinates should often be under selection to escape manipulation by dominants. If manipulative acts pre-empt escape (e.g. feeding juveniles less), then such selection cannot be effective. In contrast, if manipulation involves ongoing behavioral interactions, such as frequent aggressive nudging or enforced displays of subordinate status, then subordinates might be expected to have the option of avoiding the interactions as best they can and perhaps thereby improving their dispersal prospects. In many social insect species, subordinates attempt to avoid the dominant while at the nest site (Buckle, 1982; Michener, 1990), a behavior that is compatible with the “queen control” but not with the “queen signal” concept. This behavior could be interpreted as avoidance of reproductive suppression, aggressive manipulation or both. Moreover, in some halictine bees, some first-brood offspring of the foundress avoid her by entering diapause directly and becoming next year’s foundresses rather than this year’s workers (Yanega, 1988). Has such early diapause evolved in part as a means of escaping maternal manipulation? In *Halictus rubicundus*, directly diapausing, first-brood offspring are larger than sibs which stay at home to help (Yanega, 1989), which is consistent with the idea that small worker size tilts behavioral choices towards helping. In other halictines, most first-brood offspring stay and help, while some leave and attempt to breed independently in the same year (Stockhammer, 1967; Sakagami & Hayashida, 1968; Sakagami, 1977); the presence of such species shows that the strategies envisioned by the manipulation model (Crespi & Ragsdale, 2000) are realistic and can be investigated in natural populations. There is a continuity of aggression-dependent and chemical cue-dependent reproductive suppression of workers in primitively eusocial species. The effects of queen pheromones on worker ovary degeneration (see chapter 11.2) should be clear-cut evidence for queen suppression of worker reproduction. Moreover, the trans-species effect of queen pheromones on *Drosophila* ovary development is not compatible with the argument that queen pheromones are a queen signal to which workers are selected to respond

(obviously *Drosophila* cannot have been selected to respond). Finally, pheromones as queen-produced agents have their manipulative counterpart in the reproductive suppression of helpers enforced by dominants in vertebrate eusocial communities (see chapter 9.1).

In primitively eusocial insect species, suppression of ovarian development in workers is frequently a result of food restriction or aggressive behavior (i.e., nudging, butting) by the principal egg-layer (West, 1967; Free et al., 1969; Wheeler, 1986; Michener, 1990; Röseler & Van Honk, 1990). In primitively eusocial Hymenoptera, aggression is one of the most distinct behavioral attributes of the queen and may serve to establish dominance hierarchies in small colonies (Michener & Brothers, 1974; Breed & Gamboa, 1977; Michener, 1990; Pabalan et al., 2000). Workers may still escape dominance assertion by the queen by avoiding her and workers may lay eggs (Buckle, 1982). However, differential oophagy by the primary reproductive may prevent successful development of worker-laid eggs (Brothers & Michener, 1974; Packer & Owen, 1994). This egg-eating activity appears to bolster the queen’s reproductive dominance (Kukuk, 1992). In *Polistes* wasps and permanently queenless ants, aggression by the dominant reproductive individual limits both mating opportunities and reproduction of subordinates (Reeve, 1991; Röseler, 1991; Peeters, 1993; Premnath et al., 1996; Monnin & Peeters, 1998). However, after reproductive dominance is established, a reduction in aggression levels often is observed, which appears to be replaced by chemical cues as suppressive agents, at least in *Ropalidia marginata*, *Polistes dominulus* (Premnath et al., 1996; Sledge & Boscaro, 2001) and *Bombus terrestris* (Fletcher & Ross, 1985; Röseler & Van Honk, 1990; Sramkova et al., 2008; Amsalem & Hefetz, 2010). Thus, chemical cues can be regarded as surrogate for agonistic behavior. Candidates for such cues are cuticular hydrocarbons that are altered by ovarian activity (Cuvillier-Hot et al., 2001; Liebig et al., 2009; Peeters & Liebig, 2009; Ferveur & Cobb, 2010; Liebig, 2010; Fedina et al., 2012). In advanced eusocial insect colonies (i.e., those with extreme queen-worker dimorphism), queen-produced pheromones that maintain worker sterility are thought to be taxonomically widespread, as queens, their eggs and queen-derived chemicals have been shown to reduce or eliminate worker reproduction, and because queens typically produce chemicals that are absent or minimally expressed in workers (e.g. Wilson, 1971; Michener, 1974, 1990; Fletcher & Ross, 1985; Wheeler, 1986; Bourke, 1988a; Vargo, 1992; Peeters et al., 1999; Dietemann et al., 2003; Cuvillier-Hot et

al., 2004a; Endler et al., 2004; Monnin, 2006; Korb et al., 2009; Bhadra et al. 2010; Holman et al., 2010b; Kocher & Grozinger, 2011).

Queen pheromones are strikingly conserved across at least three independent origins of eusociality, with wasps, ants, and some bees all appearing to use nonvolatile, saturated hydrocarbons to advertise fecundity and/or suppress worker reproduction (Van Oystaeyen et al., 2014). Saturated hydrocarbons were most likely used as fertility cues in the common solitary ancestor of all ants, bees, and wasps, which lived ~145 million years ago (Johnson et al., 2013; Wilson et al., 2013; Van Oystaeyen et al., 2014). Queen pheromones underpin the proximate and ultimate causes of worker sterility: in the honeybee, they cause changes in worker gene expression (Grozinger et al., 2003; Beggs et al., 2007) and physiology (Kaatz et al., 1992; Beggs et al., 2007) and mediate the transition from reproductive suppression to worker reproduction (Wossler & Crewe, 1999; Hoover et al., 2003; Kocher et al., 2008, 2009; Maisonnasse et al., 2010). Moreover, honey and bumble bee queen pheromones inhibit rearing of new queens by workers (Butler et al., 1959; Melathopoulos et al., 1996; Pettis et al., 1997; Lopez-Vaamonde et al., 2007), delay the transition from nursing to foraging (Pankiw et al., 1998), inhibit juvenile hormone synthesis in workers (Pankiw et al., 1998), and influence comb building within the colony (Ledoux et al., 2001). Notably, reproductively active, queenless honeybee workers (and bumble bee workers) revert back to sterility when the queen is reintroduced (Alaux et al., 2007; Malka et al., 2007). Inhibitory queen pheromones and their active compounds have also been found in the ants *Camponotus floridanus* (Endler et al., 2004), pharaoh's ant *Monomorium pharaonis* (Edwards, 1987), *Aphaenogaster senilis* (Boulay et al., 2009), and *Lasius niger* (Holman et al., 2010b), and the termite *Reticulitermes speratus* (Matsuura et al., 2010). Among ants, the queen pheromone system of the fire ant *Solenopsis invicta* is particularly well studied. Pheromones initiate reproductive development in new winged females, called female sexuals (Vargo, 1999). These chemicals also inhibit workers from rearing male and female sexuals, suppress egg production in other queens of multiple queen colonies and cause workers to kill sexual larvae or execute excess queens (Fletcher & Ross, 1985; Vargo & Fletcher, 1986; Vargo, 1999; Klobuchar & Deslippe, 2002). In queenless colonies that lack such pheromones, winged females will quickly shed their wings, develop ovaries and lay eggs. These virgin replacement queens assume the role of the queen and even start to produce queen pheromones (Vargo,

1999). There is also evidence that queen weaver ants *Oecophylla longinoda* have a variety of exocrine glands that produce pheromones, which prevent workers from laying reproductive eggs (Fletcher & Ross, 1985).

### 9.3 Excursion: Pleiotropy

Haldane (1955) explained that "two genes are said to be allelomorphous if a nucleus with a single chromosome set, for example that of a spermatozoon, can only contain one of the two." Even where both the alleles are present in a single diploid organism (heterozygote), only one (the dominant allele) is expressed. In incomplete dominance, there is usually a blended simultaneous expression of the morphological phenotypes. Selfish mutants that cooperate less (cheats) can be isolated from natural populations of microorganisms or artificially generated (Velicer, 2003; West et al., 2006; Foster et al., 2007; Ross-Gillespie et al., 2009). Accordingly, extant models of kin selection suppose that the "altruistic" and selfish traits are allelomorphs. There is never environmentally contingent expression of one or the other in an alternating fashion. Where the latter happens, in modern genetics parlance this is described as phenotypic plasticity (Pigliucci, 2001). Recently, Yakubu (2012, 2013) postulated a pleiotropic plastic "sociality trait" that can express either "altruism" or selfishness depending upon the circumstances. This trait requires the capacity to judge when to be "altruistic" or behave selfishly. This suggests plasticity.

The theory of pleiotropy assumes that a particular gene may have an effect not only on one feature but on several traits of an organism. Pleiotropy is one of the most commonly observed attributes of genes, with broad implications in genetics, evolution, development, aging, disease, and drug discovery (Wright, 1968; Barton, 1990; Cheverud, 1996; Hodgkin, 1998; Waxman & Peck, 1998; Brunner & van Driel, 2004; Otto 2004; van de Peppel & Holstege, 2005; He & Zhang, 2006; Stearns, 2010; Wang et al., 2010). Pleiotropy causes compromises among adaptations of different traits, because a genetic change beneficial to one trait may be deleterious to another (Barton, 1990; Otto, 2004). Hence, pleiotropy is under strong stabilizing selection (Barton, 1990). A model showed that, when three or more characters are affected by a mutation, a single optimal genetic sequence may become common. This result may explain the low levels of variation and low rates of substitution that are observed at some loci (Waxman & Peck, 1998). Pleiotropy is expected to constrain the rate of evolution (Otto, 2004), consistent with the observation

that broadly expressed genes evolve more slowly (Hughes & Hughes, 1995; Hastings, 1996; Hurst & Smith, 1999; Duret & Mouchiroud, 2000; Hirsh & Fraser, 2001; Jordan et al., 2002; Subramanian & Kumar, 2004; Zhang & Li, 2004; Wall et al., 2005; Zhang & He, 2005; Liao & Zhang, 2006; Liao et al., 2006; Larracuenta et al., 2008). Importantly, the expression pattern-dependent substitution rates in mammalian genes are determined by selection intensity but not mutation rate (Duret & Mouchiroud, 2000). He and Zhang (2006) found that  $39.5 \pm 0.8\%$  of nonpleiotropic yeast genes (no phenotype in any condition) have detectable homologs in the fruit fly *D. melanogaster*. In comparison,  $49.2 \pm 2.3\%$  of low pleiotropic genes (with phenotypes in one to two conditions) and  $54.7 \pm 3.6\%$  of high pleiotropic genes (with phenotypes in more than two conditions) have fruit fly homologs. Pleiotropic genes are significantly more likely to be retained in long-term evolution than nonpleiotropic genes ( $\chi = 29$ ,  $P < 10^{-7}$ ).

Social behavior is a plastic trait that is regulated by environmental cues such as stress, and various other, particularly metabolic (see chapter 10), signaling networks. In eusocial insects, environmental effects on worker ovary activation are obvious, as pheromones emitted from the queen (Voogd, 1956; Hoover et al., 2003) and her brood (Jay, 1972; Mohammedi et al., 1998) strongly suppress worker reproduction. Queen pheromones are pleiotropic agents that induce “altruistic” sterility in workers and selfish monopolization of reproduction in queens (Wessler & Crewe, 1999; Hoover et al., 2003; Kocher et al., 2008, 2009; Holman et al., 2010b; Maisonnasse et al., 2010). Within queenright colonies, worker reproduction is rare (Ratnieks, 1993) but in queenless colonies, some workers activate their ovaries and begin to lay unfertilized eggs that develop into haploid males (Velthuis, 1970; Page & Robinson, 1994). Worker reproduction is therefore responsive to pheromone signals, and variation in ovary activation among workers is best modelled as a threshold response (Barron & Robinson, 2008). Beyond pheromones, environmental factors such as nutrition (Jay & Jay, 1993; Pernal & Currie, 2000), season (Lin & Winston, 1998; Hoover et al., 2006) and the presence and qualities of other workers within the colony (Wegener & Bienefeld, 2009) can likewise influence worker reproductive state. In termite colonies, workers are reproductively suppressed in queenright colonies and accordingly to current terminology are considered as “altruists”. When a breeder’s position becomes available, a subset of workers develops into neotenic replacement reproductives. Should more individuals develop than are needed to replace the queen or king,

these neotenics will fight with their siblings until death to take over the queenless colony. During the process of caste determination, genetically identical individuals develop into queens or workers (LeBoeuf et al., 2013), the former selfish and the latter “altruistic”. In singular cooperative breeders, the death of the breeding female is often followed by intense fighting between her daughters and the death or eviction of unsuccessful competitors (Clutton-Brock et al., 2006; Sharp & Clutton-Brock, 2011). In the primitive ant species, *Harpegnathos saltator*, queens are relatively short-lived, and the loss of a queen reliably triggers highly aggressive, long-lasting (up to 4 weeks) dominance fights among the remaining workers (Liebig et al., 2000; Peeters et al., 2002). As a result of these dominance fights, only one or a few inseminated workers eventually become reproductive and turn into functional queens. These examples demonstrate the pleiotropy, context dependency of alternative selfish and “altruistic” behavior.

Genetic effects on worker ovary activation also occur, as is apparent from colony patrilineages that show variation in their threshold response to pheromone signals. In such cases, workers sired by a particular drone are more likely to activate their ovaries in queenless colonies (Inbar et al., 2008), or even when a queen is present—a condition described as worker ‘anarchy’ (Barron et al., 2001). A meta-analysis of published studies that measure worker ovary activation as a function of genetic or environmental manipulations, revealed that environmental sources of variation, including real or synthetic queen pheromone, brood pheromone, social interaction, season, diet and CO<sub>2</sub> narcosis, have had a larger overall effect on ovary scores than have strictly genetic effects (Backx et al., 2012).

Epigenetics is closely linked to environmental conditions and mitochondrial bioenergetics (Xie et al., 2007; Naviaux, 2008; Smiraglia et al., 2008; Wallace & Fan, 2010; Minocherhomji et al., 2012). The epigenome provides the interface between the environment and the regulation of nuclear DNA gene expression (Feinberg, 2007, 2008). The regulation of nuclear replication and gene expression by calorie availability is mediated by mitochondrial energetics. This is achieved by coupling of nDNA chromatin structure and function by modification via high energy intermediates: phosphorylation by ATP, acetylation by acetyl-Coenzyme A (ac-CoA), deacetylation by nicotinamide adenine dinucleotide (NAD<sup>+</sup>), and methylation by S-adenosyl-methionine (SAM). Numerous characterized epigenetic marks, including histone methylation, acetylation, and ADP-ribosylation,

as well as DNA methylation, have direct linkages to central metabolism through critical redox intermediates such as NAD<sup>+</sup>, SAM, and 2-oxoglutarate (Wallace & Fan, 2010; Cyr & Domann, 2011). Stress-induced changes of DNA methylation are common (Chinnusamy & Zhu, 2009; Verhoeven et al., 2010; Richards, 2011; Verhoeven & van Gurp, 2012). While mitochondrial DNA replication appears to be required for prespore differentiation in *Dictyostelium* (Araki & Maeda, 1995, 1998; Shaulsky & Loomis, 1995), pleiotropic DIF-1 that is released by prespore cells (Kay & Thompson, 2001) suppresses prestalk cell energy metabolism. DIF-1 and DIF-3, the first metabolite produced during the degradation of DIF-1, are mitochondrial uncoupler that inhibit mitochondrial respiration and suppress cell growth (Shaulsky & Loomis, 1995; Thompson & Kay, 2000b; Kubohara et al., 2013). Honeybee worker development is associated with increased DNA methylation; larvae reared in vitro with inhibited DNA methylation show greatly increased probabilities of developing into queens (Kucharski et al., 2008).

Stress-dependent bacterial quorum sensing is a pleiotropic regulatory network of social interactions (Czárán & Hoekstra, 2009, 2010) that regulates both cooperative biofilm formation (Suntharalingam & Cvitkovitch, 2005; Irie & Parsek, 2008; Goo et al., 2012; Li & Tian, 2012) and selfish bacteriocin production (Kleerebezem & Quadri, 2001; van der Ploeg, 2005; Cornforth & Foster, 2013) (see chapter 5.3). As in many other bacteria, *Pseudomonas aeruginosa* has a Fur protein that functions as a global regulator of iron-responsive genes (Vasil & Ochsner, 1999; Ochsner et al., 2002). Since a critical level of intracellular iron serves as the signal for biofilm development, Fur is a key regulator of biofilm maturation (Banin et al., 2005). In *P. aeruginosa*, *fur* appears to be an essential gene, and the only *fur* mutants available either produce reduced levels of wild-type Fur or have missense mutations that exhibit high reversion rates (Barton et al., 1996; Ochsner et al., 1999; Banin et al., 2005). Thus, pyoverdine defective mutants, which have been isolated in natural populations, are potential cheats (De Vos et al., 2001; Visca et al., 2007). Clones that defected from cooperative production of iron-scavenging siderophores were deficient in biofilm formation (Banin et al., 2005; Harrison & Buckling, 2009). Thus *fur* has a pleiotropic role in iron homeostasis and social behavior of *P. aeruginosa* (Banin et al., 2005; Harrison & Buckling, 2009). Iron metabolism is regulated in response to oxidative stress coordinated with oxidative stress defenses (Pantopoulos & Hentze, 1995; Hanson & Leibold, 1998; Zheng et al., 1999). Iron

accumulation, dependent on metabolic and oxidative stress (Romslo, 1975; Fujimoto et al., 1982; Ceccarelli et al., 1995; Wang et al., 1995), may sensitize cells to oxidative stress (Lipinski et al., 2000) and modulate social behavior. *Myxococcus fulvus* develops by social fruiting body formation in social habitats, but switches pleiotropically to asocial spore formation from vegetative cells in asocial habitats (Zhang et al., 2005; Li et al., 2011). Deleting the gene *dimA* in *D. discoideum* allows cells to avoid death, but leads to a great reduction in spore production (Foster et al., 2004). Hence, the pleiotropic effects of *dimA* stabilize social behavior among amoeba. Given the key role of the metabolism-stress signaling network for life history strategies and their trade-offs in multicellular organisms (Dallman et al., 1995; Dantzer & Swanson, 2012; Heininger, 2012; Sparkman et al., 2012), pleiotropic social interactions add multiple dimensions of complexity to this life history network (Sinervo et al., 2008).

Non-coding small RNAs that modulate gene expression at the post-transcriptional level are plausible candidates for the regulation of pleiotropic behavior (Altuvia et al., 1997). In bacteria, regulatory small RNAs (sRNAs) are often associated with stress responses in changing environments, such as oxidative stress, iron limitation, glucose-phosphate stress and growth-substrate deprivation (Altuvia et al., 1997; Masse & Gottesman, 2002; Vanderpool & Gottesman, 2004; Yu et al., 2010; Chen et al., 2014; Taylor, 2014), and have been shown to regulate social traits such as biofilm formation (Chambers & Sauer, 2013; Taylor, 2014), quorum sensing (Bejerano-Sagie & Xavier, 2007), adaptive resistance (Taylor, 2014) and fruiting body development (Yu et al., 2010). A non-coding small RNA molecule is a key developmental gatekeeper that blocks *M. xanthus* development when food is abundant (Yu et al., 2010; Chen et al., 2014).

Reactive oxygen/nitrogen species are prototypic pleiotropic agents. Candidate genes associated with variation in sensitivity to oxidative stress form networks of genes involved in development, immunity, and signal transduction (Jordan et al., 2012). Oxidative/nitrosative stress is the final common pathway of responses to a variety of biotic and abiotic stressors (Lindquist, 1986; Sanchez et al., 1992; Finkel & Holbrook, 2000; Heininger, 2001; Mittler, 2002; Mikkelsen & Wardman, 2003; Sørensen et al., 2003; Apel & Hirt, 2004; Ardanaz & Pagano, 2006; Rollo, 2007; Miller et al., 2008; Slos & Stoks, 2008; Jaspers & Kangasjärvi, 2010; Steinberg, 2012; Choudhury et al., 2013). There is no doubt that

reactive oxygen species can be a double-edged sword: depending on the cellular context they exert signaling and executive functions in cellular survival and apoptosis decisions (Heininger, 2001; Martin & Barrett, 2002; Martindale & Holbrook, 2002; Fruehauf & Meyskens, 2007; Moreira da Silva et al., 2010; Maryanovich & Gross, 2013).

## 10. Resources and social interactions: a tale of murder, affiliation and indifference

### Summary

**Behavioral ecologists have long recognized a relationship between social behavior and the distribution and predictability of resources. In extreme resource-limited environments both kin and conspecifics can serve as food. Filial cannibalism, siblicide and sibling cannibalism are a common phenomenon in several orders of taxa. Even matricidal behavior occurs in some taxa living in extremely resource-limited habitats.**

**In unpredictable or dangerous environments, the chances of successfully raising offspring independently are limited either by predator pressure or harsh environmental conditions. Under such conditions groups are better able to find scattered food, repel enemies, care for young, and thus reduce the risk of brood loss.**

**In social bacteria and amoeba, nutrient-rich environments select for asociality. An excessive abundance of common resources deters socially responsible actions on structured populations and the excess allows defectors to free-ride well over the time horizon that is required for cooperators to die out. A similar development may be observed in modern human societies with their abundant resources that appear to promote the loss of social coherence and solidarity.**

Resource availability follows a conservation law, implying that the gains or losses in resources to individual are balanced by the losses or gains to others (Lehmann & Rousset, 2010). Behavioral ecologists have long recognized a relationship between social behavior and the distribution and predictability of resources (Crook, 1964; Horn, 1968; Bradbury & Vehrencamp, 1976; Clutton-Brock & Harvey, 1977), and increasing empirical evidence points to resource-based explanations of social organization in a variety of species (Waser, 1981; Macdonald, 1983; Wrangham et al., 1993; Chapman et al., 1994; Creel & Macdonald, 1995; Powell et al.,

1997; Johnson DDP et al., 2002). In a simulation using an adaptive multiagent system, the effect of environmental conditions on the success of distinct strategies for optimal resource management was investigated. Interestingly, in an environment with patchy and limited resources agents learned to cooperate and to harvest their resources in a moderate way, thus avoiding population crashes due to uncontrolled exploitation (Krink, 2000). Resource supply has been found to alter the cost of cooperation, which decreases with increasing resource supply, such that public-goods cooperation is more likely to evolve when resources are more abundant (Brockhurst et al., 2007, 2008, 2010). The resources hypothesis of sociality suggests that social groups form and are maintained in response to the cooperative benefits that can be obtained by extracting certain types of resource distributions (Crook, 1965; Slobodchikoff, 1984). These groups may consist of either kin or nonkin. Following and extending Crook's arguments (1965, 1970, 1972), Slobodchikoff (1984) suggested that ecological factors such as resource abundances and distributions play a role in determining whether or not a particular group of animals is going to be social (Slobodchikoff & Schulz, 1988). The relationship between resources and sociality is expressed in several different models (Crook, 1965, 1972; Wrangham, 1980, 1983; Terborgh, 1983; Van Schaik & van Hooff, 1983; Slobodchikoff, 1984). While research on non-humans demonstrates that the extent of nepotism among kin can depend critically on resources available to parents or sibships in insects (Griffin, West, and Buckling 2004; West et al., 2001) our understanding of the sensitivity of human kinship relations to resource competition derives largely from folklore.

### 10.1 Scarce resources and social behavior

In extreme resource-limited environments both kin and conspecifics can serve as food. Several theorists (Eickwort, 1973; Crespi, 1992; Mock & Parker, 1997; Pfennig, 1997; Perry & Roitberg, 2005) restated Hamilton's rule for the spread of a selfish act to investigate the conditions favoring sibling cannibalism. For example, in a dyadic interaction a cannibal must increase survival by at least 50% to profit from consuming a full sibling. In my opinion this is teleological thinking par excellence (see also chapter 19). How should organisms, given the huge stochasticity of environments and their chances of survival to maturity (see chapter 15.1; Heininger, 2015), be able to estimate the inclusive-fitness effects of their actions? Already by taking frequency-dependent effects into account (information

that is often not available to cannibals) the dynamic stochasticity of the social interactions and their fitness value become evident.

Cannibalism is a well-documented phenomenon that has been described for many animal species (Polis, 1981). Several forms of cannibalism can be distinguished (Rohwer, 1978; Smith & Reay, 1991), for example, heterocannibalism (also called 'nonkin cannibalism'; Smith & Reay, 1991) and filial cannibalism. While the former describes the eating of unrelated conspecifics, the latter describes the consumption of own offspring, either eggs or young. Filial cannibalism is extremely common in teleost fish (e.g. Dominey & Blumer, 1984; Smith & Reay, 1991; FitzGerald, 1992), having been recorded in 17 families (Manica, 2002), and in a wide range of other taxa (Polis, 1981; Elgar and Crespi, 1992; Klug & Bonsall, 2007), including snakes (Lourdais et al., 2005), skinks (Huang, 2008), mammals (Elwood, 1991; Burn & Mason, 2008), birds (Gilbert et al., 2005), crustaceans (Dumont & Ali, 2004; Gallucci & Ólafsson, 2007), spiders (Anthony, 2003) and insects (Bartlett, 1987; Thomas & Manica, 2003; Creighton, 2005). Population size in the flour beetle *Tribolium* is mainly governed by the cannibalism rate rather than differences in fertility or fecundity (Park et al., 1961, 1965; McCauley & Wade, 1980; Stevens & Mertz, 1985). Several studies suggest that filial cannibalism increases when the costs of providing care increase or the benefits of providing care decrease (Marconato et al., 1993; Neff, 2003a, b; Thomas & Manica, 2003; Manica, 2004; Lourdais et al., 2005; Klug et al., 2006; Frommen et al., 2007; Gray et al., 2007; Huang, 2008; Chin-Baarstad et al., 2009). Population-level resource competition appears to play an important role in the evolution of both parental care and filial cannibalism (Klug & Bonsall, 2007).

Mock and Parker (1997) broadly defined sibling rivalry as "any features of animals or plants that have the effect of promoting individual survival and/or reproduction at the expense of siblings." Siblicide (also termed brood reduction) falls within this definition (Hofer & East, 2008). The theory for resource-based sibling rivalry has been well developed (O'Connor, 1978; Stinson, 1979; Dickins & Clark, 1987; Parker et al., 1989; Godfray & Harper, 1990; Godfray & Parker, 1992; Forbes, 1993; Rodríguez-Gironés, 1996; Mock & Parker, 1997; Mock et al., 1998; Perry & Roitberg, 2005). Siblicide and sibling cannibalism are a common phenomenon in several orders of arthropods (Elgar & Crespi, 1992; Fincke & Hadryns, 2001; Gagne et al., 2002; Iida, 2003; Michaud & Grant, 2004; Dobler & Kölliker, 2010; Noriyuki et al., 2011, 2012; Collie et al.,

2013), fishes (Hecht & Appelbaum, 1988; van Damme et al., 1989; Smith & Reay, 1991; Bry et al., 1992; Fitzgerald & Whoriskey, 1992; Hecht & Pienaar, 1993; Folkvord, 1997; Baras, 1999), amphibians (Crump, 1992, 1996), birds (Mock & Parker, 1997; Watson et al., 1999; Drummond, 2001; Morandini & Ferrer, 2014), and mammals (Frank et al., 1991; Mock & Parker, 1997; Smale et al., 1999) and is termed facultative when it occurs only occasionally (when food resources are low) and obligate when at least one sibling is killed in virtually all broods/cohorts.

Bird rearing decisions can be described by portfolio theory on the premise that higher returns are generally associated with greater risk, and that portfolio diversification reduces risk (Forbes, 2009). Parents of altricial birds structure their brood into core (first-hatched) and marginal (later-hatched) elements that differ in risk profile. Their initial investment, in the egg and the resources required to sustain the offspring during a period of clemency (Forbes & Ydenberg, 1992), is modest as brood reduction usually occurs early before food demands are high (Forbes et al., 2002a). Thus parents can await unfolding ecological conditions to determine if the option should be exercised. Under conditions of plenty, the option is called, and marginal progeny reared. If food is insufficient, they cut their losses by allowing marginal progeny to perish early via a fatal sibling rivalry (Mock & Forbes, 1995; Mock & Parker, 1997; Forbes et al., 2001). The natural magnitude of hatching asynchrony may be adaptive in part because it moderates sibling competition and chick losses but also because it may give parents greater control over the outcome of sibling competition (Merkling et al., 2014). Death can be caused by physical damage inflicted by a sibling or by aggressive and/or non-aggressive monopolisation of food resources provided by parents (Forbes, 1993; Mock & Parker, 1997; Drummond, 2001; Drake et al., 2008; Hofer & East, 2008; Hudson & Trillmich, 2008; Trillmich & Wolf, 2008; Morandini & Ferrer, 2014). Avian models of facultative siblicide predict, and are supported by empirical evidence that fitness benefits acquired by dominant offspring through despotic behavior should increase as parental provisioning rates decline. In the blue-footed booby (*Sula nebouxii*), differential mortality of junior chicks was associated with a 20-25% weight deficiency of the senior sib, implying siblicidal brood reduction triggered at a weight threshold. Parents and senior chick cooperate in the siblicide, as if their fitness interests were congruent (Drummond et al., 1986). In contrast, fitness costs should increase and benefits associated with despotic behavior should decline as parental provisioning rates rise (Parker et al., 1989; White et

al., 2010). Food amount also influences aggression in obligate brood reducers (Osorno & Drummond, 2003). These findings have been confirmed in a mammalian context of facultative siblicide (Wachter et al., 2002; Hofer & East, 2008; Morandini & Ferrer, 2014) and non-lethal aggressive competition between offspring (Hodge et al., 2009).

Siblicide and cannibalism are a primary cause of mortality throughout nymph development (Dobler & Kölliker, 2010, 2011) in the European earwig (*Forficula auricularia*), an insect species with uniparental maternal care. Interactions among unrelated nymphs frequently occur under natural conditions due to brood mixing (Kölliker & Vancassel, 2007; Wong & Kölliker, 2013). Cues of maternal condition affect offspring behavior in terms of sibling cannibalism: cues of poor maternal condition enhanced nymph survival in early broods, but reduced nymph survival in late broods, and vice versa for cues of good condition (Wong et al., 2014). Sibling interactions also reflect cooperative behaviors in the form of food sharing in nonderived families of the European earwig. Food ingested by individual offspring was transferred to their siblings through mouth-to-anus contacts and active allo-coprophagy. Relatedness influenced the strategy used by nymphs to provide and/or obtain food from other nestmates, but the two strategies resulted in equivalent outcomes in terms of amount of food transferred (Falk et al., 2014). Together with maternal sensitivities to condition-dependent nymph chemical cues (Mas et al., 2009; Wong & Kölliker, 2012; Meunier & Kölliker, 2012), these findings establish a context-dependent reciprocal information exchange about condition between earwig mothers and their offspring that are potentially mediated by cuticular hydrocarbons and affect the rate of siblicide or offspring cooperation (Wong & Kölliker, 2012; Gómez & Kölliker, 2013).

Even matricidal behavior occurs in extremely resource-limited habitats in which the parental organism serves well to nurture the progeny. Several examples of maternal death (endotokia matricida) that occurs during matricidal hatching are provided by Caleb Finch (1990, p. 102). In a variety of spiders, juveniles eat their mother before dispersing from the communal nest (Wise, 2006). Females of the Japanese foliage spider, *Chiracanthium japonicum*, are eaten by their offspring at the end of the maternal care period (Toyama, 2003). Facultative endotokia matricida has been observed in a variety of parasitic and free-living oviparous nematodes as a response to food limitation (Ayalew & Murphy, 1986; Johnigk & Ehlers, 1999; Baliadi et al., 2001; Hirao & Ehlers,

2010).

## 10.2 Unpredictable or limited resources and sociality

Throughout this work (see chapters 4.2, 5.3.1 and 6) cumulative evidence has been presented indicating that more challenging environments with limited resources select for cooperativity. Meta-analyses and models show that many mammals, birds, fishes and insects are found living at densities at the carrying capacity of their habitats (Sibly et al., 2005; Brook & Bradshaw, 2006). Thus, in most animal species a population's growth rate is a decreasing function of density (Sibly et al., 2005) which explains the relative stability of animal populations that do not increase at rates their fertility would allow. In unpredictable or dangerous environments, the chances of successfully raising offspring independently are limited either by predator pressure or harsh environmental conditions. Under such conditions groups are better able to find scattered food, repel enemies, care for young, and thus reduce the risk of brood loss. This scenario has long been a favored explanation for evolution of eusociality in insects (Wilson, 1971; Lin & Michener, 1972), and has been termed 'life insurer' eusociality (Queller & Strassmann, 1998) in Hymenoptera, in which helpless larvae require extended care and foraging adults are under constant threat from enemies (Queller, 1989; Gadagkar, 1991b). A similar explanation has been offered for sociality in vertebrates threatened by harsh environments with unpredictable food supply. In both naked mole-rats (Faulkes et al., 1997) and certain cooperatively breeding bird families (Rubenstein & Lovette, 2007), phylogenetically controlled comparative analyses identified significant associations between sociality and unpredictable environmental conditions (Duffy & Macdonald, 2009). Habitat saturation in favorable environments with predictable resources but dense populations and strong pressure from competitors or other enemies may also limit breeding opportunities, a finding that was conceptualized by the long-standing habitat saturation hypothesis (Selander, 1964; Brown, 1974; Emlen, 1982b). Particularly in long-lived species (Hatchwell & Komdeur, 2000), offspring have few opportunities for independent breeding and little option but to live instead as helpers at the nest of parents or other relatives. A global comparative analysis of 182 species of birds supported this hypothesis, confirming that cooperative breeding was significantly associated with sedentary life in warm, invariable climates (Arnold & Owens, 1999). A somewhat similar argument has been made for sociality in 'fortress defender' insects, which include certain gall-forming aphids and thrips,

and many termites, that live in protected habitats providing both food and shelter (Alexander et al., 1991; Crespi, 1994; Queller & Strassmann, 1998). Based on findings in theoretical and experimental research (MacLean & Gudelj, 2006; Andras et al., 2007; Gore et al., 2009; Requejo & Camacho, 2011, 2012a, b, 2013; Smaldino et al., 2013a, b; Chen & Perc, 2014), cooperation has been found to be the more likely behavior if initially the common resources are limited rather than abundant. In models, harsher environments led to higher long-term frequencies of cooperators (Smaldino et al., 2013a, b), and select for reduced parasitism (Hochberg et al., 2000; Requejo & Camacho, 2011) lending theoretical support to Kropotkin's (1902) proposal that harsh environments should select for cooperation. Cheater phenotypes of bacteria and amoebae have a high risk to go extinct under conditions of unpredictable and fluctuating resource availability such as in feast and famine cycles (Hilson et al., 1994; Pál & Papp, 2000; Ennis et al., 2003; Fiegna & Velicer, 2003; Rainey & Rainey, 2003; Castillo et al., 2005; Kuzdzal-Fick et al., 2011). These findings are in agreement with data from experiments conducted on yeast (MacLean & Gudelj, 2006; Gore et al., 2009) as well as on social vertebrates (Shen et al., 2012). Similarly, experiments on social vertebrates indicate that unfavorable environmental conditions, where resources are limited, reduce social conflict and make social vertebrates more cooperative (Shen et al., 2012).

### 10.3 Abundant resources and sociality

A resource-rich, noncompetitive, r-environment selects for traits that enhance population growth rate, including early maturity, small body size, high reproductive effort, and high fecundity. Conversely, resource-limited, competitive, K-environments select for traits that enhance persistence of individuals, including delayed maturity, large body size, high investment in individual maintenance at the cost of low reproductive effort, low fecundity with a large investment in each offspring, and longer lifespan (MacArthur & Wilson, 1967). These alternative constellations of life-history traits became known as life-history strategies (Pianka 1970; 1974b; Reznick et al., 2002). The life history strategies of cooperators are biased towards the K-selected end of the r-K continuum (Brown, 1974, 1987; Gaston, 1978; Russell, 1989; Rowley & Russell, 1990; Poiani & Jermin, 1994; Arnold & Owens, 1998, 1999). On the other hand, current abundance of resources, respectively a history of resource abundance or stress, may select for asociality.

Already bacteria and protozoa have options for either

social or asocial behavior dependent on the inverse relationship of resource availability and intercellular communication. In chemostats (well-mixed, continuous systems), the selfish high growth rate strategist (at the cost of low growth yield) will always outcompete the cooperative high growth yield strategist (at the cost of low growth rate), because high growth rate strategists grow faster at every substrate concentration above zero (Kreft, 2004b). In the unstructured environment of suspension cultures, resources are a public good and accessible to every individual. In the case of batch cultures, this will select for the fastest growing, selfish organism (Bachmann et al., 2013). The asocial alternative may be pursued in stressed, socially deprived microorganisms (Boesen et al., 1992). In constant, nutrient-rich environments where benefits associated with sporogenesis (a social behavior) are absent and no longer balance the cost of constructing spores, sporulation ability of *Bacillus subtilis* was lost over 6,000 generations (Maughan et al., 2009). Propagation of *B. subtilis* for less than 2,000 generations in a nutrient-rich environment where sporulation is suppressed led to rapid onset of genomic erosion including biosynthetic pathways, sporulation, competence, and DNA repair (Brown et al., 2011). The social prokaryote *Myxococcus xanthus* loses its social behavior when propagated in nutrient-rich habitats in which their social behaviors for starvation-induced spore production or predatory efficiency were not under positive selection (Velicer et al., 1998; Velicer & Stredwick, 2002). This selective regime places no positive selection on *M. xanthus* social traits but rather on competitiveness under asocial growth conditions. The replicate lineages improved their maximum growth rates an average of 37% over 1,000 generations, but all populations incurred partial or complete losses in their capacity for social motility and social development during this period of adaptation (Velicer et al., 2006). Bacteria or protists which are shear-stressed by constant shaking (Hellung-Larsen & Lyhne, 1993; Fang et al., 1997) are deprived of humoral or cellular contacts with their siblings (Velicer et al., 1998). Bacteria cultured in such an asocial environment but exposed to abundant nutrient resources exhibit substantially attenuated capacities for social behavior following starvation (Velicer et al., 1998). Similarly, disruption of cell-cell contacts that mediate social control (Hanahan & Weinberg, 2000; Bornstein & Sage, 2002; Giacotti & Tarone, 2003) appears to be a basic requirement of carcinogenesis (Yamasaki et al., 1995; Trosko & Ruch, 1998) which can be viewed as social cheating taking advantage of the abundant nutrient resources of the internal milieu of a metazoan organism. The model

amoeba *Dictyostelium discoideum* is single-celled under conditions of nutritional abundance but aggregate under metabolic stress. Following growth with glucose, *D. discoideum* cells exhibit lowered DIF sensitivity, cheat and are overrepresented in the spores when mixed with cells grown without glucose (Leach et al., 1973; Thompson & Kay, 2000b). When the amount of glucose available in the media is increased, defective yeast that do not pay a cost for producing invertase can spread faster than cooperative yeast, even driving cooperative yeast to extinction (MacLean & Gudelj, 2006; Gore et al., 2009). At either extreme, nutrient-rich or very nutrient-poor conditions, greater numbers of cells are in the planktonic phase where they have greater access to the local nutrients or can be distributed to a new environment (Stanley & Lazazzera, 2004). Biofilm formation is inhibited and biofilm depth reduced by catabolite repression (Jackson et al., 2002; Stanley et al., 2003), possibly as an indicator to the cells that they are in a nutrient-rich environment where there is no growth advantage to being in a biofilm. When the cells are in the planktonic phase, there is greater cell surface area exposed to the nutrients (Stanley & Lazazzera, 2004).

It has been shown repeatedly that the optimal strategies in social games depend on the availability of resources (Burtsev & Turchin, 2006). A key finding is that the investment into helping decreases, and the probability of escalated conflicts increases, for individuals that are likely to inherit a valuable nest (Abbot et al., 2001; Cant et al., 2006a; Field & Cant, 2009), epitomizing a general evolutionary link between resource value and societal conflict (Hoffmann et al., 2012). Individuals following a minimal-effort (plastic) strategy are the ones that most strongly bring sustainability in commons structured in large groups and abundant public goods (Cavaliere & Poyatos, 2013).

Subjected to environmental conditions that do not require cooperation, social deficits become common; all of the experimental lineages developed such deficits (Lyon, 2007). An excessive abundance of common resources deters socially responsible actions on structured populations (Chen & Perc, 2014). If either the common resources are initially too many, if the cooperators are too effective in refilling the pool, or if the maximally allowed endowments are too low for allowing an immediate dissemination of accumulated goods, the defectors are able to take full advantage of their refrain from contributing without suffering the consequences. If sufficiently abundant, the excess allows defectors to free-ride well over the time horizon

that is required for cooperators to die out (Chen & Perc, 2014). A similar development may be observed in modern human societies with their abundant resources that appear to promote the loss of social cooperation and solidarity. Putnam (2000) argued that social capital “has eroded steadily and sometimes dramatically over the past two generations” (Putnam, 2000, p. 287). Other evidence supports his claim, including a 2006 study which concluded that not only have informal and formal networks declined, as Putnam notes, but close personal ties have also diminished in recent years (Kibert et al., 2011).

#### 10.4 Resources and sociality in plants

Most plants require a similar balance of resources—energy, water, and mineral nutrients—to maintain optimal growth. Natural environments, however, differ by at least two orders of magnitude in the availability of these resources (Chapin et al., 1987). Light intensity varies 100-fold from the canopy to the floor of a rainforest (Björkman, 1981); annual precipitation ranges 500-fold (10-5000 mm/yr) from deserts to tropical rainforests; and the amount of nitrogen available to plants varies from 0.09 g/m<sup>2</sup> x yr in polar desert (Dowding et al., 1981) to 22.8 g/m<sup>2</sup> x yr in a rich tropical rainforest (Vitousek, 1984). Among botanists there is a broad consensus that the balance between negative and positive interactions should shift along environmental gradients (Tielbörger & Kadmon, 2000), with competition prevailing under environmentally benign conditions and positive interactions dominating under harsh conditions (Bertness & Callaway, 1994; Bertness & Hacker, 1994; Bertness & Leonard, 1997; Callaway & Walker, 1997; Brooker & Callaghan, 1998; Callaway et al., 2002). The importance of facilitation should increase with increasing abiotic stress, while negative interactions should prevail under benign conditions (Bertness & Callaway, 1994; Callaway & Walker, 1997; Holmgren et al., 1997; Brooker & Callaghan, 1998; Holmgren & Scheffer, 2010). Empirical evidence for this hypothesis stems from a variety of studies investigating interactions between organisms along spatial gradients in the physical environment (Walker & Chapin, 1987; Bertness & Shumway, 1993; Bertness & Hacker, 1994; Bertness & Yeh, 1994; Greenlee & Callaway, 1996; Bertness & Leonard, 1997). Importantly, positive interactions are more prominent under moderately stressful rather than under extreme conditions (Holmgren & Scheffer, 2010).

Clonal growth in plants produces iterated modular units (ramets), each with the same genotype and each potentially capable of independent growth and reproduction. Individuals of clonal plants consist of

physically and physiologically connected ramets. In modular, clonal organisms the ability to maximise resource capture as an important characteristic of highly competitive organisms may be enhanced by the physiological integration of modules (ramets) making up the clone. In splitters, they are integrated for a time shorter than ramet generation time (i.e. the time it takes to produce the first offspring ramet), whereas in integrators connections between ramets persist for a longer time (Klimeš, 2008). Clonal integration categories are necessarily heterogeneous, as they include plants with a contrasting architecture of below-ground organs, role of vegetative multiplication and reproduction in their life cycle, storage organs, etc (Jónsdóttir & Watson, 1997). It has been predicted that integrators should prevail in stressful environments, such as habitats poor in nutrients, whereas splitters are expected to dominate in benign habitats, such as fertile areas with a moderate climate (Mágori et al., 2003). Several groups reported a prevalence of clonal integrators in stressful environments (Jónsdóttir & Watson, 1997; Klimeš, 2008; Klimešová et al., 2011). In contrast, in completely homogeneous environments, models show that plants with no clonal integration are usually favored (Oborny et al., 2000). Plants at lower temperatures and higher altitudes, where abiotic stress is high, compete less and cooperate more with their neighbors (Callaway et al., 2002). However, daughter ramets in multiple ramet clones may also compete for resources and inhibit each other (Abrahamson et al., 1991; Hellström et al., 2006; Wang P et al., 2012).

Patchiness or heterogeneity of the habitat arises due to the uneven distribution of environmental features impinging on the organism (e.g. soil quality, topography, temperature, light, food, enemies, etc.). The extent of heterogeneity may vary depending on two factors, patch size and the relative quality differences between patches (Gillespie, 1974). Numerous studies have shown that clonal integration can buffer against environmental heterogeneity (Hartnett & Bazzaz, 1985; Pitelka & Ashmun, 1985; Salzman, 1985; Alpert & Mooney, 1986; Hutchings & Bradbury, 1986; Landa et al., 1992; Stuefer et al., 1994; Wijesinghe & Handel, 1994). Physiological integration, or the sharing of resources between ramets, is considered to be of particular benefit when resources are distributed in discrete patches within the habitat (Cook, 1983; Harper, 1985; Pitelka & Ashmun, 1985; Hutchings & Bradbury, 1986). A number of studies have shown that in clonal plants water, nutrients and photosynthates can be redistributed from ramets growing in favorable patches to those growing in poor patches (Noble & Marshall, 1983; Salzman &

Parker, 1985; Slade & Hutchings, 1987; Chapman et al., 1992; Hutchings & de Kroon, 1994) and hence to allow the plants to grow better (Alpert, 1991; Alpert & Stuefer, 1997; Hutchings & Wijesinghe, 1997; Du et al., 2009). This may be true of clonal animals as well (Crowell, 1957; Rees et al., 1970; Jackson, 1977; Best & Thorpe, 1985). This type of physiological integration is thought in some cases to buffer the entire clone against adverse effects resulting from spatial and temporal changes in the quality of a habitat (Hartnett & Bazzaz, 1983; Pitelka & Ashmun, 1985; Hutchings & Bradbury, 1986; Hutchings, 1999). Intriguingly, clones of the herb *Fragaria chiloensis* from patchier habitats, where high levels of different resources tend to be spatially separated, have a greater capacity for division of labor (Roiloa et al., 2007). Populations of the same clonal species from more heterogeneous habitats can show a higher capacity for resource sharing and cooperative behavior, suggesting that physiological integration has been selected for in response to resource patchiness and that patterns of integration may thus to some extent match patterns of patchiness in the habitat of a species (Alpert, 1999; Alpert et al., 2003; Roiloa et al., 2007; Nilsson & D'Hertefeldt, 2008; He et al., 2011; Wang et al., 2011). When the relative abundance of essential resources varies within a clone each ramet specializes in a division of labor to acquire a locally abundant instead of a scarce resource (Alpert & Stuefer, 1997; Magyar et al., 2007). For example, in habitats consisting of patches with high availability of light but low availability of nutrients, and patches with high nutrients but low light, a ramet growing in high light and low nutrients will allocate a relatively high proportion of biomass, and thus of carbon, to shoots if it is connected to a ramet growing in low light and high nutrients, and that ramet in high nutrients will allocate a high proportion of biomass to roots (e.g. Alpert et al., 2003; Roiloa et al., 2007). Simulations have pointed out a number of habitat types characterized by low patch density, and high spatial and temporal variation of the patches where a splitter (displaying competitive behavior) was not viable at all, and only an integrator (displaying cooperative behavior) could persist. In constant environments, the splitter could survive being confined to clusters of good patches (Kun & Oborny, 2003).

In a uniform habitat, ramets will occupy microsites with similar levels of external resource availability. Clones from populations in relatively uniform habitats such as grassland are selected for low levels of resource sharing between ramets (Alpert, 1999). Based on literature survey and field observations, Pitelka and Ashmun (1985) expected splitting in stressful and resource-poor environments, because maintenance of

connections between ramets is costly (Caraco & Kelly, 1991). In such environments, dispersal is favored, both by seeds and vegetative propagules, which are sometimes highly specialized, such as turions, bulbils and detachable buds. The adaptive advantage of clonal splitting in desert shrubs appears to be largely a risk-spreading mechanism that enables independent mortality of integrated hydraulic units or ramets. This should be especially advantageous in heterogeneous, water-limited environments, where soil water occurs in pockets too small to support a large shrub-genet and clonal splitting may cause an increase in intracolon competition among ramets (Schenk, 1999).

Many clonal plants are colonized by arbuscular mycorrhizal fungi. Arbuscular mycorrhizal fungi are likely to reduce contrasts in effective resource levels and have been shown to partly replace the effects and benefits of clonal integration in low-nutrient and heterogeneous habitats (Du et al., 2009). The interaction between colonization by arbuscular mycorrhizal fungi and physiological integration in a clonal plant provides an intriguing example of how biotic and abiotic factors could interact in the evolution of cooperative and mutualistic behavior (Du et al., 2009).

## 11. The genetics of social interactions

### Summary

**A key goal of sociogenomics is to determine how genes and patterns of gene expression change with the shift from solitary to social life. Complex traits are products of a large number of loci with individually small and possibly context-dependent effects. Social behavior is a complex trait. Even in simple organisms such as yeast and social amoeba, the regulation is cooperation is highly polygenic and complex. Aggressive behavior is a complex trait with substantial effects on sociality, regulated by multiple genetic factors as well as by a set of neurotransmitters and neurohormones. Possibly hundreds of candidate genes have been associated with aggressive behavior in fruit flies, zebrafish, mice and humans, many of which, in *Drosophila*, have pleiotropic effects on metabolism, development, and/or other behavioral traits.**

**Insulin and insulin-like messengers signal nutritional status to the reproductive axis and thus regulate reproductive functions such as maturation and gametogenesis in metazoans. In**

**eusocial bees, wasps, ants and termites metabolism signaling pathways also regulate the division of labor. Insulin-like peptides mediate a direct and positive long-range effect on ovarian activity. Worker ovaries are inhibited by pheromones of queen and brood. Some workers dramatically increase the activity of their ovarioles in the absence of the queen indicating that signals from the queen, either directly or indirectly, suppress insulin signaling. Honeybee queen pheromones suppressed solitary fruit fly ovaries in much the same way as it suppresses bee worker ovaries. Queen-worker pheromone communication is a multicomponent, labile dialog between the castes that is independent of genetic relatedness and even works across large phylogenetic distances.**

The theories of social evolution rely on the assumption that social traits have a simple genetic basis that can be treated as a mechanistic 'black box' and largely ignored (Grafen, 1982). The main reason for this is the paucity of classical and molecular genetic tools available to biologists studying classical social organisms (Foster et al., 2007). A key goal of sociogenomics is to determine how genes and patterns of gene expression change with the shift from solitary to social life (Robinson, 1999; Robinson et al., 2005; Owens, 2006; Foster et al., 2007; Smith et al., 2008; O'Connell & Hofmann, 2011; Rittschof & Robinson, 2014). Variation in behaviors in natural populations arises from complex networks of multiple segregating polymorphic alleles, characterized by pleiotropy and widespread epistasis. These networks are sexually dimorphic and sensitive to environmental modulation. Since behaviors reflect dynamic interactions between organisms and their environments, they are central targets for adaptive evolution (Bendesky & Bargmann, 2011; Anholt & Mackay, 2015).

### 11.1 Social behavior, a complex trait

Tremendous progress has been made resolving certain well-studied "simple" traits at the molecular level (Han & Sternberg, 1990; Hobbs et al., 1992; Carroll et al., 1994; Dilda & Mackay, 2002; Rogers et al., 2003; Gutteling et al., 2007a, b; Kammenga et al., 2007; Debat et al., 2009; Dreyer & Shingleton, 2011; Manceau et al., 2011; Reed et al., 2011; Tang et al., 2011); however, an understanding of the specification of complex traits is generally lacking (Rockman & Kruglyak, 2006). Much of this complexity results from the phenotype being a convolution of the genotype and the specific environment experienced by the organism (Grishkevich & Yanai, 2013). It has been

argued that systems genetics approaches are necessary to understand complex traits (Civelek & Lusi, 2014). Genome-wide association studies have identified thousands of genetic loci that contribute to the complex trait 'disease susceptibility' in humans (Glazier et al., 2002; Hindorf et al., 2009; Civelek & Lusi, 2014). For example, more than 100 genomic cancer susceptibility regions have been identified (Stadler et al., 2010). An increasing large number of polymorphisms associated with resistance and susceptibility to malaria have been mapped both using population studies and experimental models of malaria (Fortin et al., 2002). However, aside from their typically modest value for predicting future disease occurrence, this information will provide little mechanistic insight until the loci are translated into genes and pathways. Beyond that, it will be important to understand how the alleles interact with each other or with environmental factors (Civelek & Lusi, 2014).

With regard to social behavior these approaches are still in their infancy. In budding yeast, non-sexual cell aggregation has a polygenic molecular architecture (Li et al., 2013). A genome-scale investigation of the genetic opportunities for cheating in social amoeba showed that cheating is multifaceted and complex by revealing cheater mutations in well over 100 genes of diverse types (Santorelli et al., 2008). Multiple mechanisms and pathways may be involved in cheating behavior, including GTPase regulatory activity, polyketide synthesis, nucleotide binding, and phosphoric ester hydrolase activity (Santorelli et al., 2008). If even in this rather simple organism, the actions of so many genes can be exploited for cheating, cooperation can be expected to be complex and highly polygenic (Buttery et al., 2009, 2010). It appeared that response of *D. discoideum* to social interaction involves many genes with individually small transcriptional effect (Li et al., 2014). These findings corroborate a suggestion already made by Fisher (1918) that most complex traits are products of a large number of loci with individually small and possibly context-dependent effects (Lynch & Lande, 1993). This premise has stood up to a substantial body of empirical work indicating that the number of genes affecting complex traits in populations—or even in simple mouse crosses—range from the tens to hundreds or even thousands (Falconer, 1989; Sjöblom et al., 2006; Wang et al., 2006; Chen Y et al., 2008; Reed et al., 2008; Ayroles et al., 2009; Anholt & Mackay, 2015). In *Drosophila*, quantitative analyses of new mutations have revealed large numbers of loci affecting quantitative traits (Mackay & Anholt, 2006), as have high-resolution maps of segregating quantitative trait loci (QTL) in *Drosophila* (Mackay &

Anholt, 2006) and mice (Valdar et al., 2006). A systems-genetics analysis of the genetic basis of complex traits in *Drosophila* implicated several hundred candidate genes that form modules of biologically meaningful correlated transcripts affecting each phenotype (Ayroles et al., 2009). Comparative and integrative studies suggest that social behaviors most likely evolved by acquiring new social roles for "old" genes rather than the evolution of entirely new sets of "social" genes (Robinson & Ben-Shahar, 2002). Evidence indicates that the distribution of allelic effects of quantitative traits is exponential (Mackay, 2001). A few loci with large effects (major genes) influence most of the genetic variation and an increasingly large number of loci with increasingly smaller effects (minor genes) influence the remaining variation. Numerous genes with large effects on behavior have been identified by mutation (Sokolowski, 2001), Mendelian analysis of behavioral variants (Sokolowski, 2001), QTL mapping (Anholt & Mackay, 2004) and the identification of differences in RNA or protein expression between behavioral variants (Insel & Young, 2000). These are all candidate genes for natural variation in behavior (Fitzpatrick et al., 2005). Mutations generally have small effects on social tendencies in animals, and the resulting effects of these mutations on social tendencies have been considered to be too small for selection to act strongly (Sinervo & Lively, 1996; Sinervo & Calsbeek, 2006; Sinervo et al., 2006; Ross-Gillespie et al., 2007; Wild & Traulsen, 2007).

#### 11.1.1 Aggression

Aggressive behavior is a complex trait with substantial effects on sociality, regulated by multiple genetic factors as well as by a set of neurotransmitters and neurohormones (Popova, 2006). Aggressive behavior plays a significant role in the fitness of animals, and it is widespread in the animal kingdom. Animals use aggression to defend themselves and their progeny from attack by predators, to fight for females, to feed, and to maintain the social hierarchy. The study of aggressiveness is complicated, however, by the fact that aggressive behavior is not a unitary trait (Blanchard et al., 2003). An influential classification related to aggression (Moyer, 1968) is based on the eliciting stimuli and included the following types of aggression: predatory (attacks on prey), intermale, fear-induced, irritable, territorial, maternal and instrumental aggression. The problem of searching for the genetic and neurochemical determinants of aggressive behavior is complicated by their apparent heterogeneity (Popova, 2006). Correlating variation in transcript abundance with variation in complex trait

phenotypes in 40 wild-derived inbred lines of *D. melanogaster*, Edwards et al. (2009a) identified 266 novel candidate genes associated with aggressive behavior, many of which have pleiotropic effects on metabolism, development, and/or other behavioral traits. Behavioral tests of mutations in 12 of these candidate genes showed that nine indeed affected aggressive behavior. In a screen of 170 *Drosophila*

P-element insertional mutations for quantitative differences in aggressive behavior, Edwards et al. (2009b) identified 59 mutations in 57 genes that affected aggressive behavior, none of which had been previously implicated to affect aggression. Thirty-two of these mutants exhibited increased aggression, while 27 lines were less aggressive than the control. Most of the mutations had pleiotropic effects on other complex traits (Edwards et al., 2009b). Mapping QTL affecting variation in aggression between two wild-type *Drosophila* strains, Edwards and Mackay (2009) identified a minimum of five QTL with extensive epistasis in a genomewide scan. In *D. melanogaster*, a systems genetics approach with mutational analyses together with genome-wide transcript analyses, artificial selection studies, and genome-wide analysis of epistasis revealed that a large segment of the genome contributes to the manifestation of aggressive behavior with widespread epistatic interactions (Anholt & Mackay, 2012). Combining gene expression profiling, behavioral analyses, and pharmacological manipulations, Filby et al. (2010) identified candidate genes and pathways that appear to play significant roles in regulating aggression in the zebrafish (*Danio rerio*), an animal model in which social rank and aggressiveness tightly correlate. The patterns of differentially-expressed genes between dominant and subordinate males implied multifactorial control of aggression in zebrafish, including the hypothalamo-neurohypophysial-system, serotonin, somatostatin, dopamine, hypothalamo-pituitary-interrenal, hypothalamo-pituitary-gonadal and histamine pathways (Filby et al., 2010). Comparing the genome-wide profiles of chicken brain samples from aggressive and receiver hens in a pecking hierarchy, Buitenhuis et al. (2009) observed that there were 40 differentially expressed genes. In rodents, maternal defense behavior (maternal aggression) involves attacks against intruders by lactating females that are hypothesized to protect the offspring from potential harm (Wolff, 1993; Agrell et al., 1998; Gammie & Lonstein, 2005). Gammie et al. (2007) identified ~200 genes that were differently expressed in the continuous portion of the CNS (including preoptic and hypothalamic regions) between a line of mice selected

for high maternal aggression relative to a nonselected control line. At least 39 genes have been associated with some aspects of offense in mice and humans (Maxson, 1999; 2009; Liu et al., 2014). To provide a broader view of gene-environment interaction, a recent study examined the relationship between 403 genetic variants from 39 aggression-related genes (Miczek et al., 2001; Maxson & Canastar, 2003; Maxson, 2009) and youth delinquency and violence (Liu et al., 2014). Low social control was associated with greater genetic risk for delinquency and violence and high/moderate social control with smaller genetic risk for delinquency and violence. A key implication of these findings is that the expression of multiple genes related to delinquency depends on the social environment: gene expression is likely to be amplified in low-social-control environments but tends to be suppressed in high/moderate-social-control environments (Liu et al., 2014). Intriguingly, microsatellite length polymorphisms marking regulatory variation of gene expression appear to be associated with divergent social structure and sociobehavioral traits, including aggression and dispersal propensity development, in various mammals (Trefilov et al., 2000; Hammock & Young, 2004, 2005; Krackow & König, 2008).

### 11.2 Insulin/IGF-like signaling pathways

Reproduction is an energetically costly process and its linkage to nutrient sensing is evolutionarily conserved (Hietakangas & Cohen, 2009; Jasper & Jones, 2010). Insulin-like and TOR signaling are the metazoan organisms' monitors of resource utilization. Insulin signaling is a conserved pathway in all metazoans (Barbieri et al., 2003; Piper et al., 2008). Insulin, insulin-like growth factor (IGF) and insulin/IGF-like signaling (IIS) evolved with the appearance of multicellularity, allowing primordial metazoans to respond to a greater diversity of environmental signals. The IIS pathway is split into two complementary and interacting subsystems. The functional separation of IGF and insulin signaling that is seen in mammals dates to approximately 600 million years ago, as the two distinct types of molecules are already present in the lower metazoan tunicate phylum (McRory & Sherwood, 1997). Insects have a single insulin/IGF system that may correspond to the ancestor of the dual insulin/IGF system. The pathway has diverse functions in multicellular organisms, and mutations in IIS can affect growth, development, metabolic homeostasis, fecundity and stress resistance, as well as lifespan (Broughton & Partridge, 2009). Insulin and insulin-like messengers signal nutritional status to the reproductive axis and thus regulate reproductive functions such as maturation and gametogenesis in

nematodes (Heininger, 2012), insects (Riehle & Brown, 1999; Drummond-Barbosa & Spradling, 2001; LaFever & Drummond-Barbosa, 2005; Richard et al., 2005; Tu et al., 2005; Narbonne & Roy, 2006; Hsu & Drummond-Barbosa, 2009), fishes, birds, and mammals (Heininger, 2012). Both at the gonadal and CNS/hypothalamic level, the insulin/IGF system is involved in energy homeostasis, germ cell maturation and reproductive processes in all invertebrate and vertebrate taxa (Brüning et al., 2000; Burks et al., 2000; Lackey et al., 2000; Narbonne & Roy, 2006; Jasper & Jones, 2010). In the honeybee, differential feeding of queen- and worker-destined larvae by nurse bees in the early larval stages triggers a major endocrine response, marked by pronounced differences in the hemolymph juvenile hormone (JH) titer (Rachinsky et al., 1990; Hartfelder & Engels, 1998), as well as in IIS and TOR signaling pathways (Wheeler et al., 2006; Patel et al., 2007; Azevedo & Hartfelder, 2008). JH and ecdysteroid production are dependent on IIS (Riehle & Brown, 1999; Tatar et al., 2001; Tu et al., 2002, 2005; Wu & Brown, 2006), and, in addition, the IIS controls fertility by autonomous effects on the ovaries (Richard et al., 2005). JH shows higher titers during the fourth to fifth instar in queen-destined larvae (Rachinsky & Hartfelder, 1990; Rachinsky et al., 1990). JH affects ovary differentiation from the third larval instar until the onset of metamorphosis: high JH titers in queen larvae prevent autophagic programmed cell death in the ovary (Schmidt Capella & Hartfelder, 2002), thus sustaining tissue survival and differentiation into the large queen ovaries, whereas low JH titers in worker larvae cannot inhibit programmed cell death, which removes 95–99% of the ovariole primordia and leads to the small worker-type ovaries. Functionally, JH application induces queen-like traits in larvae fed a restricted diet (Goewie, 1977; Rembold et al., 1974).

Current evidence indicates that caste development in honeybees involves a complex interaction network composed of the IIS/TOR/epidermal growth factor receptor pathways, JH and ecdysteroids (Wang et al., 2013), which are classic developmental and reproductive hormones in *Drosophila* (Mirth & Riddiford, 2007) and other insect species (Chapman, 1998). Studies of eusocial bees, wasps, ants and termites have shown that nutritional physiology and some conserved nutrient signalling pathways, especially the insulin and TOR pathways, also regulate the division of labor between queens, foraging and non-foraging individuals (Wheeler et al., 2006; Patel et al., 2007; Ament et al., 2008; Azevedo & Hartfelder, 2008; Okada et al., 2010; Azevedo et al., 2011; Daugherty et al., 2011; Mutti et al., 2011;

Wolschin et al., 2011; Hattori et al., 2013; Shao et al., 2014). Developing queens show upregulation of several IIS genes (Wheeler et al., 2006), and knockdown of the bee orthologue of the IIS gene TOR by RNAi blocks queen development (Patel et al., 2007). Wang et al. (2013) performed a functional study on insulin-like peptide genes (AmILP1 and AmILP2) in honeybee larvae by using a double-stranded RNA (dsRNA)-mediated gene knockdown approach and found that JH levels were diminished by AmILP1 dsRNA treatment, while the AmILP2 knockdown caused a reduction in ovary size. During reproductive differentiation in late oogenesis of the queenless ponerine ant, *Diacamma* sp., IIS pathways are expressed in nurse cells, oocytes, and upper germarial regions of reproductives but not of workers (Okada et al., 2010). In insects, insulin-like peptides are produced by a specialized cell cluster in the brain and mediate a direct and positive long-range effect on ovarian activity (Cao & Brown, 2001; Riehle et al., 2006). Transcriptomics data from the brain of a social wasp demonstrated that the brain of the queen expresses much higher levels of the insulin-like peptide2 than that of the workers (Toth et al., 2007).

Queen-produced pheromones that maintain worker sterility are thought to be taxonomically widespread, as queens, their eggs and queen-derived chemicals have been shown to reduce or eliminate worker reproduction (Vargo, 1992; Peeters et al., 1999; Dietemann et al., 2003; Hoover et al., 2003; Cuvillier-Hot et al., 2004a; Endler et al., 2004; Monnin, 2006; Dengler-Crish & Catania, 2007; Korb et al., 2009; Bhadra et al., 2010; Holman et al., 2010a, 2010b). Programmed cell death is observed in the ovary of workers inhibited by pheromones of queen and brood (Schmidt Capella & Hartfelder, 1998). Some workers dramatically increase the activity of their ovarioles in the absence of the queen indicating that signals from the queen, either directly or indirectly, suppress IIS and its effect on JH activity in the workers (Plettner et al., 1993; Arnold et al., 1994; Winston & Slessor, 1998; Khila & Abouheif, 2010). Intriguingly, sufficient doses of honeybee queen mandibular pheromone suppressed solitary *Drosophila melanogaster* ovaries in much the same way as it suppresses bee worker ovaries. Exposed fruit flies showed a reduction in ovary size, produced fewer eggs, and generated fewer viable offspring, relative to unexposed controls, indicating that phylogenetically distant solitary and social insects share regulatory pathways associated with female reproduction (Camiletti et al., 2013, 2014). These findings gain plausibility by the recent evidence of putative orthologues of cuticle forming enzymes in *Drosophila*

*melanogaster* and *Apis mellifera* (Wang et al., 2014) and of a striking, ~145-million-year-long conservation of nonvolatile, saturated hydrocarbons (HC) as queen pheromone fertility signals (Van Oystaeyen et al., 2014). In *D. melanogaster*, long-chain HC on the adult fly cuticle are perceived by contact or at a short distance by other flies (Jallon, 1984; Ferveur, 2005), are thought to be related to ovarian activity (Cuvillier-Hot et al., 2001; Liebig et al., 2009; Peeters & Liebig, 2009; Ferveur & Cobb, 2010; Liebig, 2010; Fedina et al., 2012) and IIS signaling (Richard et al., 2005; Fedina et al., 2012) and the large bouquet of HC is affected by mating (Everaerts et al., 2010). There is cumulative evidence that queen-worker pheromone communication is a multicomponent, labile dialog between the castes, rather than a simple, fixed signal-response system (Kocher & Grozinger, 2011) that is independent of genetic relatedness and even works across large phylogenetic distances.

## 12. The neurobiology of social interactions

### Summary

**Neurobiological signal systems are pleiotropic; social and asocial effects are context-specific and dynamic. The neurotransmitters serotonin,  $\gamma$ -aminobutyric acid, noradrenaline and dopamine, the steroids corticosteroids, testosterone and estradiol, and the peptides oxytocin and arginine vasopressin have established effects on animal and human social behaviors. There appears to be marked conservation in the molecular mechanisms regulating social behavior across diverse species. However, species and gender differences in receptor distribution and density may contribute to species/gender differences in the effects of neurotransmitters and neurohormones on behavior. Particularly, homologs of oxytocin and vasopressin play a general role in the modulation of social and reproductive behaviors in such diverse organisms as hydra, worms, insects, and vertebrates. Maternal brood care is the nucleus of any complex sociality. There is a continuum of neurobiological processes regulating maternal behavior, pair bonding and social behaviors. Intriguingly, closely related vole species differ in oxytocin and vasopressin signaling in a gender-specific fashion with profound consequences for pair bonding and sociality. Social experiences occurring during postnatal, juvenile, and in some cases, early adulthood impact on several neurobiological**

**systems with long-term, even transgenerational consequences on sociality. Like the vertebrate neurohormonal system, insect endocrine systems are plastic in response to the social environment. Both theory and empirical evidence suggest that the origin of hymenopteran worker behavior lies in parental care redirected towards siblings. From a neurobiological and physiological point of view it appears as if in workers brood care, and division of labor have taken the role of a substitute or surrogate reproductive activity.**

The term “sociality” encompasses a wide diversity of behaviors that do not evolve in a linked fashion across species. Thus grouping, monogamy, paternal care, cooperative breeding/alloparental care, and various other forms of social contact are evolutionarily labile and evolve in an almost cafeteria-like fashion, indicating that relevant neural mechanisms are at least partially dissociable (Goodson, 2013). However, there is one constant: not a single more complex social system (I exclude the temporary, targeted, alliances such as swarms or herds as anti-predator defense) evolved without maternal care as the core social relationship within these social groups. Hormones often are the proximate mechanisms by which social traits critical to life-history trade-offs are expressed, and can be helpful in gaining insights into ultimate function (van Anders et al., 2011). The social behaviors are clearly opposed to the ancient self-preservative behaviors. When these balanced social interactions are disturbed, e.g., by a stressor, the self-preservative, fight-flight response pattern takes priority (Henry & Wang, 1998). Evolutionary theories of pair bonds highlight the similarity of these types of bonds and those that exist between parents and offspring; both include attachment, intimacy, and overlapping hormonal mechanisms (Carter, 1998). Given that parent-offspring bonds are likely to be evolutionarily older, pair bonds may be predicated upon a neuroendocrine system that evolved to support parent-offspring bonds, but in general promotes nurturance (Fisher, 1992; Carter, 1998; Fernandez-Duque et al., 2009).

### 12.1 Vertebrates

The neurotransmitters serotonin,  $\gamma$ -aminobutyric acid, noradrenaline and dopamine, the steroids corticosteroids, testosterone and estradiol, and the peptides oxytocin and arginine vasopressin have established effects on animal and human social behaviors (Miczek et al., 2002; Kosfeld et al., 2005; Donaldson & Young, 2008; Heinrichs et al., 2009; Ebstein et al., 2010; Bos et al., 2012; McCall & Singer, 2012). Social behavior is affected by a variety of

factors, e.g. environmental conditions acting through sensory inputs, the hypothalamic-pituitary-gonadal axis, the hypothalamic-pituitary-adrenal stress response axis (Gordon et al., 2011), and genetics (Ebstein et al., 2010). Studies in rodents suggest that the neurohypophysial hormones in concert with steroids are key components in the central mediation of complex social behaviors, including affiliation, parental care, sexual behavior, mate guarding, and territorial aggression (Gimpl & Fahrenholz, 2001; Insel, 2010). Abundant evidence exists for hormonal control of aggression (Koolhaas et al., 1990; Ferris et al., 1997), partner preference (Arletti et al., 1992; Insel & Young, 2001), maternal bonding and affiliative behavior (Kendrick, 2000; Lim & Young, 2006; Neumann, 2008; Ross & Young, 2009; Insel, 2010), trust (Kosfeld et al., 2005; Zak et al., 2005; Baumgartner et al., 2008), and social status (Winslow & Insel, 1991; Sapolsky, 2004). From the huge amount of neurobiological data, only a limited selection will be used to outline some general patterns.

Particularly, aggression is amenable to experimental investigation. Both the serotonergic and dopaminergic systems influence aggressive behaviors in both mammals and birds (Nelson & Chiavegatto, 2001; Van Hierden et al., 2002; Kjaer et al., 2004). Elevated CNS serotonin levels lead to decreased aggression in many different species (Asberg et al., 1987; Linnola & Virkkunen, 1992; Chiavegatto & Nelson, 2003), while high dopamine levels are associated with aggression and dominance behavior (van Erp & Miczek, 2000; Ryding et al., 2008). Both human and animal studies have also identified the GABAergic system (de Almeida et al., 2004, 2005; Gourley et al., 2005), the noradrenergic system (Miczek & Fish, 2005) and the glutamatergic system, particularly N-methyl-D-aspartate (NMDA) receptors (Belozertseva & Bernalov, 1999; Duncan et al., 2004, 2009), to be related to cognitive-behavioral performance and social interaction, including prosocial, antisocial, and aggressive behaviors (Comai et al., 2012). Observations in several species indicate a role for serotonin in the modulation of prosocial behavior (Wood et al., 2006). Investigation of both peripheral and central indices of serotonin function have shown negative associations with violent and aggressive behavior in rhesus monkeys (Higley et al., 1992, 1996) and human clinical samples (Brown et al., 1979; Virkkunen et al., 1994), as well as positive associations with socially affiliative behaviors (such as grooming and approach) (Raleigh et al., 1981). Pharmacological interventions that increase serotonergic activity also attest to a prominent role in important aspects of social behavior and aggression

(Fuller, 1996). The selective serotonin reuptake inhibitor fluoxetine, increases affiliative behaviors in rodents (Knutson & Panksepp, 1996), while each of fluoxetine, quipazine (a 5-HT<sub>1</sub> and 5-HT<sub>2</sub> receptor agonist), and the amino-acid serotonin precursor, L-tryptophan, have been found to increase affiliative behaviors and decrease nonsocial behaviors (such as vigilance and avoidance) in primates (Raleigh et al., 1985). In humans, serotonin promotes social cooperation (Wood et al., 2006).

A number of studies indicate that the serotonin and dopamine systems interact closely at a basic neurophysiological level (Wong et al., 1995; Kapur & Remington, 1996; Daw et al., 2002; Seo et al., 2008). These general actions, however, are modulated by receptor subtypes and their brain regional variation (Cologer-Clifford et al., 1997; Nelson & Chiavegatto, 2001; Olivier, 2004; de Almeida et al., 2005; de Boer & Koolhaas, 2005; Nelson & Trainor, 2007; Comai et al., 2012). The interaction between low serotonin and high testosterone levels in the central nervous system has a significant effect on the neural mechanisms involved in the expression of aggressive behavior (Birger et al., 2003). Testosterone is associated with social aggression in a wide range of species, affecting such behaviors as mate guarding, territorial and dominance aggression (Mazur & Booth, 1998; Nelson & Trainor, 2007). By contrast, testosterone appears to be less involved in other non-social forms of aggression, such as predatory and anti-predatory aggression (Wingfield et al., 2000). Exposure to embryonic testosterone in birds, in particular, increases aggression and dominance in adults and hence alters fitness, even though embryonic exposure does not affect the levels of testosterone circulating in adults (Partecke & Schwabl, 2008). Testosterone disrupts collaboration by increasing egocentric choices (Wright et al., 2012). The role of testosterone in human social behavior might be best understood in terms of the search for, and maintenance of, social status (Eisenegger et al., 2012). In terms of the stress response, testosterone is traditionally associated with inhibiting the hypothalamic-pituitary-adrenal axis (Handa et al., 1994).

### 12.1.1 Oxytocin/vasopressin

Within vertebrates, a majority of work relating neuropeptides to social behavior has focused on members of the oxytocin/vasopressin family. Homologs of oxytocin and vasopressin existed at least 700 million years ago and have been identified in such diverse organisms as hydra, worms, insects, and vertebrates (Minakata, 2010). Among these distant taxa, oxytocin- and vasopressin-related peptides play

a general role in the modulation of social and reproductive behaviors. In contrast to this apparent conservation in function, the specific behaviors affected by these neuropeptides are notably species-specific (Donaldson & Young, 2008). The mammalian oxytocin (OT) and arginine vasopressin (AVP) nonapeptides, so called for their nine-amino acid composition, differ from each other at only two amino acid positions. OT, AVP, and their respective nonmammalian vertebrate lineages are thought to have arisen from a gene duplication event before vertebrate divergence. Within these lineages, peptides vary by a single amino acid, and their genes are found near each other on the same chromosome. Invertebrates, with few exceptions, have only one OT/AVP homolog, whereas vertebrates have two (Acher et al., 1995; Caldwell & Young, 2006). OT is a very abundant neuropeptide. This became obvious in a study where the most prevalent rat hypothalamic-specific mRNAs were analyzed. OT was found to be the most abundant of 43 transcripts identified (Gautvik et al., 1996). Brain OT receptor (OTR)-mediated actions were shown to be significantly involved in the regulation of a variety of behaviors. A broad variety of behaviors, including maternal care and aggression, pair bonding, sexual behavior, and social memory and support, as well as anxiety-related behavior and stress coping, are modulated by brain OT (Kenrick, 2000; Numan & Insel, 2003; Pedersen, 2004; Lonstein & Morrell, 2007; Campbell, 2008; Neumann, 2008, 2009; Insel, 2010; Anacker & Beery, 2013). While the importance of OT for social functions appears nearly universal, central OTR distribution varies between species and may relate to species-typical social behavior (Insel et al., 1994; Young, 1999; Insel & Young, 2000; Donaldson & Young, 2008). Likewise, there are substantial gender-related differences of both OT and AVP brain innervation (de Vries, 1999). Gender-specific aspects of mammalian social behavior are regulated by the steroid hormones, notably estrogens and progestogens, which determine the expression and distribution of receptors for neuropeptides such as OT and AVP (Dantzer 1998; Kalamatianos et al. 2004).

OT and OT-like hormones facilitate reproduction in all vertebrates at several levels (Gimpl & Fahrenholz, 2001). Peripheral and intracerebroventricular administration of OT reliably leads to maternal behavior in virgin mammals who would ordinarily ignore or attack pups (Pedersen & Prange, 1979; Pedersen et al., 1982; Kendrick et al., 1987; Kendrick, 2000; Francis et al., 2002). Conversely, experimental manipulations that decrease OT levels or block OTR activation within the brain reduce maternal behaviors

(Pedersen et al., 1985; Pedersen & Boccia, 2003; Caldwell & Young, 2006). OT has been shown to play a key role in processes of parent-infant bonding across a range of mammalian species, including rats, prairie voles, sheep, and primates (Kendrick et al., 1987; Holman & Goy, 1995; Kendrick, 2000; Neumann, 2008; Maestriperi et al., 2009). Pregnancy, lactation, maternal behavior and exogenous treatments with estrogen and progesterone increase OT immunoreactivity, OT mRNA expression, OTR mRNA expression and OTR binding in brain areas central for parenting and the reward parents derive from their infants (Ross & Young, 2009). AVP is involved in erection and ejaculation in species including humans, rats, and rabbits (Segarra et al., 1998; Gupta et al., 2008), and it mediates a variety of male-typical social behaviors including aggression, territoriality, and pair bonding in various species. The brain OT system is also involved to a significant extent in female sexual behavior, at least in rats, specifically promoting lordosis behavior in an estrogen-dependent manner. Moreover, in late pregnancy and during lactation, central OT is involved in the establishment and fine-tuned maintenance of maternal care. In addition to maternal care, most lactating mammals show a remarkable level of aggression (with a link to anxiety; Bosch et al., 2005), thus protecting their offspring against potential social threats.

Pair bonding is exclusive to the 3 to 5% of mammalian species that are socially monogamous. Traditional laboratory organisms such as rats and mice, however, do not display mate-based pair bonds. The mammalian genus *Microtus* provides an excellent model for investigating the evolution of social behavior. Rodents of the genus *Microtus* show dramatic species differences in social structure: prairie voles (*Microtus ochrogaster*) exhibit a monogamous social structure in nature with either communal nesting or cooperative breeding (Getz & McGuire, 1997; Roberts et al., 1998), whereas closely related meadow voles (*Microtus pennsylvanicus*) and montane voles (*Microtus montanus*) are solitary and polygamous (Gruder-Adams & Getz, 1985; Shapiro & Dewsbury, 1990). In monogamous prairie voles, both OT and AVP were demonstrated to play a major role in pair bonding in a gender-specific fashion. Although both peptides may facilitate pair-bond formation in either sex (Winslow et al., 1993; Insel & Hulihan, 1995; Cho et al., 1999; Young & Wang, 2004; Young et al., 2010), AVP seems to be more important in males, whereas OT is more critical in females. In male prairie voles, partner loss elicits anxiety-like and depression-like behaviors, disrupts bond-related behaviors, and alters neuropeptide systems that

regulate such behaviors (Sun et al., 2014). Central infusions of OT facilitate (Williams et al., 1994) whereas a selective OTR antagonist inhibits pair-bond formation in female prairie voles (Insel & Hulihan, 1995). Moreover, there are notable differences in OTR distribution patterns among prairie voles and montane voles mainly in the brain region nucleus accumbens (Insel & Shapiro, 1992), and an OTR antagonist applied directly to this region blocks mating-induced partner preference formation (Young et al., 2001). Overexpression of the OTR in nucleus accumbens accelerates partner preference formation in female prairie voles (Ross et al., 2009). Differences in potential regulatory elements in the OTR gene, which could reflect variation in gene expression, have been found between prairie and montane voles (Young et al., 1996). A recent study has found that manipulations of OT activity alter partner-directed social behavior during pair interactions in the pair-bonding primate Black-tufted Marmoset (*Callithrix penicillata*) (Smith AS et al., 2009). In humans, single nucleotide polymorphisms in OTR are also associated with traits reflecting pair-bonding in women (Walum et al., 2012), empathy and stress reactivity (Rodrigues et al., 2009). Repetitive microsatellites mutate at relatively high rates and may contribute to the rapid evolution of species-typical traits. Microsatellites in the cis-regulatory regions of genes may significantly enhance the rate of evolution of gene expression patterns and selectable phenotypic traits (King, 1994; Kashi et al., 1997; Li et al., 2004; Kashi & King, 2006). Vasopressin and the vasopressin 1a receptor (V1aR) have been implicated in social recognition and interaction processes in a variety of species (Ferguson et al., 2002; Bielsky & Young, 2004; Bielsky et al., 2005; Egashira et al., 2007; Donaldson et al., 2010). The V1aR is expressed at higher levels in the ventral forebrain of monogamous than in promiscuous vole species (Insel et al., 1994). Intracerebroventricular injection of a V1a receptor antagonist into male prairie voles abolished their mate preference demonstrating the role of vasopressin and its V1a receptor in this species-specific behavior (Winslow et al., 1993). Individual alleles of a repetitive polymorphic microsatellite in the 5' region of the prairie vole V1aR gene modify V1aR gene expression in vitro. In vivo, this regulatory polymorphism predicts both individual differences in receptor distribution patterns and socio-behavioral traits (Hammock & Young, 2004, 2005). Male prairie voles with the longest DNA microsatellite strings spend more time with their mates and pups than male prairie voles with shorter strings (Hammock & Young, 2005). Transgenic mice that have received the prairie vole V1aR gene affiliate

significantly more with their mated partners (Young et al., 1999). By using viral vector V1aR gene transfer into the ventral forebrain, Lim et al. (2004) substantially increased partner preference formation in the socially promiscuous meadow vole, showing that a change in the expression of a single gene in the larger context of pre-existing genetic and neural circuits can profoundly alter social behavior. In conclusion, a change of affiliative behavior, possibly resulting from the evolutionary history of the species (Getz & McGuire, 1997; Gadagkar, 2004b), had significant consequences for both the mating and social systems of *Microtus ochrogaster* compared to *Microtus pennsylvanicus* and possibly in humans. Both the findings of Sun et al. (2014) and the Young group argue for the joint malleability of the neuropeptide system through environmental and genetic factors.

Another example of behavioral actions of intracerebral OT is the promotion of social memory processes and recognition of conspecifics, as revealed in rats, mice, sheep and voles. OT knockout mice show deficits in social recognition, but normal nonsocial learning and memory abilities (Ferguson et al., 2000; Kavaliers et al., 2003; Takayanagi et al., 2005). These deficits are reversible by OT administration specifically into the central amygdala (Ferguson et al., 2001). OT released in response to social stimuli may be part of a neuroendocrine substrate which underlies the benefits of positive social experiences. In rats, OT exerts potent and long-term physiological antistress effects (Uvnäs-Moberg, 1998) and promotes social affiliation during threatening situations (Bowen & McGregor, 2014). In the highly gregarious zebra finch (Estrildidae: *Taeniopygia guttata*), blockade of nonapeptide receptors by an OT antagonist significantly reduced time spent with large groups and familiar social partners, independent of time spent in social contact. Opposing effects were produced by central infusions of mesotocin (avian OT homologue) (Goodson et al., 2009). Experimental evidence suggests that, in humans, brain OT exerts similar behavioral effects (Kenrick, 2000; Numan & Insel, 2003; Pedersen, 2004; Lonstein & Morrell, 2007; Campbell, 2008; Neumann, 2008). There is also evidence from neuroimaging studies suggesting effects of OT treatment on amygdala activity (Kirsch et al., 2005; Domes et al., 2007a; Petrovic et al., 2008), a brain region known to be of importance for regulation of social behaviors. Exogenously administered OT increases rates of several cooperative behaviors in genetically related meerkats (Madden & Clutton-Brock, 2011). In wild chimpanzees, OT levels were higher after grooming with bond partners compared with nonbond partners regardless of genetic relatedness or

sexual interest (Crockford et al., 2013). In genetically unrelated humans, intranasal OT increases trust (Kosfeld et al., 2005; Baumgartner et al., 2009; Mikolajczak et al., 2010), generosity (Zak et al., 2007), willingness to cooperate (Declerck et al., 2010) and promotes reciprocity (Kosfeld et al., 2005; Baumgartner et al., 2008). However, OT decreases generosity and the adherence to fairness norms in social settings where others are likely to be perceived as not belonging to one's ingroup (Radke & de Bruijn, 2012).

The commonality of pathways and genes suggests a high degree of conservation in the multi-factorial control of aggression between fish, birds and mammals (Miczek et al., 2001; Caldwell et al., 2008; Buitenhuis et al., 2009; Filby et al., 2010). On the other hand, studies on gene expression in the brain have shown that profound differences in phenotype are often associated with only small changes in gene expression (Nisenbaum, 2002). OT is involved in both acute aggressive interactions and lasting dominance relationships (Anacker & Beery, 2013). The peptide is released in the lateral septum during an acute social defeat in rats (Ebner et al., 2000), which can have lasting effects because initial interactions can be remembered for long periods of time, and thus contribute to a stable social dominance hierarchy (Adkins-Regan, 2005). In established hierarchies, something different is observed. Dominant female rhesus macaques have higher levels of serum OT than subordinates (Michopoulos et al., 2011, 2012), and dominant male squirrel monkeys exhibit greater levels of aggression when given OT infusions (Winslow & Insel, 1991). Conversely, subordinate male rats decrease OTR expression in the long-term establishment of dominance roles (Timmer et al., 2011). Dominant male cichlid fish have higher levels of isotocin, the teleost homolog of oxytocin, in the hindbrain (Almeida et al., 2012), and aggressive dominant three-spined sticklebacks have higher levels of isotocin in the brain as well (Kleszczynska et al., 2012). Also the teleost arginine vasotocin (AVT), and its mammalian homologue AVP, have well established roles in aggression and social position across vertebrate taxa (Caldwell et al., 2008). There have been conflicting findings of effects of AVT on aggression in fish (Lema & Nevitt, 2004; Santangelo & Bass, 2006; Filby et al., 2010). This may be because AVT increases aggression in non-territorial (colonial) species and decreases it in territorial species (Caldwell et al., 2008). Even within a single species, AVT can have opposite effects between behavioral phenotypes; AVT increases aggression in non-territorial males but decreases aggression in

territorial males (Semsar et al., 2001; Filby et al., 2010).

### 12.1.2 Hypothalamic-pituitary-adrenal axis

Mounting evidence suggests that corticotropin-releasing factor (CRF), CRF receptors, and the hypothalamic-pituitary-adrenal (HPA) axis may play an important role in social behaviors (Hostetler & Ryabinin, 2013). Plasma corticosteroids rise fast and early in the course of an agonistic encounter between rats (Schuurman, 1980), even before actual aggressive behavior is observed (Haller et al., 1995). There are several reasons to believe that the surge in plasma glucocorticoids caused by the confrontation with a potential adversary plays an important role in the subsequent aggressive conflict. Inhibiting corticosterone synthesis inhibits aggressive behavior (Haller et al., 1996; Mikics et al., 2004), whereas corticosterone treatment administered to metyrapone-treated rats rapidly reinstates aggressive behavior (Mikics et al., 2004). Also, injecting glucocorticosteroids (GC) into the hypothalamus of the golden hamster rapidly facilitates aggression (Hayden-Hixson & Ferris, 1991). A fast, mutual, positive feedback of the controlling mechanisms within the time frame of a single conflict may contribute to the precipitation and escalation of violent behavior under stressful conditions (Kruk et al., 2004). Stress is a major factor promoting aggression and violence in humans (Barnett et al., 1991; Tardiff, 1992). Of all of the enduring effects of GCs, the most profound might be their capacity to alter their own regulation (Martin et al., 2011). In mammals (Weaver et al., 2004), birds (Love et al., 2008), and amphibians (Denver, 2009), stressors early in life alter HPA and OT/AVP pathway regulation throughout life with long-term, even transgenerational, effects on social behavior (Champagne, 2008; Weinstock, 2008; Curley et al., 2011; Bales & Perkeybile, 2012; Veenema, 2012).

The CRF system has also been implicated in prosocial and affiliative behaviors such as parental care, maternal defense, sexual behavior, and pair bonding (Hostetler & Ryabinin, 2013). Low GC levels are also associated with antisocial behavior (Shirtcliff et al., 2009). Acute stress and activation of the HPA axis may increase prosocial behavior (Taylor et al., 2000; DeVries et al., 2002; de Waal & Suchak, 2010; Buchanan et al., 2012; Von Dawans et al., 2012; Buchanan & Preston, 2014). There is neuroanatomical and neurobiological evidence for reciprocal regulation of the HPA and OT systems balancing stress and affect (Dabrowska et al., 2011). In the rat, physical and mental stresses or central administration of CRF evoke an increase in OT secretion while AVP

secretion remains unchanged (Bruhn et al., 1986). OT appears to function as an anxiolytic, suppressing HPA axis function during periods of stress (Smith & Wang, 2012). OT was found to inhibit HPA axis responses to a wide variety of physical, emotional and pharmacological stressors, and may thus make an important contribution to the attenuated stress responsiveness found in pregnancy and during lactation. These neuroendocrine adaptations are mainly reflected by lower peak levels of corticosterone/cortisol and corticotropin in response to acute stressor exposure. In humans, OT administration enhances the stress-alleviating effects of social support (Heinrichs et al., 2003).

Social experiences occurring during postnatal, juvenile, and in some cases, early adulthood impact on social competence later in life (mammals including humans: Bastian et al., 2003; Levy et al., 2003; Margulis et al., 2005; Branchi et al., 2006, 2009; Bester-Meredith & Marler, 2007; Flinn et al., 2011; birds: Adkins-Regan & Krakauer, 2000; Bertin et al., 2009; White et al., 2010; fish: Moretz et al., 2007; Arnold & Taborsky, 2010; Taborsky et al., 2012). This early socialization affects several neurobiological systems, including monoamine (e.g. serotonin and dopamine), GABAergic, glutamatergic, vasopressin, oxytocin, estrogen sensitivity and estrogen receptors, and receptors for CRF and GC, changes that may also extend transgenerationally (Curley et al., 2011). Intriguingly, the hormonal system orchestrating social interactions entertains manifold cross-talk to the metabolic system, particularly insulin (Bobbioni-Harsch et al., 1995; Björkstrand et al., 1996). In the coral reef cleaner fish *Labroides dimidiatus*, pro- and anti-social behaviors are physiological condition-dependent involving metabolic stress response signaling pathways mediated by e.g. cortisol and vasotocin (Bshary, 2002; Bshary et al., 2011; Soares et al., 2012, 2014; Cardoso et al., 2015). These pathways establish the pleiotropic links between resource availability and social behavior (see also chapter 10).

## 12.2 Invertebrates

Like the vertebrate neurohormonal system, insect endocrine systems also respond to social stimuli (Scott, 2006a, b; Tibbetts & Huang, 2010; Tibbetts & Crocker, 2014), hence are plastic in response to the social environment. In eusocial communities, suppression of aggression is an essential aspect of communal life. Queen pheromone modulates brain dopamine (DA) function in young worker honeybees (Beggs et al. 2007; Beggs & Mercer, 2009). A key component of queen pheromone, homovanillyl alcohol, has been found to lower young worker brain DA levels

(Beggs et al. 2007; Beggs & Mercer, 2009). Reducing DA levels, changing receptor expression and activation has been suggested to reduce aggression, stinging, and aversive learning in young bees (the bees closest to the queen, feeding her); this would translate into an increase in both the queen's and the colony's fitness (Vergoz et al., 2007; Wright, 2009). In adult honeybees, aggression is associated with juvenile hormone (JH) titers (Pearce et al., 2001). Older bees, which have higher JH levels (Huang et al., 1994), are generally more aggressive than younger bees with lower JH levels (Breed, 1983). Bees treated with a JH analog exhibited an earlier response to alarm pheromone (Robinson, 1987), and the proportion of bees acting as guards also increased (Sasagawa et al., 1989). Queen pheromones suppress worker JH production (Pankiw et al., 1998). Workers reared in isolation showed higher levels of aggressiveness toward other bees (Breed, 1983), and isolated bees have elevated JH levels compared to bees reared in groups or in a colony (Huang & Robinson, 1992). Guards at the entrance that are less exposed to queen pheromones exhibit low thresholds for the expression of aggressiveness (Breed et al., 1992; Pearce et al., 2001) and JH titers of guards are higher than of all other middle-age bees except undertakers (Huang et al., 1994; Pearce et al., 2001).

The hormonal and neurochemical mechanisms modulating aggression in arthropods seem to be quite varied. In many insects, JH has a role in aggression, dominance and reproduction (Röseler, 1991; Larrere & Couillaud, 1993; Bloch et al., 2000a; Cnaani et al., 2000; Scott, 2006a; Kou et al., 2009; Tibbetts & Izzo, 2009; Tibbetts & Huang, 2010; Tibbetts et al., 2011), but not in crickets (Adamo et al., 1994). The low DA and JH levels in reproductive queenless ants are very different from what has been observed in fire ant queens, which show a rise in DA with the onset of reproduction (Boulay et al., 2001) and have high JH levels when mature (Brent & Vargo, 2003). Pharmacological reduction of JH levels in *Bombus terrestris* workers decreased ovarian activation, irrespective of the bees' dominance rank within the group, an effect that was remedied by JH replacement therapy. Low JH also decreased aggressiveness and increased ester-sterility signal production; these changes were rank-dependent, and affected mainly the most reproductive and the least aggressive workers, respectively, and could not be remedied by JH replacement therapy (Amsalem et al., 2014). Aggressiveness was depressed in crickets depleted of octopamine (a biogenic monoamine structurally related to noradrenaline) and dopamine, and was restored by an octopamine agonist (Stevenson et al.,

2005). Octopamine has also been reported to correlate with dominance and aggressiveness in bumblebees (Bloch et al., 2000b); in fruit flies, octopamine increases aggressiveness and dopamine is negatively correlated (Baier et al., 2002) while serotonin seems to promote aggression in crustaceans (Kravitz, 2000; Kravitz & Huber, 2003).

Queenless ant species have colonies composed exclusively of monomorphic workers, each one capable of mating and laying eggs, forming societies with a more plastic mode of organization (Peeters, 1993). In these colonies, the division of labor depends on interindividual behavioral interactions that determine not only gathering tasks but also more importantly, reproductive roles. Since queenless ant species are restricted by ecological constraints from forming new, independent colonies, their access to reproduction is entirely dependent on their rank in the dominance hierarchy (Cuvillier-Hot & Lenoir, 2006). The potential reproducers in a queenless ant colony form a dominance hierarchy through confrontations. Because castes are determined through behavioral interactions, the social position of individual workers changes frequently and rapidly. *Streblognathus peetersi* is a monogynous queenless ant with colonies organised in three distinct groups: the alpha ant is the most dominant worker and the only one to mate and lay eggs; workers of high social ranks are behaviorally dominant (while submissive to the alpha), are rather young and do not mate or lay eggs; workers of low social ranks are subordinate to the other two groups, can be of any age and also remain infertile. Fertile alpha workers are clearly characterised by higher levels of octopamine; this monoamine, thus, seems to correlate with reproductive activity in *Streblognathus*.

The present results suggest a shift through which DA no longer regulates reproduction but has been co-opted for polyethism regulation in eusocial species. This major physiological transition of the role of DA is similar to the well-documented change in JH activity in honeybees. In insects, JH serves as a gonadotropin to regulate the biosynthesis of vitellogenin and/or its uptake by the developing oocytes (Nijhout, 1994; Gilbert et al., 2000). JH is broadly correlated with fertility, and treatment with JH increases fertility (e.g. Tibbetts & Izzo, 2009; Tibbetts et al., 2011). JH has also a clear gonadotropic role in primitively eusocial species [*Bombus* (Bloch et al., 2000a), *Ropalidia* (Agrahari & Gadagkar, 2003) and *Polistes* (Tibbetts et al., 2011)]. Queens produce a pheromone that inhibits the activity of workers' corpora allata, resulting in low JH titers and thus in restricted ovarian development and inhibition of egg laying (van Honk et al., 1980;

Röseler et al., 1981). Once the queen loses control over her workers, or when the queen dies, the corpora allata of a few dominant workers are reactivated and this allows them to lay eggs and to inhibit the corpora allata of other workers (van Honk et al., 1980; Röseler et al., 1981; van Honk & Hogeweg, 1981). In at least some insects, high JH seems to inhibit parental care (Rankin et al., 1997). However, in many taxa, JH may have no effect or a positive effect on parental care (Mas & Kolliker, 2008; Trumbo, 2002). JH seems to have lost its reproductive function in honeybees, and instead, regulates colony polyethism (Hartfelder, 2000; Robinson & Vargo, 1997). As opposed to the pattern of JH levels in *Bombus*, JH levels in both honeybees and queenless ants are low in reproductive castes (and in honeybee nurses) and high in foragers in both cases (Robinson et al., 1991; Sommer et al., 1993). This double inversion of JH and DA roles suggests that DA in queenless ants plays an allatotropic role, as it does in several species [e.g., *Locusta migratoria* (Lafon-Cazal & Baehr, 1988), *Apis mellifera* (Kaatz et al., 1994; Rachinsky, 1994)]. Both theory and empirical evidence suggest that the origin of hymenopteran worker behavior lies in parental care redirected towards siblings (Wheeler, 1928; Kennedy, 1966; Michener, 1969; Wilson, 1971; Hamilton, 1972; Alexander, 1974; West-Eberhard, 1987; Alexander et al., 1991; Bourke & Franks, 1995; Linksvayer & Wade, 2005; Amdam et al., 2006; Boomsma, 2007; Toth et al., 2006; Boomsma et al., 2011). Taken together it appears as if in workers, from a neurobiological and physiological point of view, brood care, and division of labor have taken the role of a substitute or surrogate reproductive activity.

### 13. The ecology of kin recognition

#### Summary

**Social recognition abilities have evolved for a host of functional reasons. Familiarity as the sole mechanism to determine kin and used as a proxy of relatedness has been shown for diverse organisms and contexts. Cooperation based on genetic cues, on the other hand, would be a conundrum because it requires polymorphic recognition loci, yet cooperation is predicted to erode this genetic variation. In many species, olfactory information provides salient information about species identity, kin, sex, social status, and/or reproductive condition. Nestmate recognition based on cuticular hydrocarbons is common among the eusocial insects. Nestmate**

**recognition cues have a substantial hereditary component but are also modulated by environmental factors that may override genetically based ones. A highly polymorphic major histocompatibility complex (MHC) encodes proteins that target foreign molecules for immune cell recognition. Animals are capable of converting this genetic code into olfactory information that is used for social recognition. The odorants are the same MHC peptides used during immune recognition, which provides the molecular logic linking selection acting on MHC-mediated behaviors with selection acting on immune recognition.**

**Accurate discrimination of conspecifics with regard to genetic relatedness is a crucial prerequisite for nepotistic behaviors (preferential treatment of kin). However, kin discrimination and nepotistic behavior are only rarely associated. Thus, there is no evidence that evolution of kin recognition/discrimination and prosocial behavior are interdependent. This prompts the question whether kin discrimination may serve another purpose. A totalitarian system, such as a unitary metazoan organism or eusocial colony, requires effective means of information and communication and compliant agents that enforce the despotic system. Throughout phylogenesis, allorecognition, the self/nonself discrimination, served the purpose to ensure the reproductive monopoly of the germline and to prevent germline parasitism. The importance of selfish/cheater behavior in the activation of the immune system is demonstrated by the ability of the immune system to tolerate allogeneic cooperative microbiota and fight syngeneic selfish cells (tumors) by responding to "selfish/cheater signals". Thus, similar to metazoan organisms that have evolved systems to control cancer, the evolution of insect societies requires mechanisms to control selfish worker reproduction. There is a nearly perfect analogy of the eusocial nestmate recognition and worker policing systems to the function of the immune system in multicellular organisms.**

Social recognition abilities have evolved for a host of functional reasons (Colgan, 1983; Sherman et al., 1997; Pfennig et al., 1999; Mateo, 2004; Tibbetts & Dale, 2007; Gabor et al., 2012) such as inbreeding avoidance (Sherborne et al., 2007), mate choice (Brown, 1997; Tregenza & Wedell, 2000; Candolin, 2003), mother-offspring recognition (Beecher, 1991; Booth & Katz, 2000), dominance hierarchies (Barnard & Burk, 1979; d'Ettorre & Heinze, 2005; Gherardi & Atema, 2005), and territory establishment and defense

(Temeles, 1994; Tibbetts & Dale, 2007; Grether, 2011). Visual, olfactory and auditory cues are prominent in many cognitive systems. Kin recognition, the differential treatment of conspecifics varying in genetic relatedness, has been documented in multiple animal and plant taxa (Fletcher & Michener, 1987; Waldman, 1988; Hepper, 1991; Pfennig & Sherman, 1995; Penn & Frommen, 2010). Familiarity as the sole mechanism to determine kin and used as a proxy of relatedness has been shown for diverse organisms and contexts (Schausberger, 2007): Association attractiveness among salmon varies with familiarity and odor concentration (Courtenay et al., 2001), guppies choose shoal mates based on familiarity (Griffiths & Magurran, 1999), familiar piglets show less aggressiveness than unfamiliar ones irrespective of genetic relatedness (Stokey & Gonyou, 1998), juvenile sticklebacks compete less with familiar individuals without any indication that genetic relatedness plays a role (Utne-Palm & Hart, 2000), and penguin chicks discriminate between familiar and unfamiliar calls but not between calls of familiar kin and nonkin (Nakagawa et al., 2001). On the other hand, there is no evidence for the use of **genetically** determined recognition cues or templates (Komdeur et al., 2008). Kin discrimination as a means to perceive certainty of paternity cannot be exerted by birds (Kempnaers & Sheldon, 1996; DeWoody et al., 2001; Sheldon, 2002; Komdeur et al., 2004) and fish (Svensson et al., 1998). A simple spatially based recognition rule, such as 'feed anything in my nest or territory', is widespread and successfully exploited by bird species that are brood parasites or in which extrapair paternity occurs (Komdeur & Hatchwell, 1999; Aktipis & Fernandez-Duque, 2011). In other bird species (e.g. dunlocks, *Prunella modularis* and alpine accentors, *Prunella collaris*) males use indirect cues and behavioral 'rules of thumb', adjusting their parental care based on the amount of attempted extrapair copulations or exclusive sexual access they had to the female, which correlates with degree of paternity (Burke et al., 1989; Davies et al., 1992; Hartley et al., 1995; Ewen & Armstrong, 2000). There is a continuum of social behavior in spiders from small subsocial mother-offspring-sibling groups to complex, cooperative societies of thousands of individuals (Buskirk, 1981; Avilés, 1997; Lubin & Bilde, 2007). Most social spiders, despite multiple evolutionary origins, share a suite of traits that includes the acceptance of alien spiders (unrelated and unfamiliar conspecifics) into the group without overt aggression (Lubin & Bilde, 2007). These social spider species do not appear to differentiate between conspecific aliens and members of their own colony

(Pasquet et al., 1997; but see Yip et al., 2009), between silk from kin or nonkin (Bilde et al., 2002; Buser, 2002), or even between heterospecific from conspecific spiders in the same genus (Seibt & Wickler, 1988).

Ever since Hamilton (1964) proposed his concept of kin selection to explain social evolution and the evolution of “altruistic” behaviors, there has been a strong interest in kin recognition and the mechanisms by which animals may be able to distinguish between their kin (genetically-related individuals) and nonkin (genetically-unrelated individuals) (e.g., Holmes & Sherman, 1983; Sherman & Holmes, 1985; Waldman, 1988; Waldman et al., 1988; Hepper, 1991; Sherman et al., 1997; Neff & Gross, 2001; Tang-Martinez, 2001; Krupp et al., 2011). However, Hamilton later modified his thinking to suggest that an innate ability to recognize actual genetic relatedness was unlikely to be the dominant mediating mechanism for kin altruism: “But once again, we do not expect anything describable as an innate kin recognition adaptation, used for social behaviour other than mating...” (Hamilton 1987, p. 425).

The prevailing categorization lists four different mechanisms of ‘kin recognition’: (i) spatially based recognition; (ii) association or familiarity; (iii) phenotype matching (Hauber & Sherman, 2001); and (iv) recognition alleles, *sensu* Hamilton (1964). The classical mechanisms of kin recognition have been criticized (Fletcher, 1987; Waldman, 1987; Waldman et al., 1988; Barnard, 1990). As Grafen (1990) pointed out, the conclusions that can be drawn when an animal is observed to behave differently on first encounter towards differently related groups of conspecifics are limited. We can conclude that individuals are able to detect some feature of conspecifics or their environment which correlates with their genotype, but it does not necessarily follow that this ability has evolved to distinguish kin from nonkin or has anything to do with kin selection (Grafen, 1990). Thus, although there are undoubtedly many examples of kin bias (e.g. cooperative breeding in certain bird species), only those involving recognition of relatedness *per se* (i.e. genetic similarity), with the purpose of biasing responses towards relatives (kin discrimination), deserve the label ‘kin recognition’ (Grafen, 1990, 1991; Barnard, 1991; Barnard et al., 1991). Barnard (1999) argued that the four categories of recognition mechanisms are not helpful for two reasons: first they do not constitute a set of mutually exclusive alternatives (Fletcher, 1987; Waldman, 1987), and second they confuse questions about the development and expression of traits indicating

genetic similarity with those about the processes of perceiving and acting upon this information (Fletcher, 1987; Waldman, 1987; Barnard, 1990).

Cooperation based on genetic cues, if it exists, would be a conundrum because it requires polymorphic recognition loci, yet cooperation is predicted to erode this genetic variation (e.g. Crozier, 1986; Grosberg & Quinn, 1989; Tsutsui, 2004; Gardner & West, 2007; Rousset & Roze, 2007; Boomsma & d’Ettorre, 2013; Holman et al., 2013). This problem, sometimes termed Crozier’s paradox, applies whenever individuals with common recognition cues receive greater average fitness returns from social interactions. Crozier pointed out that those individuals bearing a common marker more readily enter into social interactions, and hence enjoy a higher reproductive success than those individuals bearing rare markers. Disproportionate fitness benefits for individuals with common recognition alleles should produce positive frequency-dependent selection at recognition loci, depleting the genetic variance necessary for kin recognition (Holman et al., 2013). Thus, already common markers become more common still, and eventually all individuals carry the same marker. At this point, it fails to be diagnostic of kinship, and there has been a breakdown of kin recognition. Alexander and Borgia (1978) pointed out that “fixation for ‘genetic recognition’ alleles would lead to rather uniform distribution of benefits to all interactants, and relatives would be preferred only while such traits were on their way to fixation. Such systems could account for variations in nepotistic behavior associated with social structure only if there is (a) rapid recurrence of mutations leading to genetic recognition or (b) common association with disadvantageous characters through either pleiotropy or linkage. The first condition is unlikely because of the necessity of complex recognition mechanisms, and there is no reason to expect the second.” On the other hand, theoretical models suggest that many recognition loci likely have some primary function such as histocompatibility or inbreeding avoidance that is subject to diversifying selection, keeping them variable (Holman et al., 2013). Overall, genetic kin recognition is inherently unstable, explaining its rarity (Gardner & West, 2007).

### 13.1 Kin recognition by olfactory cues

In many species, olfactory information provides salient information about species identity, sex, social status, and/or reproductive condition (Brown, 1979; Halpin, 1986; Johnston, 2003; Wyatt, 2003; Kavaliers et al., 2005). Members of vertebrate species commonly use olfactory signatures to distinguish between individual members and to denote various subgroups, including

the recognition of kin versus nonkin (Porter, 1998; Yamazaki et al., 1999, 2000; Mateo, 2002; Reynolds & Sheldon, 2003). Kin recognition is triggered by olfactory cues in a variety of vertebrates (e.g. Porter et al., 1978; Holmes 1984; Quinn & Busack, 1985; Waldman, 1985; Todrank et al., 1998; Gerlach et al., 2008; Mehlis et al., 2008; Bonadonna & Sanz-Aguilar, 2012; Krause et al., 2012). Several of these species do not form cooperative alliances with their kin. Olfactory cues appear to be important in kin recognition mechanisms as they function to facilitate inbreeding avoidance and the attainment of optimal outbreeding (e.g., in mice, Gilder & Slater, 1978; D'Udine & Partridge, 1981).

### 13.1.1 Hydrocarbons as olfactory cues in nestmate recognition

Nestmate recognition is common among the eusocial insects (Wilson, 1971; Singer & Espelie, 1992; Clément & Bagnères, 1998; Vander Meer & Morel, 1998; Strassmann et al., 2000; Tapy et al., 2004). Eusocial insects commonly rely on olfactory cues for making social discriminations. The olfactory pathway of Hymenoptera is well investigated (Kirschner et al., 2006; Zube et al., 2008; Kleineidam & Rössler, 2009; Galizia & Rössler, 2010; Nakanishi et al., 2010). For example, all annotated ant, bee and wasp species have several-fold more odorant receptors than most solitary insects, suggesting that enhanced olfactory abilities may contribute to complex social organization (LeBoeuf et al., 2013).

The most studied, and probably the most widespread, intracolony chemical messengers are cuticular hydrocarbons (Richard & Hunt, 2013). Insects cover their cuticles with a complex mixture of organic chemicals that is thought to have evolved to protect against desiccation and/or to prevent microbial infection (Gibbs, 2002; Howard & Blomquist, 2005). These chemicals are predominantly hydrocarbons, though substances such as wax esters, aldehydes, ketones, sterols and alcohols are also often found (Lockey, 1988; Copren et al., 2005; Monnin, 2006; van Wilgenburg et al., 2011). Many of these cuticular chemicals have been evolutionarily co-opted to function in communication, and, as signals for species-, gender-, and mate-recognition, dominance and fertility cues, have pivotal roles in the social lives of their bearers (Howard & Blomquist, 2005; Blomquist & Bagnères, 2010; Babis et al., 2014). In eusocial insects these cuticular hydrocarbons have been co-opted to function in recognition and are perceived by other individuals by direct antennal contact or at a short distance (Cuvillier-Hot et al., 2005; Brandstaetter et al., 2008). The pattern of cuticular hydrocarbons

can be complex and dynamic, with many compounds varying both qualitatively (different species typically have different compounds) and quantitatively (different colonies of the same species have different relative proportions of the same hydrocarbons) (Guerrieri et al., 2009). In ants (Beye et al., 1998; Lahav et al., 1999; Wagner et al., 2000; Roulston et al., 2003; Martin et al., 2008), bees (Paxton et al., 1999), wasps (Dani et al., 2001; Ruther et al., 2002) and termites (Polizzi & Forschler, 1999; Weil et al., 2009) the determination of self versus nonself in the context of nestmate recognition is frequently based on the expression of cuticular hydrocarbon profiles (Liang et al., 2001; Suarez et al., 2002; Blomquist & Bagnères, 2010). Nestmate recognition cues have a substantial hereditary component (van Zweden et al., 2009, 2010) but are also modulated by environmental factors. Three major sources of nestmate recognition cues are identified as: (i) queen dominant (Carlin & Hölldobler, 1983, 1986); (ii) worker-produced (Stuart, 1988; Soroker et al., 1994; Dahbi & Lenoir, 1998; Lahav et al., 1998; van Zweden & d'Ettorre, 2010), and (iii) environmentally derived (Obin, 1986; Crosland, 1989; Heinze et al., 1996). These chemicals may then be distributed throughout the membership of the colony via allogrooming and trophallaxis resulting in a colony-specific odor blend or "gestalt" (Crozier & Dix, 1979; Crozier, 1987; Dahbi & Lenoir, 1998).

The presence of the queen's pheromones that serve as recognition cues can influence nestmate recognition and intraspecific interactions in several ant species (Carlin & Hölldobler, 1987; Provost, 1987; Keller & Passera, 1989; Lahav et al., 1998; Vander Meer & Alonso, 2002). In orphaned *Solenopsis invicta* colonies, worker aggression toward non-nestmate conspecifics drops (but still exists with interspecific interactions) and re-establishes following acceptance of a newly mated queen (Vander Meer & Alonso, 2002). The new queen exposes workers to her queen primer pheromone, the level of which correlates with workers' sensitivity to colony-level differences in cuticular hydrocarbons. Increased sensitivity is linked to higher levels of octopamine in workers' brains of queenright colonies compared with orphan colonies (Vander Meer et al., 2008). However, the presence of the queen does not influence nestmate recognition cues in several other ant species (Boulay et al., 2004; Caldera & Holway, 2004; Richard et al., 2004; van Zweden et al., 2009).

Sources for environmental cues include diet (Gamboa et al., 1986; Obin & Vander Meer, 1988; Crosland, 1989; Le Moli et al., 1992; Liang & Silverman, 2000; Silverman & Liang, 2001; Florane et al., 2004; Richard

et al., 2004; Buczkowski et al., 2005; Sorvari et al., 2008) nesting substrate (Jutsum et al., 1979; Crosland, 1989; Heinze et al., 1996; Richard et al., 2007) and abiotic conditions (Wagner et al., 2001). Environmental cues may override genetically based ones (Gamboa et al., 1986; Bennett, 1989; Beye et al., 1997, 1998; Downs & Ratnieks, 1999). Due to their strong environmental modulation, cuticular hydrocarbons do not appear to be an optimal choice as a tool for genetic kin recognition. Thus, within-colony kin discrimination does not appear to be an important factor organizing honeybee societies (Breed et al., 1994; Keller, 1997; Kryger & Moritz, 1997; Underwood et al., 2004; Rangel et al., 2009). Likewise, studies of ants (Carlin et al., 1993; Snyder, 1993; DeHeer & Ross, 1997; Holzer et al., 2006; vanWilgenburg et al., 2007; Zinck et al., 2009; Kellner & Heinze, 2011; Friend & Bourke, 2012), wasps (Queller et al., 1990; Strassmann et al., 1997, 2000b; Solís et al., 1998; Goodisman et al., 2007), termites (Clément & Bagnères, 1998; Kitade et al., 2004; DeHeer & Vargo, 2006; Atkinson et al., 2008), and aphids (Aoki et al., 1991; Foster & Benton, 1992; Miller, 1998; 2004; Shibao, 1999) failed to demonstrate within-colony kin discrimination. In ant colonies, “workers are able to discriminate between nestmates and intruders, but they also tend to treat all nestmates as colony members, regardless of the degree of relatedness” (Hölldobler & Wilson, 1990, p. 197). Virtually all recognition studies involve between-colony discrimination (nestmate recognition) (Torres et al., 2007; Brandt et al., 2009; Guerrieri et al., 2009; van Zweden & d’Ettorre, 2010) instead of within-colony discrimination (kin recognition) (Vander Meer & Morel, 1998). However, comparison of two allodapine bees, the highly eusocial allodapine *Exoneurella tridentata* and the facultatively social *Exoneura robusta*, using a standardised circle-tube apparatus found that (i) discrimination between nestmates and non-nestmates was much more strongly expressed in the facultatively social species and (ii) principal components analyses did not indicate suites of behaviors that permit clear interpretations as being agonistic, cooperative, or avoidance (Dew et al., 2014). The authors concluded that nestmate recognition is not an essential ability for social species (Dew et al., 2014).

Social parasites are able to break the hydrocarbon code and integrate into the normally closed colony of a social insect (Lenoir et al., 2001; Nash & Boomsma, 2008; Bagnères & Lorenzi, 2010; van Zweden & d’Ettorre, 2010). Social parasite species can use either chemical camouflage (recognition cues are acquired from its host) or chemical mimicry (recognition cues are synthesized by the parasite), or a combination of

both (Lenoir et al., 2001). However, the result is the same: they overcome detection as non-nestmates. The staphylinid termitophile beetles *Trichopsenius frosti*, *T. depressus*, *Xenistusa hexagonalis*, and *Philoterme howardi* are guests in termite nests and were found to have hydrocarbon profiles similar to those of their respective hosts (Howard et al., 1980, 1982). Similarly, the paper wasp *Polistes atrimandibularis* is an obligate social parasite of another paper wasp, *P. biglumis bimaculatus*. It was shown that, at the point of the colony life cycle that the parasite needs to integrate into its host colony, the hydrocarbon profile of the parasite changes from one that is characterized by unsaturated hydrocarbons into one that matches the host’s profile: characterized by the same saturated methyl-branched hydrocarbons, without any unsaturated hydrocarbons (Bagnères et al., 1996). Likewise, another paper wasp, *P. sulcifer*, was found to adopt a colony-specific hydrocarbon profile of its host, *P. dominulus* (Sledge et al., 2001). The ant *Polyergus rufescens* can achieve social integration in nests of multiple hosts of the genus *Formica* (subgenus *Serviformica*) by adopting a hydrocarbon profile that is similar to that of their host, even if the experimental host is not a natural host, like *Formica selysi* (d’Ettorre et al., 2002).

Drifting, that is leaving the nest to enter a foreign one, is a surprisingly widespread phenomenon among flying social insects (Free 1958; Jay, 1966; Akre et al., 1976; Kasuya, 1981; Paar et al., 2002; Seppa et al., 2002; Birmingham et al., 2004; Lopez-Vaamonde et al., 2004; Blacher et al., 2013) that may be made possible either by a lack of nestmate recognition or social tolerance of colonies. In *Apis mellifera* drifting can be extensive, with drifters sometimes comprising more than half of the workforce (Free 1958; Jay, 1966; Pfeiffer & Crailsheim, 1998; Neumann et al., 2000, 2001; Chapman et al., 2010). In *Bombus terrestris*, depending on colony orientation, up to 50% of the workforce can be composed of drifters (Lefebvre & Pierre, 2007; Blacher et al., 2013; O’Connor et al., 2013). In a natural population of the eusocial paper wasp *Polistes canadensis* 56% of females drifted (Sumner et al., 2007). For *Bombus occidentalis* and *Bombus impatiens*, an average of 28 % of workers was discovered to be drifters (Birmingham & Winston, 2004).

### 13.1.2 Histocompatibility polymorphism

Allorecognition—the ability of an individual organism to distinguish its own tissues from those of another—has been described in all uni- and multicellular phyla (Burnet, 1971), including bacterial self/non-self recognition systems (Gibbs et al., 2008; Budding et al.,

2009), kin discrimination in social amoebae (Ostrowski et al., 2008; Benabentos et al., 2009), fungal mating types and heterokaryon incompatibility (Buss, 1982; Glass et al., 2000; Fraser & Heitman, 2003, 2004; Idnurm et al., 2008), and plant self-incompatibility systems (Takayama & Isogai, 2005). For example, self/nonself discrimination and social recognition has been reported in bacteria *Myxococcus xanthus* (Fiegna & Velicer, 2005; Vos & Velicer, 2009), *Proteus mirabilis* (Pfaller et al., 2000; Gibbs et al., 2008) and *Pseudomonas aeruginosa* (Munson et al., 2002). In the ascidian *Botryllus schlosseri*, histocompatibility assays between randomly collected colonies suggest the presence of a highly polymorphic locus with hundreds of different allotypes (Karakashian & Milkman, 1967; Mukai & Watanabe, 1975; Scofield et al., 1982a, b; Grosberg & Quinn, 1986; Rinkevich et al., 1992; Yund & Feldgarden, 1992; Rosengarten & Nicotra, 2011). Sibling planktonic larvae of the sessile colonial settle in aggregations that are much stronger than expected from dispersal distance effects alone. Laboratory experiments indicate that larvae distinguish kin on the basis of shared alleles at the histocompatibility locus known to regulate fusion between adult colonies. This kin recognition mechanism, along with limited dispersal of larvae, promotes co-settlement of histocompatible individuals (Grosberg & Quinn, 1986). Likewise, in the cnidarian *Hydractinia symbiolongicarpus* allorecognition specificity is determined by highly polymorphic cell-surface molecules that control fusion or rejection when colonies grow into contact (Rosengarten & Nicotra, 2011). Allorecognition systems are thought to have evolved to limit fusion to self or close kin, thereby reducing the potential cost of germline parasitism (Buss, 1982, 1987).

In vertebrates, histocompatibility is a function of the immune system controlled by a highly polymorphic major histocompatibility complex (MHC), which encodes proteins that target foreign molecules for immune cell recognition. The association of the MHC and immune function suggests an evolutionary relationship between metazoan histocompatibility and the origins of vertebrate immunity. The hypothesis that there is a connection between the immune system and social behaviors such as mate choice mediated via olfactory cues is now four decades old (Thomas, 1975). Specifically, it was proposed that the MHC is involved in cell-cell recognition and the adaptive immune response is in addition responsible for the production of characteristic chemical signals in bodily secretions that enable individual recognition in social contexts such as mate or kin recognition by olfaction (Yamazaki et al., 1976; Beauchamp et al., 1985;

Brown & Eklund, 1994; Eggert et al., 1998; Penn & Potts, 1998; Penn, 2002; Leinders-Zufall et al., 2004; Boehm, 2006; Ruff et al., 2012; Overath et al., 2014). The MHC, designated H2 in mice and HLA in humans, is a genomic region on chromosomes 17 and 6, respectively, which harbors the highly polymorphic MHC class I and class II genes as well as many non-polymorphic genes (Murphy, 2012). The MHC is a family of ~50 genes that are known in mammals for their interindividual variability. Although MHC social signaling is thought to occur in over 20 species of vertebrates (Ruff et al., 2012), studies into its molecular mechanism have been predominantly performed with mice and more recently in fish, reptiles, birds and man (Wedekind & Penn, 2000; Milinski, 2006). At three of the more variable human MHC loci, HLA-A, HLA-B and HLA-DRB1, 243, 499 and 321 alleles have been resolved worldwide, respectively, and nucleotide diversity in the human MHC is up to two orders of magnitude higher than the genomic average (Gaudieri et al, 2000; Garrigan & Hedrick, 2003). It seems that animals are capable of converting this genetic code into olfactory information (Hurst et al., 2001; Leinders-Zufall et al., 2004) that is able to activate olfactory sensory neurons at exceedingly low concentrations (Leinders-Zufall et al., 2004). MHC differences are correlated with social recognition in many vertebrate species. The prevalence of this phenomenon (e.g. Olsén et al., 1998; Villinger & Waldman, 2008; Zelano & Edwards, 2002) suggests that the use of MHC-correlated odors in social recognition may be a characteristic in this clade. MHC genes can affect the concentration of volatile acids that produce odor in sweat or urine (Yamazaki et al, 1979; Singh et al, 1987; Wedekind et al, 1995; Wedekind & Furi, 1997; Hurst et al, 2001; Beauchamp & Yamazaki, 2003; Santos et al, 2004; Piertney & Oliver, 2006). Individual variation in volatiles and peptides, which becomes larger with a decrease in the degree of relatedness, can explain attraction or aversion in behavioral contexts such as mating, kin and parent-progeny recognition, as well as inbreeding avoidance without invoking a specific influence of the MHC class I and II genes (Overath et al., 2014). It has been pointed out (Boehm, 2013) that this variability may provide “a universal mechanism of olfactory assessment of genetic individuality even for animals that do not possess an MHC”. The finding that specialized sensory neurons can bind peptides in an MHC-like fashion (Boehm & Zufall, 2006; Spehr et al., 2006) has revealed the long-sought odorants used to recognize the MHC genotype and phenotype of other individuals. The odorants are the same MHC peptides used during immune recognition, which provides the

molecular logic linking selection acting on MHC-mediated behaviors with selection acting on immune recognition (Slev et al., 2006).

### 13.2 Kin discrimination and nepotism

Accurate discrimination of conspecifics with regard to genetic relatedness is a crucial prerequisite for nepotistic behaviors (preferential treatment of kin) (Hamilton, 1987). There is only very rare unambiguous evidence for both kin discrimination and nepotism. Nepotism among closely related female kin ('close' kin), including cooperative defense of territories has been well documented in Belding's ground squirrels, *Spermophilus beldingi* (Sherman, 1977, 1980, 1981). Females with close kin (e.g. mothers, daughters, sisters) are more likely to give potentially risky alarm calls than females with no close kin. Although *S. beldingi* adults do not treat distant female kin (e.g. grandmothers, aunts or cousins) and male kin nepotistically, they are able to recognize these individuals as relatives (Mateo, 2002). These findings indicate a dissociation in the evolution of recognition components, such that all *S. beldingi* kin classes produce discriminable cues, but only close female kin are recipients of nepotism. Males, like females, produce kin labels and can recognize their kin but are not treated nepotistically, nor do they act nepotistically (Mateo, 2002). Golden-mantled ground squirrels (*S. lateralis*), an asocial species which are closely related to *S. beldingi* but are not nepotistic, are also able to discriminate among classes of their kin (Mateo, 2002).

In many species, the overall rates at which adult individuals direct aggression towards kin and nonkin are simply indistinguishable. This is the case for meerkats, *Suricata suricatta* (Madden et al., 2012), European badgers, *Meles meles* (Hewitt et al., 2009), ringtailed coatis, *Nasua nasua* (Hirsch et al., 2012), spotted hyaenas (Smith et al., 2010; Wahaj et al., 2004), bonnet macaques, *Macaca radiata* (Silk et al., 1981b) and rhesus macaques (Widdig et al., 2002). Kinship also fails to curtail aggression in Belding's ground squirrels (Holmes, 1986; Mateo, 2003) despite strong evidence indicating that kin selection favors alarm calling in this species (Sherman, 1977, 1980, 1981). Kinship also generally fails to protect individuals from becoming victims of coalitionary attacks in mammals with strict linear dominance hierarchies for which social ranks are often established and reinforced within maternal lineages (e.g. baboons: Alberts, 1999; rhesus macaques: Widdig et al., 2001; spotted hyaenas: Smith et al., 2010; Wahaj et al., 2004). Although inter-pride relatedness can be high, response to intruders was influenced by both environmental and social factors,

whereas kinship had no detectable effect on territorial conflicts among groups of lions (Spong & Creel, 2004). On the other hand, the low level of aggression within coalitions of male lions is not affected by the degree of genetic relatedness (Packer & Pusey, 1982). Overall, rates of aggression were reduced among kin for only 8 out of the 31 (26%) species reviewed (Smith, 2014) such that species were significantly less likely to be socially tolerant of genetic relatives than expected by chance (binomial test:  $N = 31$  species,  $P < 0.0001$ ). That is, most species either directed higher rates of aggression towards kin or failed to preferentially tolerate groupmates on the basis of kinship. Moreover, this lack of nepotistic tolerance was statistically indistinguishable between primates and nonprimates ( $N = 31$  species,  $P = 0.926$ ).

Many social insect colonies are composed of multiple matriline (progeny from different mothers and, typically, fathers) and/or patriline (progeny from different fathers). Inclusive fitness theory (Hamilton, 1964), therefore, predicts that nepotism within full-sister groups would be beneficial if this does not incur excessive costs. In eusocial species, however, unambiguous direct evidence for nepotism has so far only been found in drywood termites (Korb, 2006), whereas evidence for the absence of nepotism has been found in numerous species (Queller et al., 1990; Woyciechowski, 1990; Carlin et al., 1993; Breed et al., 1994; Balas & Adams, 1996; Bernasconi & Keller, 1996; DeHeer & Ross, 1997; Keller, 1997; Strassmann et al., 1997; Solís et al., 1998; Mohammedi & Le Conte, 2000; Tarpy et al., 2004; Châline et al., 2005; Ratnieks et al., 2006; Goodisman et al., 2007; Koyama et al., 2007, 2009; Atkinson et al., 2008; Rangel et al., 2009; Zinck et al., 2009; Kellner & Heinze, 2011). In contrast to the lack of evidence for a role of kin recognition in nestmate nepotism, there is abundant evidence for the role of kin recognition in non-nestmate aggression and intracolony "cheater" detection (e.g. Wilson, 1971; Henderson et al., 1990; Adams, 1991; Vander Meer et al., 1998; Liebig et al., 1999, 2000; Monnin & Peeters, 1999; Dani et al., 2001; Ruther et al., 2002; Roulston et al., 2003; Endler et al., 2004; Dietemann et al., 2005; Cuvillier-Hot et al., 2004a, b; Buchwald & Breed, 2005; Ozaki et al., 2005; Cini et al., 2009; Smith SM et al., 2009; Sturgis & Gordon, 2012). This pattern is exactly what can be expected when kin discrimination is only used to eliminate non-self as can be found in the interactions of metazoan immune-competent cells with intruders (e.g. parasites) and social cheaters (e.g. cancer cells).

In conclusion, there is no evidence that evolution of kin

recognition/discrimination and prosocial behavior are interdependent. All conceivable combinations of the two factors occur: (i) kin recognition with and without cooperation; and (ii) cooperation, even eusociality, with and without kin recognition. Thus, kin recognition is neither a necessary nor sufficient condition for prosocial behavior.

### **13.3 Excursion: An Orwellian Big Brother society needs an effective system of communication and surveillance**

In an Orwellian society individuals are oppressed with the mechanics of fear and/or the sedatives of pleasure (Orwell's "1984" and Huxley's "A Brave New World" are good examples of this). A totalitarian system requires effective means of information and communication and compliant agents that enforce the despotic system. Most importantly, it should be made sure that the information is understood correctly by each member of the society, so that transgressions of the "rules" can be prevented in the first place. In metazoan organisms, a common "language" as effective communication system is ensured by common genetic descent. At least as important as discrimination of "self" and "nonself" is for the fight against external hazards, it is for the maintenance of internal homeostasis. In multicellular organisms, the immune system performs a large list of "nonimmunological" tasks such as (i) management of the cooperation of syngeneic cells, which may explain the numerous functions of the immune system in the development and maintenance of organisms in the absence of infection; (ii) detection of selfish/cheater behavior of syngeneic or allogeneic cells; and (iii) elimination and memorization of cheaters (Muraille, 2013). The importance of selfish/cheater behavior in the activation of the immune system is demonstrated by the ability of the immune system to tolerate allogeneic cooperative microbiota and fight syngeneic selfish cells (tumors) by responding to "selfish/cheater signals" (Matzinger, 2002; Cremer & Sixt, 2009; Vance et al., 2009; Muraille, 2013). Each unitary metazoan organism (that falls under Weismann's doctrine) is a totalitarian society in which the soma and each of its cells ultimately serve the final mission of the germline cells, reproduction. It is obvious that autonomy of cell growth is potentially very dangerous to the survival of the organism if not closely regulated (Hull, 1982; Chigira et al., 1990). Therefore, autonomous proliferation of each somatic cell that does not serve this ultimate goal is strictly controlled. Normal tissues carefully control the production and release of growth-promoting signals that instruct entry into and progression through the cell

growth-and-division cycle, thereby ensuring a homeostasis of cell number and thus maintenance of normal tissue architecture and function (Hanahan & Weinberg, 2000, 2011). Moreover, cell adhesion molecules and the extracellular matrix milieu keep the cells under tight social control (Hanahan & Weinberg, 2000; Bornstein & Sage, 2002; Giacotti & Tarone, 2003). This social control is even exerted in bacterial communities (Hori & Matsumoto, 2010). Circumvention of this proliferation control is the basic cause of carcinogenesis (Hull, 1982; Chigira et al., 1990; Hanahan & Weinberg, 2000, 2011). Cancer can be considered a social parasite and cheat (Nunney, 1999; Crespi & Summers, 2000; Michor et al., 2004; Dobata & Tsuji, 2009; Bourke, 2011b; Ghoul et al., 2014).

A defining characteristic of eusocial colonies (as of metazoan organisms) is their closed membership. Like a multicellular organism, membership of the colony is "self" and nonmembers, even if they are of the same species, are treated as "nonself" (Krasnec & Breed, 2012). Separation of "self" from "nonself" allows eusocial colonies to prevent invasion by parasites and predators (Vander Meer et al., 1998). Kin discrimination and nepotistic behavior are only rarely associated. This prompts the question whether kin discrimination may serve another purpose. Beehives, wasp and ant nests are police states (Foster & Ratnieks, 2001; Monnin & Ratnieks, 2001; Cuvillier-Hot et al., 2004b) in which selfish and despotic queens, by means of their pheromones, suppress the reproductive activity of their daughters and enforce their reproductive monopoly by murder, torture and imprisonment (Whitfield, 2002). Just as a metazoan organism is vulnerable to parasitism by renegade cells that form tumors (Weinberg, 1998), an insect society is susceptible to exploitation by rogue reproductive workers that can harness the brood-rearing capacity of a colony to enhance their personal reproductive success. It is thought that an insect colony is more likely than a metazoan organism to experience such problems because although the cells of an individual are considered clonal (but see e.g. Muotri et al., 2005; Flores et al., 2007; Lam & Jeffreys, 2007; Bruder et al., 2008; Liang et al., 2008; Piotrowski et al., 2008; Coufal et al., 2009; Quinlan & Hall, 2012), an insect colony comprises a genetically heterogeneous family in which the interests of individuals are not identical, especially in reproductive matters (Beekman & Ratnieks, 2003). Thus, similar to metazoan organisms that have evolved systems to control cancer, the evolution of insect societies requires mechanisms to control selfish worker reproduction (Frank, 1995; Amdam & Seehuus, 2006;

Ratnieks et al., 2006; Cremer et al., 2007; Cremer & Sixt, 2009). There is a nearly perfect analogy of the eusocial nestmate recognition and worker policing systems to the function of the immune system in multicellular organisms.

## 14. Stochasticity and selection: duality in evolution

### Summary

**Here I refer to the abstract of my recent work (Heininger, 2015) elaborating a cybernetic theory of evolution that was already outlined in an earlier work (Heininger, 2013). Stochasticity and natural selection are the input, respectively, output levels of the evolutionary Black Box. Stochastic environments fundamentally change the rules how evolution works (compared to Darwinian theory that assumed stable environments). Ashby's 'Law of Requisite Variety' describes the behavior of cybernetic systems in variable environments: create internal variety that matches the external variety to fight variation with variation. Particularly, individual-level and population-level selective pressures act jointly dependent on ecological variables. Stochastic environments coerce organisms into lotteries. Risk-avoidance or -spreading are individual- or population-level biological insurances in response to the vagaries of an uncertain, unpredictable environment. The evolution of cooperation is a bet-hedging (risk spreading) strategy of risk-averse individuals.**

Darwin's theory is based on the assumption of a stable environment. Stable environments favor selfish individuals that try to maximize their fitness (the survival of the fittest). Hamilton's rule allegedly explains the paradox of altruism, that selfish individuals forego their fitness for the benefit of others. Kin selection/inclusive fitness was his explanation for this conundrum. There is an important difference between breeding (Darwin's role model of evolution) and evolution itself: while in breeding the final goal is preset and constant, adaptation to varying biotic and abiotic environmental conditions is a moving target and selection can be highly fluctuating. Evolution is a cybernetic process whose Black Box can be understood as learning automaton with separate input and output channels (Heininger, 2013, 2015). Cybernetics requires a closed signal loop: action by the system causes some change in its environment and that change is fed to the system via information (feedback) that enables the system to change its

behavior. The input signal is given by a complex biotic and abiotic environment. Natural selection is the output/outcome of the learning automaton.

Abiotic and biotic environments are not stable, but variable, often unpredictable. Particularly, density- and frequency-dependent coevolutionary interactions generate chaotic and stochastic dynamics. Environmental stochasticity changes fundamentally the rules for the "gamble of life". Stochastic environments coerce organisms into risky lotteries. Chance favors the prepared. Ashby's (1956) 'Law of Requisite Variety' holds that cybernetic systems must have internal variety that matches their external variety so that they can self-organize to fight variation with variation. Both conservative and diversifying bet-hedging are the risk-avoiding and -spreading insurance strategies in response to environmental uncertainty. The bet-hedging strategy tries to cover all bases of plausible evolutionary scenarios in an often unpredictable environment where it does not make sense to "put all eggs into one basket". In this sense, variation is the bad/worst-case insurance strategy of risk-averse individuals. Variation is pervasive at every level of biological organization and is created by a multitude of processes: mutagenesis, epimutagenesis, recombination, transposon mobility, repeat instability, gene expression noise, cellular network dynamics, physiology, phenotypic plasticity, behavior, and life history strategy. Importantly, variation is created condition-dependently, when variation is most needed – in organisms under stress. The bet-hedging strategy also manifests in a multitude of life history patterns: turnover of generations, reproductive prudence, iteroparity, polyandry, and sexual reproduction.

Cybernetic systems are complex systems. A system is a set of inter-related elements and a complex system is one in which, in plain English, the whole is greater than the sum of its parts (Byrne & Callaghan, 2014). Complexity is conceived as a system's potential to assume a large number of states, i.e., variety. Nothing novel can emerge from systems with high degrees of order and stability — for example, crystals, incestuous communities, or regulated industries. On the other hand, complete chaotic systems, such as stampedes, riots, rage, or the early years of the French Revolution, are too formless to coalesce. Generative complexity takes place in the boundary between rigidity and randomness (Pascale et al., 2000). Only within an intermediate level of stochastic variation, somewhere between determined rigidity and literal chaos, local interactions can give rise to complexity. Complex systems have both stochastic and deterministic

properties and, in fact, generate order from chaos. Nonlinearity, criticality, self-organization, emergent properties, scaling, hierarchy and evolvability are features of complex systems. Emergent properties are features of a complex system that are not present at the lower level but arise unexpectedly from interactions among the system's components. Nonlinearity is a product of emergence (Byrne & Callaghan, 2014). The duality of stochasticity and selection is the organizing principle of evolution. Both are interdependent. The feedback between output and input signals inextricably intertwines both stochasticity and natural selection, and the individual- and population-levels of selection. Sexual reproduction with its generation of pre-selected variation is the paradigmatic bet-hedging enterprise and its evolutionary success reveals the selective signature of stochastic environments. Sexual reproduction is the proof of concept that (epi)genetic variation is no accidental occurrence but a highly regulated process and environmental stochasticity is its evolutionary "raison d'être".

Stochastic environments change the rules of evolution. Lotteries cannot be played and insurance strategies not employed with single individuals. These are emergent population-level processes that exert population-level selection pressures generating variation and diversity at all levels of biological organization. Together with frequency and density-dependent selection, lottery- and insurance-dependent selection act on population-level traits. Within this theoretical framework, Spencer's (1864) "the survival of the fittest" and Kimura's "survival of the luckiest" (Kimura, 1989) are replaced by the "survival of the fitter and luckier", emphasizing both the duality of stochasticity and natural selection.

#### 14.1 Cooperation and multilevel selection

The phrase 'group selection' still evokes shudder and frowning among some evolutionary biologists (and incredible polemics, e.g. Dawkins, 2012) yet when properly applied it is mathematically equivalent to kin selection (Wade, 1978, 1979, 1980a, 1980b, 1985; Grafen, 1984; Queller, 1992b; Dugatkin & Reeve, 1994; Frank, 1998; Michod, 1999; Rousset, 2004; Foster et al., 2006; Lehmann et al., 2007b; Marshall, 2011). Thus, that kin selection is a type of group selection is defended by Hamilton (1975a, b), Uyenoyama and Feldman (1980), Nunney (1985), Queller (1992b), Sober and Wilson (1998) and others (Okasha, 2005) (but see van Veelen et al., 2012). Traulsen (2010), however, argued that the underlying mathematics of game theory as the basis of many multilevel selection models is fundamentally different

from the approach of inclusive fitness.

Multilevel selection operates if, in addition to competition between individuals in a group, there is also competition between groups (Wilson, 1975; Boyd & Richerson, 1990; Sober & Wilson, 1998; Boyd et al., 2003; Traulsen & Nowak, 2006; Bowles, 2009; Bowles & Gintis, 2011). Typically, individual fitness and population fitness are in conflict. While selfish behavior is favored by individual selection, cooperation can evolve in many models of multilevel/group selection (Eshel, 1972; Wilson DS, 1975; Uyenoyama, 1979; Slatkin, 1981; Leigh, 1983; Wilson, 1983; Boyd & Richerson, 1990, 1992, 2002; Binmore, 1992, 1994a, b; van Baalen & Rand, 1998; Bergstrom, 2002; Goodnight, 2005; Killingback et al., 2006; Traulsen & Nowak, 2006; Nowak et al., 2010; see Heininger, 2015). According to Goodnight (2005), the evolution of an "altruistic" trait is driven by the ratio of the heritability at the group level to the heritability at the individual level. Experimental studies have shown that both artificial and natural group selection can be effective (Wade, 1976, 1977, 1982; Colwell, 1981; Craig DM, 1982; Goodnight, 1985; Breden & Wade, 1989; Bourke & Franks, 1995; Seeley, 1995; Stevens et al., 1995; Craig & Muir, 1996; Goodnight & Stevens, 1997; Miralles et al., 1997; Brookfield, 1998; Swenson et al., 2000; Goodnight, 2005).

Although couched in terms of inclusive fitness, the design of Griffin et al.'s (2004) and Kümmerli et al.'s (2009b) experiments are nearly identical to the classic group selection experiments of Wade (1976, 1977, 1982). As Queller (2004) pointed out in a comment to the work of Griffin et al. (2004): "Curiously, however, their experiment is perhaps more easily understood from a group-selection standpoint. The conditions of low and high relatedness correspond exactly to the presence and absence of within-group selection. The conditions of global and local competition correspond exactly to the presence and absence of between-group selection. The two-by-two crossing of these treatments therefore leads to the most basic group-selection experiment possible. The results confirm that cooperation is favored by between-group selection and disfavored by within-group selection." The local competition treatment is analogous to the non-group selection controls of Wade, while the global competition treatment mirrors Wade's group selection protocol. As predicted, when group selection is turned off, cooperation cannot evolve. These experiments, along with the present theoretical analysis, support the theoretical conclusion of Bijma & Wade (2008) that kin selection requires both relatedness and group selection.

## 15. Stochasticity and cooperation

### Summary

**In stochastic environments, reproductive success is unpredictable and highly variable. In taxa without parental brood care, particularly insects, larval survivorship is typically low. Even in eusocial insects with independent colony foundation, the vast majority of attempts to establish a colony will fail. The extent to which we opt for immediate gains over future rewards is known as future discounting. Future discounting is a functional and adaptive response to specific situations, particularly uncertainty or the low probability of reaping delayed benefits. Future discounting in adverse environments with uncertain reproductive success should have hampered the evolution of eusociality. If the basic assumptions of kin selection/inclusive fitness theory would be right, eusociality should have evolved in (i) less adverse environments with more predictable reproductive success, and (ii) in taxa with more predictable reproductive success and, hence, less uncertain inclusive fitness benefits.**

**An uncertain, unpredictable environment selects for evolutionary gambling, and either conservative or diversifying bet-hedging as individual- or population-level insurance to individual risk. A large body of literature shows taxonomic ubiquitous risk-sensitive behavior that is variance-sensitive behavior. In stochastic environments, cooperation trades individual fitness maximization for less variability and greater reliability of evolutionary outcomes. Both extrinsic and intrinsic noise/stochasticity can promote collective behavior in a variety of model and experimental systems. Cooperative breeding appears to be a risk-averse strategy to optimize fitness by reducing environmentally induced variance of reproductive success.**

**Given the manifold advantages of prosocial behavior at the population level and the manifold incentives to defect at the individual level, processes have evolved that mediate between the selection level conflicts. From microbes to humans, natural selection stabilizes cooperative behavior in resource-limited environments. A multitude of these interactions have been identified: direct and indirect reciprocity, sanctions, partner choice and fidelity.**

An uncertain, unpredictable environment selects for

evolutionary gambling, and either conservative or diversifying bet-hedging as individual- or population-level insurance to individual risk. In a model where kin selection and tag-based selection are dominant, mutualism is promoted by introducing environmental fluctuations (Uitdehaag, 2011). These fluctuations cause reduction in reproductive success by the mechanism of variance discount. The best strategy to counter variance discount is to share with agents who experience the most anticorrelated fluctuations, a strategy called bet-hedging. In this way, bet-hedging stimulates cooperation with the most unrelated partners, which is a basis for mutualism. Analytic results and simulations revealed that, if this effect is large enough, mutualistic strategies can dominate kin selective strategies. In addition, mutants of these mutualistic strategies that experience fluctuations that are more anticorrelated to their partner, can outcompete wild type, which can lead to the evolution of specialization. In this way, the evolutionary success of mutualistic strategies can be explained by cooperation based on bet-hedging strategies (Uitdehaag, 2011).

### 15.1 The unpredictability of reproductive success in stochastic environments

In a review of published studies on variation in recruitment, Hairston et al. (1996) found that reproductive success of long-lived adults varied from year to year by factors up to 333 in forest perennial plants, 4 in desert perennial plants, 591 in marine invertebrates, 706 in freshwater fish, 38 in terrestrial vertebrates, and 2200 in birds. These figures represent the variation among years when some reproduction occurred; many of the studies also report years in which reproduction failed completely. Similarly, the recruitment success of diapausing seeds or eggs varied by factors of up to 1150 in chalk grassland annual and biennial plants, 614 in chapparal perennials, 1150 in freshwater zooplankton, and 31,600 in insects (Ellner, 1997). A life-history model predicted the occurrence of skipped reproduction only for intermediate environmental qualities, with high reproductive investment being optimal at both ends of a gradient of environmental quality (Fischer, 2009). Skipped reproduction is frequently observed in nature (in fish: Bull & Shine, 1979; Engelhard & Heino, 2005; Rideout et al., 2005; Jørgensen & Fiksen, 2006; Jørgensen et al., 2006; in amphibians: Bull & Shine, 1979; Harris & Ludwig, 2004; in reptiles: Bull & Shine, 1979; Brown & Weatherhead, 2004; in birds: Illera & Diaz, 2006). Poor individual condition and/or poor environmental quality are thought of as the main causes for skipped reproduction (Bull & Shine, 1979;

Dutil, 1986; Rideout et al., 2005; Illera & Diaz, 2006). In taxa without parental brood care, particularly insects, the number of embryos entering a habitat is usually far in excess of its carrying capacity, and larval survivorship is typically low (e.g., Berryman, 1988; Ohgushi, 1991; Willis & Hendrick, 1992; Tinkle et al., 1993; Duffy, 1994; Dempster & McLean, 1998; Dixon et al., 1999) and unpredictable (Madsen & Shine, 1998; Fincke & Hadrys, 2001; Haugen, 2001; Rollinson & Brooks, 2007). Ecological factors such as deterioration of larval habitats or fluctuations in the density of food, predators, cannibals, or parasites can result in unpredictable windows of offspring survivorship (e.g., Smith, 1987; Newman, 1989; So & Dugeon, 1989; Morin et al., 1990; Messina, 1991; Anholt, 1994; Dixon et al., 1999). In insects, "while lifetime egg production is largely determined by chance" (Thompson, 1990), the numbers of mature offspring produced (fitness) is largely unpredictable (Fincke & Hadrys, 2001) and in natural populations, crucially, is poorly correlated with behavioral observations of mating, particularly for females (Thompson et al., 2011).

Hamilton's rule is a deterministic statement: A cooperative behavior can only evolve if the benefit-to-cost ratio of the "altruistic" act is larger than the relatedness between the donor and recipient (Hamilton 1964; Traulsen, 2010). An obstacle for the evolution of "altruistic" behavior in the population is that the costs must be paid now but the payoff in terms of inclusive fitness lies more or less far in the future. Since natural selection lacks foresight and is a blind causal process operating over random mutations, it can only operate on actual past causal contributions (Neander, 1991). But how could a trait evolve in the first place when the costs paid by the donor are certain but the benefits for the recipient (and hence the inclusive fitness gains of the donor) in the future may be highly uncertain, adding to the donor's uncertainties regarding kin recognition (see chapter 13) and recipient cheating (Sachs & Rubenstein, 2007; Chapuisat, 2009; Heinze & d'Etorre, 2009)? And the choice between cooperation/defection of the recipient (in terms of its reproductive success) may not even be under the control of the recipient but of an uncertain, unpredictable environment. In addition, the environments that coerce individuals into some type of cooperative behavior/"altruism" can be characterized as uncertain, harsh ecological conditions that constrain independent breeding (see chapter 5) and render reproductive success unpredictable. Particularly in insects, larval survivorship is typically low (e.g., Berryman, 1988; Ohgushi, 1991; Willis & Hendrick, 1992; Tinkle et al., 1993; Duffy, 1994; Dempster & McLean, 1998; Dixon et al., 1999) and

unpredictable (Madsen & Shine, 1998; Fincke & Hadrys, 2001; Haugen, 2001; Rollinson & Brooks, 2007).

Eusocial insect colonies typically go through three different phases in their life cycle: a founding stage in which new nests are founded by recently mated queens (and kings, in the case of termites), an ergonomic growth stage in which the colony produces workers only and increases in size, and a reproductive stage in which the colony produces new sexuals (males and gynes) (Oster & Wilson 1978). The transition from ergonomic growth to reproduction is generally marked by the attainment of a certain colony size, which varies from species to species. The cooperation that makes eusocial species so successful is, however, conspicuously absent when new colonies begin: The mortality of the eusocial foundresses is very high from the moment they leave the mother nest and mate until they finish constructing a nest. The agents of the increased mortality during exposure are many, both biological (chiefly through predation) and physical (because of the scarcity of nest sites and hour-by-hour vicissitudes in the environment). The large magnitude of the resulting hecatomb of would-be foundresses has been commonly observed in species that release large numbers in nuptial flights (Hölldobler & Wilson, 2014). Most species use independent colony foundation during which the queen (queen and king in termites) is alone as she attempts to establish a new nest and produce the first generation of workers. This vulnerable solitary stage can last several weeks, and the vast majority of attempts will fail (Myles, 1988; Hölldobler & Wilson, 1990, 2008; Greene, 1991; Tschinkel, 1992a, 1992b, 2006; Herbers, 1993; Peeters, 1997; Brown & Bonhoeffer, 2003; Korb & Schneider, 2007; Cole, 2009; Peeters & Molet, 2010; Cronin et al., 2013). Tschinkel (2006), for example, has described the death of the vast majority of imported fire ant (*Solenopsis invicta*) queens from the first minute they take flight, subjecting themselves to "predation by birds and insects and the chance of heat death, starvation, execution, and usurpation." As the queens settle to the ground, "a further fraction is taken by ground-based predators, especially other ants" (Tschinkel, 2006). When predators are abundant, as few as five percent of the queens succeed in building a nest (Whitcomb et al., 1973). Similar mortality rates have been observed in the mating swarms of other ant species with large mature colonies, including representatives of the genera *Atta*, *Pheidole*, and *Pogonomyrmex* (Hölldobler & Wilson, 2009, 2011). Survival is particularly poor in environments that provide low or unpredictable resources. In a long-term

study of colony founding in the red harvester ant, *Pogonomyrmex barbatus*, less than 1% of queens were estimated to succeed (Gordon & Kulig, 1996; Ingram et al., 2013). High rates of mortality also exist for dispersing queens of primitively eusocial species, such as the facultatively eusocial wasps. Among 19 species studied, 38–100% of the nests constructed by lone foundresses, who then were subjected to high risk both on the nest and during foraging, failed before the first brood emerged (Queller, 1996). Even in honeybees with dependent colony foundation by swarms (Cronin et al., 2013), a 70% mortality of swarms before they found a nest has been reported (Oldroyd et al., 1997). It is hardly conceivable that a behavior, the helper's "altruism", could have played a role in the evolution of eusociality when its putative evolutionary *raison d'être*, the worker's inclusive fitness gain, can be more or less annihilated by an uncertain and stochastic environment.

#### 15.1.1 Discounting future uncertain benefits

Intertemporal choices—decisions involving tradeoffs among costs and benefits occurring at different times—are important and ubiquitous. It is intuitively obvious that the subjective value of an outcome decreases as the time until its occurrence increases and that subjective value also decreases as the odds against an outcome increase: People would generally prefer to receive \$100 now rather than in a month and would prefer \$100 for sure rather than a 1-in-10 chance of receiving the same amount (Green et al., 1999). When offered the choice of a smaller reward now or a larger reward at a certain point in the future, some are better than others at resisting the temptation of instant gratification. But when the long-term future is uncertain, it's rational to discount it and take what you can get today (MacGregor, 2014). The extent to which we opt for immediate gains over future rewards is known as future discounting (Frederick et al., 2002; Daly & Wilson, 2005). Future discounting is a functional and adaptive response to specific situations, particularly uncertainty or the low probability of reaping delayed benefits (Rogers, 1994; Charlton, 1996; Wilson & Daly, 1997). Studies with animals, such as wasps, honeybees, and scorpionflies, have shown that organisms tend to discount the future under certain situations (i.e., they bet on risky behaviors and present gains based on environmental cues that indicate low life expectancy or narrow future options) (Roitberg et al., 1992, 1993; Woyciechowski & Kozłowski, 1998; Engqvist & Sauer, 2002). For example, reciprocal altruism (Trivers, 1971) can evolve as long as the cost of aiding another individual is outweighed by the benefit of receiving aid from that individual later,

devalued by the probability that aid will be returned (Boyd, 1992). Among nonhuman primates, investigations demonstrated that feeding ecology could explain some differences between species with regard to the capacity to wait for rewards (Stevens et al., 2005a). Other studies verified that monkeys avoid risky options with increasing delay (Hayden & Platt, 2007), and they tend to choose a small reward when the large one is delayed (Hwang et al., 2009). Apes show a higher ability for future-oriented decisions than other animals, presenting temporal discounting preferences that are similar to humans under comparable conditions (Rosati et al., 2007). Individuals who grow up in environments where resources are scarce, competition is intense, and mortality is high should discount the future more heavily than individuals who grow up in abundant, supportive, long-lived locales (Wilson & Daly, 1997). Studies demonstrated an association between socioeconomic deprivation and faster life-history strategies involved in reproductive decisions (Ellis et al., 2009; Nettle, 2010), environmental unpredictability and risk taking (Hill et al., 2008), and between low income and choices for smaller-sooner amounts of money (Lawrance, 1991; Loewenstein & Elster, 1992; Green et al., 1996; Harrison et al., 2002; Reimers et al., 2009; Leitão et al., 2013). A recent study with a Brazilian sample showed that slum-dwelling young people discounted the future more than university students from middle-class neighborhoods in Rio de Janeiro, indicating that the young adapted their psychology and behavior to their living conditions (Ramos et al., 2013). Individuals with low discount rates will be more likely to cooperate than people with high discount rates. In other words, patient people will be more trusting, and more trustworthy (Curry et al., 2005).

In economy, when the costs have to be paid now and the benefits of this investment can only be reaped in the distant, particularly intergenerational, future the benefits have to be discounted taking into account the uncertainty of the benefits of the investment (Arrow et al., 2012). With simplifying assumptions, this leads to the Ramsey discounting formula. The Ramsey formula results in a declining certainty-equivalent discount rate if the rate of growth in consumption is uncertain and if shocks to consumption are correlated over time (Cropper, 2012). Overall, the discount factor, the reciprocal of the factor by which capital would grow over unit time by compound interest, should be rising with the long-term nature of the investment. Brown (1987) suggested that inclusive fitness might be usefully broken into direct and indirect, current and future components. The most difficult components of

inclusive fitness to conceptualize and estimate are the future effects; several authors discussed the ways in which 'future indirect' fitness components might arise (Mumme et al., 1989; Creel, 1990b; Lucas et al., 1997). Emlen & Wrege (1991) and Creel et al. (1991) suggested partial solutions to the problem of estimating future fitness components, both direct and indirect. However, under certain conditions, Creel's approach yields even negative fitness (Lucas et al., 1996).

There are clusters of correlated life history traits (e.g., timing of puberty, age at sexual debut and first birth, parental investment strategies) that lie on a slow-to-fast continuum (Ellis et al., 2009; Heining, 2012). Harshness (externally caused levels of morbidity-mortality) and unpredictability (spatial-temporal variation in harshness) are the most fundamental environmental influences on the evolution and development of these life history strategies (Ellis et al., 2009). This continuum indicates that microbes, animals and plants sense environmental stochasticity and time their reproductive investments according to their future discounting (Ellis et al., 2009). Thus, the standard life history response to increased environmental stochasticity is discounting of future reproduction (Klinkhamer et al., 1997; Williams & Day, 2003; Jones et al., 2008; Ratcliff et al., 2009; Heining, 2012; Frank, 2014). Insects appear also to be able to discount the future (Roitberg et al., 1992, 1993; Woyciechowski & Kozłowski, 1998; Engqvist & Sauer, 2002). In eusocial societies, individual worker lifespan is significantly shorter (e.g. in honeybees 15 to 38 days) than the reproductive interval of the colony (2–3 swarms/colony per year). Within the conceptual framework of inclusive fitness theory (and if the analogy of economic and evolutionary reasoning holds) agents should exert transgenerational discounting of inclusive fitness benefits. Stochasticity-related devaluation charges of inclusive fitness returns for new workers in newly founded colonies (and their incentive to reproduce) should be higher than that for workers towards the end of a reproductive cycle caring for new reproductives, resulting in an increased selfish reproduction of workers during the founding period of a colony when the long-term inclusive fitness benefits of helping are particularly uncertain. However, no such colony-reproductive-cycle-specific worker behavior in terms of selfish reproduction has been reported to date. This, again, questions the validity of the inclusive fitness theory. If the basic assumptions of kin selection/inclusive fitness theory would be right, eusociality should have evolved in (i) less adverse environments with more predictable reproductive success, and (ii) in taxa with more predictable

reproductive success and, hence, less uncertain inclusive fitness benefit. Future discounting in adverse environments with uncertain reproductive success should have hampered the evolution of eusociality.

Imagine, a close relative asks you for a big favor (so big that if you meet her/his request your own aspirations would be impaired) and she/he promises to reward your investment in the future. You know from past experience that there is a 1:50 chance that she/he will keep her/his promises. Would you do her/him this favor? Probably not if you are not a complete idiot. And for sure, evolution is not such an idiot (remember Orgel's rule).

## **15.2 Cooperation as bet-hedging response to environmental stochasticity**

### **15.2.1 Empirical evidence**

Uncertainty can be measured as the variance of a distribution of environmental quality, and adversity as the mean (Andras et al., 2003; Fronhofer et al., 2011). Both adversity and uncertainty have been conceptualized as aspects of environmental 'risk' (Daly & Wilson, 2002). A large body of literature now has shown taxonomic ubiquitous risk-sensitive behavior (Heining, 2015). Risk-sensitive behavior is variance-sensitive behavior (Smallwood, 1996; Ydenberg, 2007; Mayack & Naug, 2011; Ratikainen, 2012). Cooperation as a risk-spreading response to environmental stochasticity is a byproduct of selfish action (West-Eberhard, 1975; Brown, 1983; Connor, 1986; Morris et al., 2012). Both extrinsic and intrinsic noise/stochasticity can promote collective behavior in a variety of model and experimental systems (Chen et al., 2005; Rudge & Burrage, 2008; Yates et al., 2009). Environmental variation selects for cooperative behavior (Rubenstein & Lovette, 2007; Rubenstein, 2011). Empirical evidence from plant and animal communities and human societies suggests that there is a correlation between adverse conditions and cooperation (e.g. Knight, 1984; Wilkinson, 1984; Rytönen & Soppela, 1995; Avilés, 1999; Spinks et al., 2000; De Bono et al., 2002; Andras et al., 2003, 2007; Spieler, 2003; Krams et al., 2010; Shen et al., 2012). Social species disproportionately occur in heterogeneous and unpredictable environments (Wilson, 1971; Solomon & French, 1997; Costa, 2006; Jetz & Rubenstein, 2011). In more adverse and fluctuating environments individuals perceive their resources to be more unpredictable, and this unpredictability favors cooperation (Avilés, 1999; Andras & Lazarus, 2005; Andras et al., 2007; Shen et al., 2012). In addition to the mean amount of food, the variance of a given resource influences foraging decisions (Caraco, 1980; Caraco et al., 1980;

Stephens, 1981; Real & Caraco, 1986; Schmitz & Ritchie, 1991). For example, game in the optimal diet breadth has many high-yield but high-variance targets so that one may go several days without capturing sufficient game to meet the dietary needs of a hunter's family. Sharing among hunters provides a solution to the problem by reducing the variance across hunters through pooling risk (Kaplan et al., 1984; Kaplan & Hill, 1985; Hames, 2004). Using an experimental design in which food distribution was either clumped or dispersed, in combination with individuals that varied in exploratory behavior, Tanner and Jackson (2012) showed that social structure can be induced in the otherwise non-social European shore crab (*Carcinus maenas*). Prey consumption variance is reduced in group foraging (Caraco, 1981; Clark & Mangel, 1986; Caraco et al., 1995), i.e. foraging success becomes more reliable in groups. Risk-sensitive foraging theory (Bateson, 2002; Bednekoff, 1996; Kacelnik & Bateson, 1996; Smallwood, 1996) can be used to explain cooperative foraging and breeding (Poethke & Liebig, 2008), as in social spiders (Wenzel & Pickering, 1991; Caraco et al., 1995; Avilés, 1997; Whitehouse & Lubin, 2005; Agnarsson, 2006). In the context of risk-sensitive foraging theory, group formation has been interpreted as a mechanism of risk avoidance (Caraco, 1981; Clark & Mangel, 1986; Wenzel & Pickering, 1991; Caraco et al., 1995; Uetz, 1996; Uetz & Hieber, 1997; Fronhofer et al., 2011). Spatial self-structuring leads to selection of cooperative traits (Boerlijst & Hogeweg, 1991; Kümmerli et al., 2009a).

Using a synthetic yeast cooperator-cheater system engineered to supply or exploit essential nutrients, A.J. Waite (2013) found in his doctoral thesis that despite cooperators being less fit than cheaters, some cocultures rapidly purged cheaters, while in others cheaters dominated and drove cocultures and themselves extinct. The nutrient-limited cooperative environment acted as a stress on both cooperators and cheaters and this stress created a selective pressure which triggered an "adaptive race" between cooperators and cheaters to sample from the same pool of fitness-enhancing mutations. Although cooperators and cheaters sample from the same pool, this symmetry is soon broken: The best cooperators purge cheaters and continue to grow, whereas the best cheaters cause rapid self-extinction due to the tragedy of the commons (Waite & Shou, 2012). In a model, Waite (2013) showed that stress can synergize with a spatially-structured environment to promote cooperation. Together with Ben Kerr's lab at University of Washington, he showed that cooperation in the natural cooperative *Pseudomonas aeruginosa* can be stabilized even when spatial structure is random and

transient, but only when an environmental stress—antibiotics in this case—elicits an adaptive race between cooperators and cheaters (Waite, 2013). Social unicellular prokaryotes and eukaryotes (see chapter 5) and the nematode *Caenorhabditis elegans* aggregate in response to stressors (De Bono et al., 2002); animals form more cohesive or larger groups, with consequent greater mutualistic benefits under greater predation risk (Seghers, 1974; Farr, 1975; Dunbar, 1988; Lima & Dill, 1990; Spieler, 2003; Heg et al., 2004; Zöttl et al., 2013b); mole-rats delay dispersion more in arid than in mesic habitats (Spinks et al., 2000); human in-group solidarity is greatest when the group is under threat or in a harsh environment (Levine & Campbell, 1972; Goody, 1991; Hogg, 1992; Hewstone et al., 2002).

#### 15.2.1.1 Cooperative breeding

Cooperative breeding behavior appears to be a risk-averse strategy to maximize fitness by reducing environmentally induced fecundity variance. Such a within-generation bet-hedging hypothesis for social evolution predicts that (i) variance in reproductive success should be related to environmental variation, (ii) variance in reproductive success should be related to the potential for cooperation in a group, and (iii) the potential for cooperation should be related to environmental variation (Rubenstein, 2011). It has been proposed that there may be a link between bet-hedging as response to environmental uncertainty and cooperative breeding (Cockburn & Russell, 2011).

Consider a situation where two individuals nesting together can rear more brood than the sum of their individual capabilities and further that the roles of fertile queen and sterile worker among these two individuals is decided by the toss of a coin, so to speak (Gadagkar & Bonner, 1994). In such a situation an average individual that nests in the group may obtain more fitness than a solitary individual. If we replace the concept of alleles programming individuals into workers with alleles programming individuals to take the risk of being part of the group, then it is possible to show that under certain ecological conditions the 'gamblers' will be fitter than the risk-averse solitary individuals (Gadagkar, 1990d, 1991a, 1994b). The losers in the 'gamble' will leave behind no offspring and we will see them as sterile workers. Nevertheless, it is a form of mutualism that has given rise to this situation. One advantage of such a model is that it requires no assumption of increased genetic relatedness or parental manipulation. The fact that foundress associations in primitively eusocial species may consist of distant relatives and that workers can become queens before they die suggests

that the possibility of direct reproduction at some future point of time may itself drive the evolution of group living. Likewise, Seger (1993) argued that cofoundresses that initially join the group may put their lives at risk in a gamble in which, however, they may be also the one to survive (Seger, 1993). An important assumption of this so called 'gambling hypothesis' is that the per capita productivity in the group mode is higher (or more reliable; see Wenzel & Pickering, 1991) than in the solitary mode. Even if the probability of becoming a queen may be quite small for any given individual, the fitness gained by those who succeed can be so great that it offsets the cost incurred by the other, unsuccessful bearers of the hypothetical 'gambling' allele, which makes its bearers stay in a social group and await their chances of becoming queen (Gadagkar, 1990d, 1991a, 1994b).

Increased group productivity and strong ecological constraints have previously been suggested to favor pleometrotic associations in social insects, for example faster colony growth (Bartz & Hölldobler, 1982; Tschinkel & Howard, 1983; Rissing & Pollock, 1987; Sommer & Hölldobler, 1995), increased protection against predators and usurpation (Gamboa, 1978; McCorquodale, 1989; Balas & Adams, 1996) and a shortage of nest sites (e.g. Pfennig, 1995). In the wasp *Ropalidia marginata* a solitary foundress produces on the average no more than one or two offspring whereas a queen of a multi-female colony produces on the average 76 offspring (Gadagkar 1990a). Simultaneous polygyny in *R. cyathiformis* (Gadagkar & Joshi, 1982), serial polygyny due to queen supersedure, the process by which a colony of bees/wasps replaces its queen without swarming, in *R. marginata* (Gadagkar et al., 1993), the causes and consequences of colony fission in *R. cyathiformis* (Gadagkar & Joshi, 1985), the complex behavioral caste differentiation in *R. marginata*, *R. cyathiformis* (Gadagkar & Joshi, 1983, 1984), and in *Polistes versicolor* (Gadagkar, 1990b) all add up to make mutualism and gambling plausible models for the origin of sociality in primitively eusocial species such as *R. marginata* and *R. cyathiformis* (Gadagkar, 1990d, 1991a, 1994b). In the primitively eusocial wasp species *Belonogaster juncea juncea* multiple foundress colonies were significantly more successful than single foundress colonies in producing at least one adult (Tindo et al., 2008). The total productivity of the colonies increased significantly with the number of associated foundresses, but the productivity per capita did not. No single foundress colony (out of 13) reached the sexual phase, while eight (out of 36, 21.6%) multiple foundress colonies did. The decreasing per capita productivity concomitant with an

increasing number of females noted in this study illustrates once again Michener's paradox (1964). The coefficient of variance of the per capita productivity significantly decreased with group size, as Wenzel and Pickering (1991) suggested in the model they created to explain the paradox (Tindo et al., 2008). Several studies reported a survival advantage of multiple foundress colonies compared with single foundress colonies of the genera *Polistes* (Metcalf & Whitt, 1977; Gibo, 1978; Tibbetts & Reeve, 2003), *Belonogaster* (Keeping & Crewe, 1987; Tindo et al., 1997a), and *Ropalidia* (Shakarad & Gadagkar, 1995), Allodapine bees (Hogendoorn & Zammit, 2001) and social shrimps (Duffy, 2002). Likewise, the increase in total productivity as a function of group size is in line with previous findings reported on primitively eusocial species (Michener, 1964; Shakarad & Gadagkar, 1995; Tindo et al., 1997b; Tibbetts & Reeve, 2003). The decrease in per capita productivity as a function of group size, however, illustrates Michener's paradox in primitively eusocial insects (Michener, 1964; Noonan, 1981; Strassmann et al., 1988; Shakarad & Gadagkar, 1995; Gadagkar, 1996; Hogendoorn & Zammit, 2001; Seppä et al., 2002; Soucy et al., 2003). A widely accepted explanation for Michener's paradox is the model by Wenzel and Pickering (1991) suggesting that individuals in larger groups might trade lower per capita productivity for less variability and greater predictability. Risk-sensitive reproductive strategies may reduce the average (arithmetic mean) of individual reproductive output, while yet maximizing the population geometric mean; this trade-off in terms of average reproduction is 'bet hedging' (Slatkin, 1974; Seger & Brockmann, 1987; Philippi & Seger, 1989; Simons, 2009). To understand the adaptive value of cooperative breeding behavior in heterogeneous and unpredictable environments, both the mean and environmentally induced variance in reproductive success has to be taken into account. In addition to within-generation bet-hedging, social evolution has to be considered in the context of among-generation bet-hedging, or risk spreading over multiple generations to maximize geometric mean lifetime reproductive success (Rubenstein, 2011).

Stochasticity promotes cooperation at least at two levels. Stochastic availability of resources stabilizes cooperative acquisition of resources. Stochastic determination of fate e.g. in the spore-stalk lottery of *D. discoideum* (Chattwood & Thompson, 2011) and in cell differentiation in organisms ranging from bacteria to humans (Losick & Desplan, 2008) ensures participation in the lottery. Lotteries are considered fair procedures. In fact, when a fair (unbiased) procedure is feasible and a fair allocation is not, selection of a fair

procedure is acceptable whereas there is resistance to the imposition of biased outcomes (Bohnet et al., 2008), much as when a fair (unbiased) allocation is available (Rawls, 1971 p. 86; Bolton et al., 2005). Certainly, none of the losers would voluntarily take part in a "lottery" when the outcome is biased, e.g. if the winners and losers in that lottery would be determined by a weighted dice.

### 15.2.2 Evidence from models

It is now generally accepted that stochastic models are necessary to properly capture the multiple sources of heterogeneity needed for modeling biosystems in a realistic way (Wilkinson, 2009). Cooperating groups might provide mutual advantages for their members, so that the net benefits to all participants outweigh the costs. In essence, game theoretic models of cooperation tacitly postulate (see e.g. Axelrod & Hamilton, 1981; Maynard Smith, 1984, 1989), that cooperation is not equivalent to altruism and does not by definition require sacrifices, or genes for altruism, which is why game theory formulations are largely indifferent to the degree of relatedness, if any, between the cooperators (Corning, 1997).

As the most stringent situation of reciprocal behavior through pairwise interactions, the prisoner's dilemma has long been considered as a paradigmatic example for studying the dilemmas between individual interests and collective welfare. In its original form, the prisoner's dilemma is a two-player non-zero-sum game, where each player decides simultaneously whether to cooperate (C) or defect (D) without knowing a priori how its opponent will act. There are four possible outcomes for this game: (1) mutual cooperation (C, C) yields the largest collective payoff by offering each a reward R, (2) mutual defection (D, D) pays each a punishment P, and (3) the mixed choices (C, D) or (D, C) give the defector a temptation T and the cooperator the sucker's payoff S (Zhang et al., 2011; Stewart & Plotkin, 2013), with the payoff ranking satisfying  $T > R > P > S$  and  $2R > T + S$  (Li & Duan, 2014). A basic evolutionary problem posed by the Iterated Prisoner's Dilemma game is to understand when the paradigmatic cooperative strategy Tit-for-Tat can invade a population of pure defectors. Deterministically, this is impossible (Doebeli et al., 1997). Historically, the evolution of cooperation has been studied in the absence of diversity (Hardin, 1968; Axelrod & Hamilton, 1981; Hofbauer & Sigmund, 1998; Nowak & Sigmund, 2004; Nowak, 2006a, 2006b; Sigmund, 2010). It was found more reasonable to deal with the evolution of cooperation in a population of (primitively) identical individuals, as defined by conventional evolutionary game theory (EGT)

(Maynard Smith, 1982; Hofbauer & Sigmund, 1998; Sigmund, 2010). However, the dynamical randomness stemming from diverse factors of stochasticity in a variety of interactions and biological systems constitutes an important mechanism to establish and maintain cooperation and mutualism (Fudenberg & Maskin, 1990; Nowak, 1990; Nowak & Sigmund, 1990, 1992, 1993a, 1993b; Bendor et al., 1991; Goodnight, 1992; Nowak et al., 1994, 1995, 2004; Wu & Axelrod, 1995; Doebeli & Knowlton, 1998; Wahl & Nowak, 1999; Mitteldorf & Wilson, 2000; Eriksson & Lindgren, 2002; Lorberbaum et al., 2002; McNamara et al., 2004; Imhof et al., 2005; Szabó et al., 2005; Lehmann et al., 2006; Perc, 2006a, 2006b, 2007a; Perc & Marhl, 2006; Vukov et al., 2006; Ren et al., 2007; Tanimoto, 2007; Chen X et al., 2008a, b; Perc & Szolnoki, 2008; Santos et al., 2008, 2012; Szolnoki & Perc, 2008; Szolnoki et al., 2008; Helbing & Yu, 2009; Wu & Holme, 2009; Iliopoulos et al., 2010; Imhof & Nowak, 2010; Jia et al., 2010; Wu et al., 2010; Yaari & Solomon, 2010; Delton et al., 2011; Fronhofer et al., 2011). It was noted that "...stochasticity itself is a factor favoring the selection of altruism" (Mitteldorf & Wilson, 2000).

Cumulative evidence from models supports the intuition that complex networks are also entities with some degree of stochastic dynamics such that the coevolution of the networks with the dynamical processes they host strongly influences the overall system behavior (Bornholdt & Rohlf, 2000; Skyrms & Pemantle, 2000; Ito & Kaneko, 2001; Skyrms, 2004; Gross et al., 2006; Holme & Newman, 2006; Kossinets & Watts, 2006; Pacheco et al., 2006; Santos et al., 2006b; Garlaschelli et al., 2007; Szabó & Fátth, 2007; González et al., 2008; Gross & Blasius, 2008; Fehl et al., 2011; Rand et al., 2011; Wang J et al., 2012). Complex networks, having the connectivity structure and stochastic dynamics similar to that of social networks, are very beneficial for the evolution of cooperation (Abramson & Kuperman, 2001; Santos & Pacheco, 2005; Ohtsuki et al., 2006; Santos et al., 2006a, 2008, 2012; Tang et al., 2006; Gómez-Gardeñes et al., 2007, 2008; Lehmann et al., 2007a; Taylor et al., 2007; Gómez-Gardeñes et al., 2008; Poncela et al., 2007; Tomassini et al., 2007; Kuperman & Risau-Gusman, 2008; Lozano et al., 2008; Perc & Szolnoki, 2008; Wang S et al., 2008; Du et al., 2009; Pacheco et al., 2009; Szolnoki & Perc, 2009; McNamara & Leimar, 2010; Tomassini & Pestelacci, 2010; Fu et al., 2010; de Weerd & Verbrugge, 2011; Du & Fu, 2011; Pruitt et al., 2012). Thus, populations in which individuals exhibit diversity in behavior or handling their social contacts end up being more cooperative than those in which individuals

exhibit no such diversity (McNamara et al., 2004; Van Segbroeck et al., 2009).

More generally, heterogeneity or diversity allows for cooperative behavior to prevail even if the temptations to defect are large (Fishman et al., 2001; Brockhurst et al., 2006; Perc, 2007b; Szabó & Fátth, 2007; Fu & Wang, 2008; Perc & Szolnoki, 2008; Santos et al., 2008, 2012; Szolnoki et al., 2008). Likewise, heterogeneity/diversity of resource availability, acquisition or investment (Killingback et al., 1999; Killingback & Doebeli, 2002; Chadeaux & Helbing, 2010; Santos et al., 2012; Kun & Dieckmann, 2013) will promote the evolution of cooperation. In nature, payoffs for certain acts vary according to the levels of supply and demand for various commodities—e.g. the need for cooperation or help (Noë et al., 1991; Dunbar, 1992; Barrett et al., 1999; Stopka & Macdonald, 1999)—and variation in the payoffs are more likely to coerce individuals into mutual cooperation (Stopka & Johnson, 2012). Likewise, spatial structure will promote the evolution of cooperation (Nowak & May, 1992; Nowak et al., 1994; Ferriere & Michod, 1996; van Baalen & Rand, 1998; Brauchli et al., 1999; Pfeiffer et al., 2001; Boza & Scheuring, 2004; Kreft, 2004b; Grim et al., 2006; Langer et al., 2008). Again, there is “overwhelming evidence indicating that heterogeneity, almost irrespective of its origin, promotes cooperative actions” (Perc & Wang, 2010). On the other hand, cheating will prevail in homogeneous populations (Axelrod & Hamilton, 1981; Pfeiffer et al., 2001; Frick & Schuster, 2003; Kreft, 2004b).

After years of attempting to explain cooperation by dyadic models assuming static individuals (both developmentally within the same individual and across different individuals), it has been acknowledged that cooperation may involve more than two individuals (Brosnan & Bshary, 2010; Connor, 2010; Earley, 2010). Game theory and other models that incorporate choice among multiple potential partners (and hence another stochastic element) are more realistic representations of many mutualisms than are the two-player Prisoner's Dilemma scenarios (Noë & Hammerstein, 1995; Leimar & Hammerstein, 2010). Game theory models allow for broader stability of mutualistic interactions when multiple players are incorporated into the model (Bull & Rice, 1991; Noë & Hammerstein, 1994, 1995). While models of mutualistic communities show little dependence on stochastic population fluctuations, predator-prey models show strong dependence on the stochasticity that is a major cause of population extinctions (Murase et al., 2010).

Stochasticity, although only rarely explicitly stated, is also intrinsic to model scenarios like iterated games (Axelrod, 1984; Aumann & Maschler, 1995; Nakamaru et al., 1997). Cooperation can be supported by repeated interactions (Trivers, 1971; Axelrod & Hamilton, 1981; Axelrod, 1984). The most important condition necessary for the evolution of direct reciprocity is that interactions between pairs of agents be sufficiently repeated (Axelrod & Hamilton, 1981). For reciprocity to operate, after one agent delivers a benefit, the partner must forgo the immediate gain offered by cheating—that is, of not incurring the cost involved in returning a comparable benefit. In general, selection can only favor forgoing this gain and incurring the cost of reciprocating when the net value to the partner of the future series of exchange interactions (enabled by reciprocation) exceeds the benefit of immediate defection (which would terminate that future series). If there were no future exchanges—if an interaction was one-shot—then the equilibrium strategy would be always defect. In deciding whether to engage in dyadic reciprocity, these systems must balance (i) the costs of mistaking a one-shot interaction for a repeated interaction (hence, risking a single chance of being exploited) with (ii) the far greater costs of mistaking a repeated interaction for a one-shot interaction (thereby precluding benefits from multiple future cooperative interactions). This asymmetry builds organisms naturally selected to cooperate even when exposed to cues that they are in one-shot interactions (Delton et al., 2011). Stochasticity may, at least in part, be introduced by the compelling empirical evidence of random variation in individuals' decisions (Boyd, 1989; Camerer, 1989; Starmer & Sugden, 1989; Hey & Orme, 1994; Wu, 1994; Wu & Axelrod, 1995; Ballinger & Wilcox 1997; Hey, 2001; Eriksson & Lindgren, 2002; Blavatsky, 2007; Van Segbroeck et al., 2009; Iliopoulos et al., 2010; Cavaliere & Poyatos, 2013) and as many competitive games favor “mixed” (stochastic) strategies (Miller, 1997). For example, Camerer (1989) reports that 31.6% of subjects reversed their choices when presented with the same binary choice problem for the second time. Starmer and Sugden (1989) found that 26.5% of all choices are reversed on the second repetition of a decision problem. Hey and Orme (1994) report an inconsistency rate of 25% even when individuals are allowed to declare indifference. Wu (1994) found that 5% to 45% of choice decisions are reversed (depending on a lottery pair) when a decision problem is repeated. Ballinger and Wilcox (1997) report a median switching rate of 20.8%. There are a number of systems from single neurons and synapses (Lowen et al., 2001; Stein et al., 2005) to invertebrate

(Brembs et al., 2002; Briggman et al., 2005; Maye et al., 2007) and vertebrate animals including humans (Grobstein, 1994; Glimcher, 2005; Raichle, 2006), which even generate variable output despite no variations in input at all, leading to difficulties reproducing even tightly controlled experiments (Crabbe et al., 1999). As such, dynamic heterogeneity/diversity is instrumental not only to promote cooperation, but also to sustain it, even in the absence of complex community enforcement mechanisms, reputations or punishment (Hamilton, 1964; Wilson DS, 1975; Ostrom, 1990; Fehr & Gächter, 2000; Milinski et al., 2002; Skyrms, 2004; Nowak, 2006a; West et al., 2007a; Sigmund et al., 2010).

While in an additive context the emergence and survival of cooperation requires special conditions (especially some level of reward, punishment, reciprocity), Yaari & Solomon (2010) found that in the multiplicative random context the emergence of cooperation is much more natural and effective. The fundamental feature of multiplicative processes is the fact that the expected gain of the players taking part in this iterative process depends in a crucial way on the number of players considered (number of independent realizations) and the number of time steps that the game is played. For long times (the number of time steps played in the game), the expected wealth of the players follows the geometric mean and not the arithmetic mean of the game (keep in mind that “geometric mean  $\leq$  arithmetical mean”) (Yaari & Solomon, 2010).

### 15.3 Natural selection stabilizes cooperation

Given the manifold advantages of prosocial behavior at the population level (Wilson & Wilson, 2007a, b) and the manifold incentives to defect at the individual level, processes should have evolved that mediate between the selection level conflicts. In microbes, sociality is under strong natural selection. In constant, nutrient-rich environments where benefits associated with sporogenesis (a social behavior) are absent and no longer balance the cost of constructing spores, sporulation ability of *Bacillus subtilis* was lost over 6,000 generations (Maughan et al., 2009). Propagation of *B. subtilis* for less than 2,000 generations in a nutrient-rich environment where sporulation is suppressed led to rapid initiation of genomic erosion including biosynthetic pathways, sporulation, competence, and DNA repair (Brown et al., 2011). The social prokaryote *Myxococcus xanthus* loses its social behavior when propagated in nutrient-rich habitats in which their social behaviors for starvation-induced spore production or predatory efficiency were not under positive selection (Velicer et

al., 1998; Velicer & Stredwick, 2002). Social behavior is an evolutionary burden in asocial habitats (Velicer et al., 1998; Velicer & Stredwick, 2002; Zhang et al., 2005; Li et al., 2011). Kraemer et al. (2010) argued that the globally widespread presence of developmentally competent strains (Vos & Velicer, 2008) indicates that social proficiency is highly beneficial in many habitats. Natural variation in developmental timing of strains recovered from different sites, suggests that variation in selective forces across different environments may contribute to the persistence of such variants (Kraemer et al., 2010).

Corning (1996) listed some of the common assumptions in Prisoner’s Dilemma games: “The games are always voluntary and “democratic”; each player is free to choose his/her own preferred strategy, and the opposing player has no means available for coercing choices, or compliance. Also, the players are not allowed to communicate with one another in an effort to reduce the uncertainties in the interactions. Furthermore, defectors are usually rewarded handsomely for cheating while the co-operators are denied the power to prevent defectors from enjoying the rewards, much less punishing them for defection. Such “grade inflation” for defection biases the game in favor of cheating. Worse yet, in iterative games the players are forced to continue playing; they cannot exclude or ostracize a defector. They can only retaliate by themselves defecting and hoping thereby to penalize the other player. [...] This reasoning is reflected in a new Prisoner’s Dilemma model developed by Nowak and Sigmund (1993b) called “Pavlov”, which the authors suggest can outperform Tit-For-Tat. They call their strategy “win-stay, lose-shift,” and the significance of this innovation is that, in contrast with an iterated game in which the players must continue playing regardless of the outcome, in Pavlov they have the choice of leaving the game if they don’t like the results. In other words, a player may also have the power to exercise some control over the behavior of a defector by denying to that player future access to the game and its potential benefits. Punishments as well as rewards may be utilized as a means of keeping the game honest and, more important, as a means of restricting the game over time to mutual co-operators.” Not surprisingly, evolution employed a variety of these strategies, e.g. punishment, reward, and partner fidelity/choice to ensure cooperative behavior.

A multitude of interactions can stabilize cooperative behavior: direct and indirect reciprocity, sanctions, partner choice and fidelity (Gurven, 2004; Weyl et al.,

2010; Archetti et al., 2011; Nowak & Highfield, 2011; Frederickson, 2013). Several natural mechanisms of promoting/enforcing cooperation have been explored such as sanctions and policing (Axelrod & Hamilton, 1981; Axelrod, 1984; Boyd & Richerson, 1992; Clutton-Brock & Parker, 1995; Denison, 2000; Sigmund et al., 2001, 2010; Yu, 2001; West et al., 2002b, 2002c; Kiers et al., 2003, 2006, 2011a; Gächter et al., 2008; Rockenbach & Milinski, 2009; Boyd et al., 2010; Helbing et al., 2010; Manhes & Velicer, 2011; Hilbe & Traulsen, 2012; Jandér et al., 2012; Raihani et al., 2012; Shutters, 2012). The evolution of individually costly punishment has been difficult to explain. Several studies in isolated groups have found clear evidence that while costly punishment increases the level of cooperation, the net effect in terms of material pay-off is often negative, decreasing the success of groups and individuals (Sefton et al., 2007; Dreber et al., 2008; Egas & Riedl, 2008; Wu et al., 2009). However, there is ample evidence that intergroup competition can be a powerful force for promoting within-group cooperation (Bornstein et al., 1990; Erev et al., 1993; Gunnthorsdottir & Rapoport, 2006; Tan & Bolle, 2007; Puurtinen & Mappes, 2009; Gneezy & Fessler, 2011; Sääksvuori et al., 2011; Voors et al., 2012; Böhm & Rockenbach, 2013; Rand & Nowak, 2013). Generally, group-selected systems can be expected to evolve policing against cheats (Frank, 1995). Group competition enhances the effectiveness of punishment so that when groups are in direct competition, individuals belonging to a group with punishment opportunity prevail over individuals in a group without this opportunity (Sääksvuori et al., 2011). Punishment can function as a form of reproductive leveling that is likely to change the selective environment so that it becomes more favorable to the evolution of behaviors that increase the success of the group relative to other groups (Bowles, 2006). In addition to competitive superiority in between-group competition, punishment reduces within-group variation in success, creating circumstances that are highly favorable for the evolution of accompanying group-functional behaviors (Sääksvuori et al., 2011). Experience with real-world intergroup conflict supports the results of mathematical models (Gneezy & Fessler, 2011; Voors et al., 2012).

Direct reciprocity (Trivers, 1971; Bowles & Gintis, 2004; Kiers et al., 2011b; Fellbaum et al., 2012), indirect reciprocity that works through reputation (Alexander, 1987; Boyd & Richerson, 1989; Nowak & Sigmund, 1998; Leimar & Hammerstein, 2001; Milinski et al., 2002; Fehr & Fischbacher, 2003; Ohtsuki & Iwasa, 2004, 2006; Panchanathan & Boyd, 2004; Suzuki & Akiyama, 2005; Bshary & Grutter, 2006), pleiotropy

(Foster et al., 2004; Banin et al., 2005; Xavier & Foster, 2007; Harrison & Buckling, 2009; Dandekar et al., 2012), voluntary participation (Hauert et al., 2002; 2007; Szabó & Hauert, 2002; Semmann et al., 2003; Szabó & Vukov, 2004), or spatial extensions (Nowak & May, 1992) stabilize cooperative behavior. Tit-for-tat-like strategies can sustain mutualistic cooperation in the presence of cheaters (Frank, 1994; Doebeli & Knowlton, 1998; Bergstrom & Lachmann, 2003; Yamamura et al., 2004). Theoretical and empirical studies of indirect reciprocity show that people who are more helpful are more likely to receive help (Wedekind & Milinski, 2000; Leimar & Hammerstein, 2001; Milinski et al., 2002; Fishman, 2003; Hauser et al., 2003; Brandt & Sigmund, 2004; Gurven, 2004; Ohtsuki & Iwasa, 2004; Panchanathan & Boyd, 2004; Nowak & Sigmund, 2005; Nowak, 2006a). In his extensive work about the sharing of blood among vampire bats (their exclusive food-source) (Wilkinson 1984, 1988, 1990), Wilkinson concluded: "Reciprocity is likely to be more beneficial than kin selection – provided that cheaters can be detected and excluded from the system" (1990, p. 82). On the other hand, individuals may prefer close kin to distant kin and nonkin as partners for reciprocity. Relatives can make ideal candidates for reciprocal exchanges due to factors such as familiarity, trust, proximity, a high probability of future interaction, or an expectation that relatives will cooperate (Allen-Arave et al., 2008). When choosing among potential reciprocity partners, individuals should generally prefer partners who will provide the highest expected return benefit. Familiarity and emotional bonds fostered over time may make close kin easier to "read" and trust than distant kin and nonkin (Allen-Arave et al., 2008). Familiarity, emotional bonds, trust, and proximity can promote an expectation among kin that a relative will cooperate, and experimental research has shown that expectations of cooperation promote and stabilize "altruistic" behavior (Dawes, 1980; Messick & Brewer, 1983; Allen-Arave et al., 2008). Would-be transgressors likely experience more guilt from cheating victims with whom they have emotional ties (Frank, 1988).

However, relatively few examples of cooperation and mutualism in non-human species seem to fit reciprocity concepts (Hauser et al., 2003; Stevens & Gilby, 2004; Brosnan et al., 2010b; Connor, 2010; Leimar & Hammerstein, 2010; Melis & Semmann, 2010). It has even been suggested that the specific mechanism of reciprocity is unlikely to be of general importance outside of humans, because the conditions required can be extremely restrictive (Connor, 1995; Dugatkin, 1997; Clutton-Brock, 2002; Hammerstein,

2003; Stevens & Hauser, 2004; Stevens et al., 2005b). Trivers (2004) argued that reciprocity in all its aspects is very difficult to demonstrate, especially in nature. For example, it is not sufficient to demonstrate a positive correlation in beneficent acts across pairs of unrelated individuals (which is sometimes achieved). "Contingency" has also to be shown: that withholding a benefit by one results in a similar action by the other (which is rarely established).

A mechanism that has not been considered sufficiently in all models, at least to my knowledge (but see Queller, 1994a), is that, in a world of limited resources, the fitness gain associated with cooperative behavior results in a relative fitness loss due to competitive/solitary behavior. Resource availability follows a conservation law, implying that the gains or losses in resources to one individual are balanced by the losses or gains to others (Schluter, 1996, 2010). For instance, the huge success of eusocial insects should come at the expense of solitary organisms. Within the nervous system, cooperative synapses also have a competitive side: when some synapses grow stronger and prosper, others, which left to themselves would also have strengthened, instead weaken. Cooperation and competition between postsynaptic cells during correlation-based development determine the arrangement or maps of receptive field properties across the postsynaptic structure (Miller, 1996; Bhaumik & Mathur, 2003).

Many researchers have found it useful to separate reciprocity into two components; repeated interactions of partners, partner fidelity, and the ability of interactants to alter their response based on the other's behavior—partner choice or sanctions (Noë, 1990; Bull & Rice, 1991; Nowak & May, 1992; Noë & Hammerstein, 1994; Doebeli & Knowlton, 1998; Simms & Taylor, 2002; West et al., 2002a; Sachs et al., 2004). Individuals often discriminate among partners according to the quantity of rewards they provide and associate differentially with higher reward producers (Bull & Rice, 1991; Christensen et al., 1991; Mitchell, 1994; Anstett et al., 1998; Ferriere et al., 2002). Plants and mycorrhizal fungi appear to be able to distinguish and selectively reward better symbionts (e.g., Hammer et al., 2011; Kiers et al., 2011b; Lekberg et al., 2010), although this ability may differ among plant species, depend on the spatial distribution of co-occurring fungi (Bever et al., 2009), and be moderated by bet-hedging (Lekberg & Koide, 2014). Hosts respond differentially to strains varying in their mutualistic benefit, reducing the fitness of less beneficial strains relative to more beneficial strains. Such 'sanctions' have been reported in soybean (Kiers

et al., 2003), lupine (Simms et al., 2006), and in alfalfa and pea (Oono et al., 2011). Partner choice and partner fidelity are mechanisms for dealing with cheaters, and can theoretically allow mutualisms to persist despite cheaters (Simms & Taylor, 2002; Sachs & Simms, 2006). Partner fidelity involves long-term or repeated interactions among partners that promote correlated fitness interests between them (Trivers, 1971; Axelrod & Hamilton, 1981; Bull & Rice, 1991; Frank, 1994; Doebeli & Knowlton, 1998; Sachs et al., 2004; Foster & Wenseleers, 2006) such as microbial mutualists that are vertically transmitted in a host lineage (Axelrod & Hamilton, 1981; Bull & Rice, 1991; Frank, 1994; Herre et al., 1999; Sachs et al., 2004). By far the most common tool to enforce cooperation is partner choice. Partner choice or sanctions occur when an interacting party is able to alter its response based on the behavior of the other (Bull & Rice, 1991; Denison, 2000; Simms & Taylor, 2002; Kiers et al., 2003; Sachs et al., 2004; Foster & Wenseleers, 2006; Simms et al., 2006). For instance, in the mutualism between client fish and cleaner fish in which cleaner fish obtain food from removing client parasites, client fish recognize and avoid cheating cleaners that also bite healthy tissues (Bshary, 2002). Models in public goods games show that both external rewards and punishment enhance cooperation in a society (Hilbe & Sigmund, 2010; Szolnoki & Perc, 2010). It has been proposed that a good way of increasing cooperation would be to use a reward first (the carrot), and a punishment later (the stick) (Hilbe & Sigmund, 2010).

Punishing non-cooperative partners or rewarding cooperative ones can help maintain cooperation between species (Clutton-Brock & Parker, 1995) if the behavior of the partners can be observed. In some cases discrimination may not be possible and one may only be able to react to the collective action of its partners, either because there is no way to detect the behavior (or its effects) of individual partners or because the differences between cooperators and non-cooperators are too small to be detected. Archetti and Scheuring (2013) showed that if the benefit of the public goods traded by the two species is a nonlinear saturating function of the individual contributions, cooperators and defectors can coexist in sizeable groups, in the absence of assortment and of discrimination mechanisms, and mutualism can be maintained in well-mixed population without punishing the free riders. Momeni et al. (2013) conducted a study with two genetically engineered species of yeast that mutually cooperate, each providing a metabolite that is essential to the other, but are not able to recognize each other (this means that these

populations cannot rely on partner choice to combat cheaters), and a third species of yeast that cheated by consuming one of the metabolites without releasing any metabolite of its own. Momeni et al. found that as long as there was space for the yeast cells to grow into, the two species that cooperated self-organized into mixed clusters, with the cheating species being excluded from these clusters. The self-organization was driven by a positive feedback loop involving the two species that cooperated, with each species helping to increase the fitness of the other. The results demonstrate that it is possible for two genetically unrelated populations to cooperate and combat cheaters without the use of partner choice (Momeni et al., 2013).

There is ample evidence that partner choice is a strong coevolutionary force in cooperative and mutualistic systems (Noë & Hammerstein, 1994; Noë, 2001; Bshary & Grutter, 2002; Simms & Taylor, 2002; Simms et al., 2006; Johnstone & Bshary, 2008; Leimar & Hammerstein, 2010). Unsatisfactory relationships can be abandoned and replaced by ones with greater benefits. For example the choice of a more desirable aphid species draws ant protection away from the less desirable aphid species which, as a result, experience a higher level of predation and population decline (Fischer et al., 2001). With each individual shopping for the best partners and selling its own services, the framework becomes one of supply and demand, as formalized in Noë and Hammerstein's (1994) Biological Market theory. This theory applies whenever trading partners can choose with whom to deal. Market mechanisms are an effective way of sidelining profiteers (de Waal & Suchak, 2010). Partner choice has long been considered sufficient for the maintenance of cooperation both within and among species (Noë, 1990; Bull & Rice, 1991; Noë & Hammerstein, 1994; Dugatkin & Sih, 1995; Noë et al., 2001; Bshary & Noë, 2003; Sachs et al., 2004; Sachs, 2006). Models have predicted that partner choice mechanisms can act alone to support intra-specific cooperation (Eshel & Cavalli-Sforza, 1982; Noë, 1990; Noë & Hammerstein, 1994) and empirical examples appear to fulfil these predictions. Examples include nuptial gifts in scorpionflies (Thornhill, 1976, 1984) and bushcrickets (Gwynn, 1988), as well as coalitions in baboons (Noë, 1990) and common eiders (Ost et al., 2003, 2005). Partner choice in a market of potential symbionts can constrain cheating, but only if the following conditions apply: (i) A range of partners is available, (ii) there is a mechanism for effecting choice, and (iii) the cost of evaluating partners is less than the benefit derived from choosing a good partner (Simms & Taylor, 2002).

## 16. Stochasticity, complex systems and self-organization

*A striking difference between linear and nonlinear laws is whether the property of superposition holds or breaks down. In a linear system the ultimate effect of the combined action of two different causes is merely the superposition of the effects of each cause taken individually. But in a nonlinear system adding two elementary actions to one another can induce dramatic new effects reflecting the onset of cooperativity between the constituent elements. This can give rise to unexpected structures and events whose properties can be quite different from those of underlying elementary laws, in the form of abrupt transitions, a multiplicity of states, pattern formation, or an irregularly markedly unpredictable evolution of space and time referred to as deterministic chaos. Nonlinear science, is therefore, the science of evolution and complexity.*

*Nicolis 1995, pp 1–2*

### Summary

**Complex systems are characterized by interacting units that display global properties not present at the lower level. Complex adaptive systems also require stochastic factors, e.g. noise and fluctuations. For self-organization to arise, a system needs to exhibit two properties: it must be both dissipative and nonlinear. Generally, the polarity of randomness and law characterizes the self-creating natural world. Only with an intermediate level of stochastic variation, somewhere between determined rigidity and literal chaos local interactions give rise to complexity. Cooperative behavior on various levels is an emergent phenomenon of self-organized systems. Both the formation of swarms and division of labor in a colony are self-organized behaviors at the group level as an emergent consequence of individuals' interactions.**

To begin with, the term complex is a relative one. Individual organisms may use relatively simple behavioral rules to generate structures and patterns at the collective level that are relatively more complex than the components and processes from which they emerge. Systems are complex not because they involve many behavioral rules and large numbers of different components but because of the nature of the system's global response. Complexity and complex systems, on the other hand, generally refer to a system of interacting units that displays global

properties not present at the lower level. These systems may show diverse responses that are often sensitively dependent on both the initial state of the system and nonlinear interactions among its components. Since these nonlinear interactions involve amplification or cooperativity, complex behaviors may emerge even though the system components may be similar and follow simple rules (Camazine et al., 2001). Life reflects all the key characteristics of complex systems: living organisms have a large number of interdependent constituents that often behave chaotically, span across several organizational scales, show collectivity and emergence, and maintain a balance between cooperation and competition (Baranger, 2000; Baffy & Loscalzo, 2014). Complex biological systems manifest a large variety of emergent phenomena among which prominent roles belong to self-organization and swarm intelligence (Proulx, 2007). Complexity, in Ashby's sense, is essentially conceived as a system's potential to assume a large number of states, and we also have a measure for it: variety, the number of states a system can assume (Schwaninger, 2004).

Complex systems, by their very nature, do not yield to a traditional reductionist approach (Hartwell et al., 1999; Kitano, 2002; Vendruscolo et al., 2003). Such systems are made up of a large number of distinct parts which interact and are often organized hierarchically (Weng et al., 1999; Csete & Doyle, 2002; Milo et al., 2002; Oltvai & Barabasi, 2002). The complexity of a system scales with the number of its elements, the number of interactions between them, the complexities of the elements, and the complexities of the interactions (Gershenson, 2002, 2005). This can be confirmed mathematically in certain systems. As a general example, random Boolean networks (Kauffman 1969; 1993; Gershenson, 2004) show clearly that the complexity of the network increases with the number of elements and the number of interactions. The result is a dazzling multiplicity of possible patterns of behavior that makes it extremely difficult to predict and control the course of events, as is well known in weather or in financial market forecasting (Goldenfeld & Kadanoff, 1999; Vendruscolo et al., 2003).

For self-organization to arise, a system needs to exhibit two properties: it must be both dissipative and nonlinear. Generally, the polarity of randomness and law characterizes the self-creating natural world (Carr, 2004). Heinz von Foerster (1960) formulated the principle of "order from noise". He noted that, paradoxically, the larger the random perturbations ("noise") that affect a system, the more quickly it will

self-organize (produce "order"). Another reason for this intrinsic robustness is that self-organization thrives on randomness, fluctuations or "noise". An important factor to consider when understanding the collective behaviors of animal groups (and self-organized pattern-forming processes in general) is the influence of stochastic (random) events. Animal behavior is inherently probabilistic, and stochastic properties of animal movement are likely to strongly influence the structure of many groups. It is becoming increasingly evident that self-organized patterns often arise because of the amplification of random fluctuation (Nicolis & Prigogine, 1977; Seeley, 1995). By developing stochastic computer models of animal groups the essential statistical mechanics of the system may be captured (Grünbaum, 1998; Couzin & Krause, 2003).

Self-organization is a set of dynamical mechanisms whereby structures appear at the global level of a system from interactions among its lower-level components, without being explicitly coded at the individual level (Garnier et al., 2007). "It relies on four basic ingredients: (1) The first component is a positive feedback that results from the execution of simple behavioral "rules of thumb" that promote the creation of structures. For instance, trail recruitment to a food source is a kind of positive feedback which creates the conditions for the emergence of a trail network at the global level.

(2) Then we have a negative feedback that counterbalances positive feedback and that leads to the stabilization of the collective pattern. In the example of ant foraging, negative feedback may have several origins. It may result from the limited number of available foragers, the food source exhaustion, and the evaporation of pheromone or a competition between paths to attract foragers.

(3) Self-organization also relies on the amplification of fluctuations by positive feedbacks. Social insects are well known to perform actions that can be described as stochastic. Such random fluctuations are the seeds from which structures nucleate and grow. Moreover, randomness is often crucial, because it enables the colony to discover new solutions. For instance, lost foragers can find new, unexploited food sources, and then recruit nest mates to these food sources.

(4) Finally, self-organization requires multiple direct or stigmergic interactions among individuals to produce apparently deterministic outcomes and the appearance of large and enduring structures.

In addition to the previously detailed ingredients, self-organization is also characterized by a few key properties:

(1) Self-organized systems are dynamic. As stated

before, the production of structures as well as their persistence requires permanent interactions between the members of the colony and with their environment. These interactions promote the positive feedbacks that create the collective structures and act for their subsistence against negative feedbacks that tend to eliminate them.

(2) Self-organized systems exhibit emergent properties. They display properties that are more complex than the simple contribution of each agent. These properties arise from the nonlinear combination of the interactions between the members of the colony.

(3) Together with the emergent properties, non linear interactions lead self-organized systems to bifurcations. A bifurcation is the appearance of new stable solutions when some of the system's parameters change. This corresponds to a qualitative change in the collective behavior.

(4) Last, self-organized systems can be multi-stable. Multi-stability means that, for a given set of parameters, the system can reach different stable states depending on the initial conditions and on the random fluctuations" (Garnier et al., 2007).

According to the self-organization approach, by studying interactions on a lower level, the emergence of a macrostructure on a higher level is perceived and, therefore, better understood (Hogeweg, 1988). Patterns of interactions at a group level arise from local interactions between individuals and their environment. By interacting, individuals change each other and, therein, their social environment. In turn, the developing social structure feeds back to the individuals and shapes their interactions, etc. Individual and group behaviors become a product of social dynamics (Moore et al., 1997; Wolf et al., 1998; Fewell & Page, 1999; Camazine et al., 2001; Clark & Fewell, 2014). Experiments with robots have demonstrated that cooperative behavior which looks complex and sophisticated to an observer can be nothing more than the result of straightforward, simple interactions between agents and their local environment (Maris & te Boekhorst, 1996). Consequently, this approach attributes the complexity of social interaction patterns to interactions between entities rather than their internal complexity (Hemelrijk, 1999, 2002). This reflects a shift of focus from objects to relationships (Cohen & Stewart, 1994), whereby relationships are often considered to be self-reinforcing. Moreover, natural selection will often operate, not on single traits, but on self-organized patterns (Boerlijst & Hogeweg, 1991; Hemelrijk, 1999). To gauge the complexity-generating effects of interindividual interactions, Hemelrijk (1996, 1997) investigated the 'social organisation' of a group of

simple, artificial agents by means of an individual-oriented model. In a virtual world, cooperation emerged as a self-organized phenomenon. These effects arose without considering any particular costs or benefits associated with acts of cooperation and defection but were due to the intertwined effects of displaying dominance and social cohesion (Hemelrijk, 1997). With self-organization, complexity and emergence, the realization increasingly shared by many scientists is that behavior at one 'level' is then more than the 'sum' of the behavior of individual entities (Skår & Coveney, 2003).

Cooperative behavior on various levels is associated with self-organization phenomena (Deneubourg et al., 2002; Hemelrijk, 2002, 2005; Miramontes & DeSouza, 2014; Szolnoki et al., 2014). Models of self-organized systems are able to explain the emergent cooperative behavior of microorganisms (Ben-Jacob et al., 1994, 2000, 2004) and groups of animals such as insects (Dussutour et al., 2004; Jeanson et al., 2005; Detrain & Deneubourg, 2006), fishes (Couzin et al., 2005; Ward et al., 2008), birds (Hildenbrandt et al., 2010; Hemelrijk & Hildenbrandt, 2012), primates (Puga-Gonzalez et al., 2009; Hemelrijk & Puga-Gonzalez, 2012) and humans (Moussaid et al., 2010). *D. discoideum* aggregation following metabolic stress (see chapter 5.2) displays emergence of cooperative behavior as a result of self-organization (Marée & Hogeweg, 2001). To this date, the wavelike patterns observed during *D. discoideum* aggregation represent one of the most beautiful and best understood examples of spatiotemporal self-organization at the cellular level (Goldbeter, 2006; Gregor et al., 2010). The wavelike nature of aggregation (Gerisch, 1968; Alcantara & Monk, 1974; Gerisch et al., 1975) results from the existence of an oscillatory cellular rhythm in the production of cAMP (Gregor et al., 2010; Prindle & Hasty, 2010).

## 16.1 Stochasticity of swarms

### 16.1.1 Swarm behavior

Groups of many kinds of fishes show a characteristic social aggregation, school (Shaw, 1978). The problem of why fish groups make schooling behaviors has often been studied based on the evolutionary assumption that schools must increase the survivorship or reproductive success of individuals in the school (Breder, 1967; Cashing & Harden-Jones, 1968; Magurran, 1990; Pitcher & Parrish, 1993). Selection forces related to the location and acquisition of food and predator-prey interactions may have played very important roles in shaping the evolution of aggregating behavior (Zheng et al., 2005).

Schools make frequently sharp turns or accelerations in which every individual within the school appears to react simultaneously. However, it has been revealed (Partridge, 1981, 1982) that individuals within a school do not all respond instantaneously to course change by other individuals but there is a well-defined latency or lag. The properties of a shoal are the product of local rules between neighboring fish that, via self-organization, generate behavior at the group level as an emergent consequence of individuals' interactions (Parrish et al., 2002; Vabø & Skaret, 2008; Rieucau et al., 2014). Intriguingly, the role of stochasticity extends to features like facilitation of coherence in collective swarm motion (Yates et al., 2009). An individual's response to a loss of alignment in the group is increased randomness of its motion, until an aligned state is again achieved. The phenomena of using randomness to keep the group ordered appears counterintuitive but has been reported at the level of an individual (Douglass et al., 1993) and at the collective level in an ecological system (Yates et al., 2009). Furthermore, the lack of sources of environmental noise indicates that the noise-induced alignment seems to be an intrinsic characteristic of collective coherent motion. The frequency of stochastic asynchronous updating of individual positions and orientations increases with perceived threat and leads to more synchronized group movement, with speed and nearest-neighbor distributions becoming more uniform (Bode et al., 2010a, b). In fact, experiments with three-spined sticklebacks (*Gasterosteus aculeatus*) that were exposed to different threat levels suggest that the behavior of fish (at different states of agitation) can be explained by a single parameter in the model, the updating frequency.

A widely appreciated benefit of group membership is the reduction in cost of locomotion for individuals that trail behind others, taking advantage of the vortices, e.g. birds flying in a V formation or fish schooling (Weihs, 1973; Cutts & Speakman, 1994; Weimerskirch et al., 2001; Marras et al., 2014; Portugal et al., 2014), or zones of low pressure (e.g. bicyclists drafting in a peloton or vehicles on a motorway) created by their leading group mates (McCole et al., 1990; Dominy, 1992; Fish, 1999). Such energetic savings can be significant enough to be considered one of the main benefits of group membership for schooling fish, flocking birds and cycling humans (Fish, 1999; Krause & Ruxton, 2002; Liao et al., 2003).

### 16.1.2 Swarm intelligence

Stochastic environments confront organisms with unfamiliar situations. As one solution to the problem of

uncertainty, organisms can attempt to reduce the uncertainty associated with key features of their environments by collecting and storing information. By sampling each of its options regularly, animals gain from being able to exploit them when they are productive and avoid them otherwise. In this way, collecting information can be thought of as a solution to the uncertainty problem that maximizes potential opportunities (Stephens, 1989; Mangel, 1990; Dall & Johnstone, 2002). Unpredictable or variable environments favor the evolution of cognition and learning (Bergman & Feldman, 1995; Richerson & Boyd, 2000; Godfrey-Smith, 2002; Mery & Kawecki, 2002; Brown et al., 2003; Kerr & Feldman, 2003; Borenstein et al., 2008; Kotschal & Taborsky, 2010; Clarin et al., 2013; Tebbich & Teschke, 2014) and cognition/learning is thought to enable organisms to deal with environmental heterogeneity (Godfrey-Smith, 2002). Reviews of the factors contributing to the emergence of social learning emphasize the role played by a spatially and temporally changing environment (Laland et al., 2000; Richerson & Boyd, 2000; Alvard, 2003; Henrich & McElreath, 2003; Aoki et al., 2005). Social learning has been observed in a wide range of species in diverse taxa including mammals (Perry & Manson, 2003; Galef & Laland, 2005; Perreault et al., 2012), birds (Lefebvre, 2000; Benskin et al., 2002), fish (Brown & Laland, 2003), and invertebrates (Leadbeater & Chittka, 2007a, b). Social interactions form one part of a complex environment and intelligence and learning may have evolved to navigate the social world (Humphrey, 1976; Byrne, 1996; Byrne & Bates, 2007; Borenstein et al., 2008; Hamblin & Giraldeau, 2009; Arbilly et al., 2010; Dubois et al., 2010; Katsnelson et al., 2012; Smead, 2014).

The study of swarm intelligence is deeply embedded in the biological study of self-organized behaviors in social insects (Garnier et al., 2007). Social animals choose between alternative actions (Conradt & Roper, 2005; King & Cowlshaw, 2009) that is vital if a group is to remain a cohesive unit and accrue the many advantages of group living (Krause & Ruxton, 2002). Couzin and Krause (2003) wrote: "Information transfer among individuals is likely to influence their response to stimuli, such as the positions of resources, or favorable regions within a heterogeneous environment. In aquatic habitats, for example, resources such as phytoplankton, the temperature or salinity of the water, and concentrations of dissolved gases are all known to vary in a nonuniform way, and over both small and large length scales. Individuals are therefore expected to modify their positions with respect to these properties so as to maximize resource intake and minimize physiological stress. However, this is a

nontrivial task: unpredictability and local fluctuations make finding and moving up or down such environmental gradients (taxis) difficult when an individual has only local knowledge on which to base its motion. Grünbaum (1998) used computer simulation to investigate the theoretical consequences of grouping to such taxis behavior. He assumed individuals use a simple form of taxis, known as klinotaxis, whereby a moving individual modifies its probability of making a turn as a function of whether conditions are perceived to improve or deteriorate over a given time interval. Such behavior is known to facilitate taxis in even simple organisms, such as bacteria (Keller & Segel, 1971; Alt, 1980; Tranquillo, 1990). Although they are not directly detecting the gradient, individuals performing such taxes will, on average, spend more time moving in favorable directions than in unfavorable ones. By simulating groups of individuals performing this behavior under conditions in which they do not interact with one another (asocial taxis) and do interact by balancing the tendency for taxis with a simple schooling behavior (social taxis), Grünbaum (1998) demonstrated that such social interactions improve the motion of individuals up a gradient. The alignment of individuals, and thus transfer of information, when schooling, allows averaging of individual errors in gradient detection, and therefore results in reduced deviations in motion from the desired direction of travel. This information sharing within schools of fish has been likened to a 'sensory array' (Kils, 1986), which allows information to be gathered over a wider spatial range than would be possible for a solitary or noninteracting individual, and dampens the influence of small-scale fluctuations in the environment. The model also predicts that the benefits of such information sharing are dependent on group size. As group size is increased the efficiency of taxis shows an asymptotic increase: initially it increases steeply, but then the rate of increase reduces over time, leading to a plateau where further increases in group size have little effect on taxis accuracy."

A large amount of work suggests that a social-insect colony is a decentralized system comprised of cooperative, autonomous units that are distributed in the environment, exhibit simple probabilistic stimulus response behavior, and only have access to local information (Deneubourg & Goss, 1989; Bonabeau et al. 1997; Theraulaz et al. 1998, 2003; Camazine et al. 2001). Without centralized control, workers are able to work together and collectively tackle tasks far beyond the abilities of any one individual. The resulting patterns produced by a colony are not explicitly coded at the individual level, but rather they emerge from

myriads of simple nonlinear interactions between individuals or between individuals and their environment (Theraulaz et al., 2003). The decisive factor favoring social learning in insects may not be coloniality, as suggested by the comparison between colonial and solitary bees (Dukas, 1987; Dukas & Real, 1991), but more simply the opportunity to interact with organisms sharing similar ecological needs and constraints (Coolen et al., 2005; Worden & Papaj, 2005). Social interaction can provide a solution to a cognitive problem via two potential mechanisms: (i) individuals can aggregate information, thus augmenting their 'collective cognition', or (ii) interaction with conspecifics can allow individuals to follow specific 'leaders', those experts with information particularly relevant to the decision at hand. For repeated decisions—where individuals are able to consider the success of previous decision outcomes—the collective's aggregated information is almost always superior (Katsikopoulos & King, 2010). Social/swarm intelligence can facilitate solving cognitive problems that go beyond the capacity of single animals (Kennedy et al., 2001; Garnier et al., 2007; Hinchey et al., 2007; Moussaid et al., 2009; Katsikopoulos & King, 2010; Krause et al., 2010). In most cases, the collective decisions and patterns arise as a result of competition between different sources of information which can be amplified in different ways (De Schutter et al., 2001). As shown in ants and honeybees, quorum sensing is used to collate individual assessments and form them into a collective decision (Pratt et al., 2002; Seeley & Visscher, 2004). Individual animals show irrational changes in preference (Latty & Beekman, 2011). The collective decisions of insect societies are immune to irrationality due to the colonies' decentralized decision mechanism that may prevent systematic errors that would otherwise arise from the cognitive limitations of individuals (Edwards & Pratt, 2009). Research on collective behavior and group-decision-making in animals has shown that individuals in groups can outperform solitary individuals (Bonabeau et al., 1999; Camazine et al., 2001; Couzin, 2009; Krause et al., 2010). Group-living has important consequences for the performance of individuals in anti-predator contexts (Krause & Ruxton, 2002; Beauchamp, 2013). In predator detection, groups achieve higher true positives (Pulliam, 1973; Powell, 1974; Siegfried & Underhill, 1975; Kenward, 1978; Lazarus, 1979; van Schaik et al., 1983b; Cresswell, 1994; Wolf et al., 2013) and diminish the negative consequences of false positives by using a behavioral rule that does not respond to single but only to multiple other individuals (Lima, 1994; Roberts, 1997; Proctor et al., 2001;

Beauchamp & Ruxton, 2007; Beauchamp, 2010; Wolf et al., 2013).

Brains, e.g. of mammals, can be considered as societies of neurons and similar adaptive network processes may be involved during cognitive processes generated by central nervous systems and social insects (Schall, 1999, 2001; De Schutter et al., 2001; Shadlen & Newsome, 2001; Fewell, 2003; Heekeren et al., 2004; Couzin, 2009). In the case of social insect societies, the insects must organize their workforce efficiently in order to survive. This organization involves making collective decisions that optimize the colony's fitness (Sumpter & Beekman, 2003). Thus, both ants and honeybees are capable of choosing collectively the best of several possible new nest sites during migration or swarming (Seeley, 1995; Sumpter & Beekman, 2003) or turn individual and collectively gathered information into foraging success (Wilson, 1971; Hölldobler, 1976; Aron et al., 1989; Traniello, 1989; Crist & MacMahon, 1991; Mull & MacMahon, 1997; Flanagan et al., 2012; Letendre & Moses, 2013). Even bacterial colonies, swarms and films exhibit an unanticipated complexity of behaviors that can undoubtedly be characterized as based on biogenic cognition (Ben-Jacob et al., 2004, 2006; Waters & Bassler, 2005; van Duijn et al., 2006; Ben-Jacob, 2008, 2009; Ng & Bassler, 2009).

During a century of research on social learning, the focus has been largely on interactions between conspecifics. Examples of studies on learning from members of other species are rare (e.g. Seyfarth & Cheney, 1990; Coolen et al., 2003; Rainey et al., 2004; Seiler et al., 2013), yet, there is no a priori reason to treat those cases differently. In fact, where resources are shared or where generalist predators lurk, picking up information from heterospecifics may be just as valuable as from members of the same species (Leadbeater & Chittka, 2007b).

## 16.2 Division of labor due to self-organization

In nature, division of labor, in the broad sense of the expression, is widespread. The main evolutionary transitions, such as those from prokaryotes to eukaryotes and from unicellular to multicellular organisms, were accompanied by division of labor (Szathmáry & Maynard Smith, 1995). Within social groups, division of labor is also common. In species with biparental care, males and females frequently have different roles in raising the offspring. In hornbills, for example, breeding females seal themselves in the nest, and males must feed them during this time (Kemp & Woodcock, 1995). Group hunting (e.g., Gazda et al., 2005), sentinel behavior in group foragers such as meerkats (Manser, 1999), and

specialization in either predator defense or provisioning in noisy miners (Arnold et al., 2005) are other examples of division of labor. Division of labor occurs when individual members of a group specialize by performing particular tasks toward some common goal. Division of labor is an important aspect of cooperative behavior (Robinson, 1992; Crespi, 2001; Wahl, 2002a, 200b; Arnold et al., 2005) that increases the entire group's productivity (Michod & Roze, 2001; Lnger et al., 2004; Pruitt & Riechert, 2011). Among vertebrates, division of labor is not strictly caste based, but rather varies by age, sex and size (such behavioral differences between categories of individuals are known as 'polyethisms'; e.g. naked mole rats *Heterocephalus glaber*; Lacey & Sherman, 1991, 1997; meerkats; Clutton-Brock et al., 2003; white-winged crows *Corcorax melanorhamphos*; Heinsohn & Cockburn, 1994; and cichlids *Neolamprologus pulcher*; Bruintjes & Taborsky, 2008).

The ecological success of social insects can be mainly attributed to their division of labor (Oster & Wilson, 1978; Wilson, 1985, 1987; Hölldobler & Wilson, 1990; Myerscough & Oldroyd, 2004). Highly specialized individuals are thought to contribute to colony fitness by working more efficiently than less specialized workers (Oster & Wilson, 1978; Heinrich, 1979; Calabi & Traniello, 1989; Beshers & Fewell, 2001; Chittka & Muller, 2009; Pruitt & Riechert, 2011). The fittest populations are those that divide tasks fairly and associate in large, highly specialized groups. Generalists have a distinct advantage in small groups, but the presence of generalists lowers group fitness. A model (Wahl, 2002) suggested a tendency for populations to evolve increasingly unfair divisions of labor. This implies that an evolutionary ratchet favors disparity between the workload of specialist populations (Wahl, 2002). *Temnothorax longispinosus* ant colonies with more intracolony behavioral variation as an important component of division of labor in brood care, aggression and exploration of novel objects were more productive under standardized conditions than colonies with less variation (Modlmeier & Foitzik, 2011; Modlmeier et al., 2012). Importantly, the concept of specialization is a statistical one, reflecting an individual's tendency to perform particular tasks more often than others. The strength of this tendency may vary greatly, ranging from temporary behavioral differentiation to fixed morphological differentiation in insect species that form large societies (Robinson, 1992).

Changes in division of labor can be induced experimentally by altering colony size (Winston & Fergusson, 1985) or demography (Rösch, 1930) or by

increasing the need for nest maintenance (Gordon, 1991), nest repair (O'Donnell & Jeanne, 1990), additional storage comb (Rösch, 1930; Kolmes, 1985; Fergusson & Winston, 1988), and defensive behavior (Gordon, 1991). Proximate analyses of division of labor generally are based on the concept of self-organization (Duarte et al., 2011). According to this view, division of labor emerges spontaneously at the origins of sociality, before becoming a target of natural selection, due to the interaction of individuals obeying simple behavioral rules (Bonabeau et al., 1997; Page & Mitchell, 1998). This concept has been supported by behavioral experiments showing that normally solitary harvester ant queens and halictine bees exhibit task specialization when forced to associate, i.e., paired individuals dedicated most of their time to different tasks (Page, 1997; Fewell & Page, 1999; Beshers & Fewell, 2001; Camazine et al., 2001; Helms Cahan & Fewell, 2004; Jeanson et al., 2005, 2008; Jeanson & Fewell, 2008; Holbrook et al., 2009; Helms Cahan & Gardner-Morse, 2013). The division of labor among cofounding queens results from dominance interactions in wasps (Pratte, 1989; Strassmann, 1989) and in small ant societies (Bourke, 1988b; Ito & Higashi, 1991). These aggressive interactions occur when the cofounding queens are both related (Bourke, 1988b; Pratte, 1989; Strassmann, 1989; Ito & Higashi, 1991) or unrelated (Kolmer & Heinze, 2000). In the ant *Cerapachys biroi*, where genetic variation within colonies is constrained by parthenogenesis, individual experience and learning is crucial for self-organized task specialization (d'Ettorre, 2007; Ravary et al., 2007). In addition, increasing evidence supports the role of genetic factors in the process of caste determination and division of labor in several species (Calderone & Page, 1988; Frumhoff & Baker, 1988; Page & Robinson, 1991; Dreller et al., 1995; O'Donnell, 1996; Julian & Fewell, 2004; Anderson et al., 2008; Crozier & Schlüns, 2008; Lo et al., 2009; Schwander et al., 2010; Libbrecht et al., 2011). For example, in species with multiply mated queens or multiple queens per colony, different patriline and matriline tend to differ in their tendencies to perform certain tasks, demonstrating a genetic component in response threshold (e.g. Robinson & Page, 1988; Page & Robinson, 1991; Page et al., 1998). Epigenetic DNA methylation is associated with differential gene expression in castes of the honeybee, *Apis mellifera*, and ants (Kucharski et al., 2008; Elango et al., 2009; Chittka & Chittka, 2010; Bonasio et al., 2012; Chittka et al., 2012; Foret et al., 2012; Smith et al., 2012; Shao et al., 2014). Worker development is associated with increased DNA methylation; larvae reared in vitro with RNAi

knockdown of DNA methyl transferase 3 show greatly increased probabilities of developing into queens (Kucharski et al., 2008). DNA methylation might serve as a developmental switch to regulate the expression of many downstream genes involved in determining caste fate, including IIS-related genes (Smith et al., 2008). In addition, neural network processes have been proposed to account for the emergence of intracolony task allocation on the basis of variation in response thresholds (Lichocki et al., 2012).

It has been shown (Simpson, 2012) that at the transition from unicellularity to multicellularity, a reproductive division of labor will evolve first in a majority of cases, and that the total extent of functional differentiation will be larger if there is a reproductive division of labor. Accordingly, specialization of cells in reproductive (germ cells) and vegetative functions (soma) is an universal feature of unitary multicellular life. Conflicts between units arise when the selection pressures on some of the units favor one outcome, whereas those on other units favor another. The most basic conflict is between units of the same species or organism when selection pressure on one of the units favors the survival of its own lineage over survival of the lineage of the other unit. These conflicts with their Red Queen coevolutionary dynamics underlie the evolutionary dynamics of functional differentiation within and between organisms and their speciation.

## 17. Stochasticity, lotteries and insurance

### Summary

**Stochastic environments force organisms into risky lotteries (see chapter 5.4). On the other hand, insurance is the risk-sharing strategy of risk-averse agents that have to compete in lotteries. It is a common observation that people/foragers exhibit risk-aversion when making some choices while also exhibiting risk-preference in other cases. Swarm formation in response to predator pressure is a prototypic insurance against idiosyncratic risk. The defense-worthy fortress providing shelter from predation, a favorable microclimate, and sometimes food, is a life insurance. Social queuing processes, i.e. waiting peacefully in line to potentially acquire dominant status in the future, seem to occur in a wide variety of taxa and life histories. Queuing can be regarded as conservative bet-hedging strategy compared to the risky alternative, dispersal. In a range of queuing species, offspring that delay**

**dispersal and wait on their natal territory either gain better quality territories or are more likely to breed than their siblings that disperse as juveniles. Assured fitness returns models argue that patterns of adult mortality combine with offspring dependence on parental care to select for group living. Assured fitness return represents a type of conservative bet-hedging strategy in a general sense, because a solitary female that survives the period of her brood's dependence would have the highest reproductive success, but brooding females in multifemale colonies trade the possibility for maximum reproductive success for a greater mean reproductive success.**

In nature, individuals have to choose from sets of risky alternatives. Stochastic environments force organisms into lotteries. The lotteries may involve either idiosyncratic risk or aggregate uncertainty or both (Robson, 1996). Idiosyncratic risk, respectively uncertainty, is risk or uncertainty to which only specific agents are exposed, in contrast to systematic or aggregate risk/uncertainty that is faced by all agents in the market. For example, the weather is a standard example of aggregate risk—a very harsh winter may kill all members of a population. In evolution, often risk is a combination of systemic component stemming primarily from the impact of unfavorable weather events and of an idiosyncratic component depending on individual characteristics and events. Cooper and Kaplan (1982) have demonstrated that when lotteries are aggregate, the optimal decision rule involves randomization. Via the law of large numbers, evolution generated a form of automatic biological insurance against idiosyncratic risk, whereas this insurance is inoperative in the same sense against aggregate uncertainty (Robson, 1996).

### **17.1 Swarm formation as insurance**

Animals form more cohesive or larger groups, with consequent greater mutualistic benefits under greater predation risk (Seghers, 1974; Farr, 1975; Dunbar, 1988; Spieler, 2003; Krams et al., 2010). Empirical and theoretical studies suggest an antipredation-function of animals forming aggregations (Hamilton, 1971; Pulliam, 1973; McNamara & Houston, 1992; Krebs & Davies, 1993; Lima, 1995; Fréon & Misund, 1999; Coleman et al., 2004; Caro, 2005; Brierley & Cox, 2010; Ioannou et al., 2012). It has been shown that the perception of an increase in the risk of predation can induce cooperative behavior in some bird species (Krams et al., 2010) and other taxa with and without kinship (Lavalli & Herrnkind, 2009). Although most studies focused either on the prey or the predator side, the few studies that tackled both

sides of the mechanisms simultaneously showed an optimization of the grouping strategies for both prey and predators (Major, 1978; Lett et al., 2004, 2014; Fryxell et al., 2007; Vaughn et al., 2010).

Attacks at high prey densities may decrease when prey has active or inducible defense behavior such as aggregation or swarming that is induced by predators as emergent behavior at high prey densities (Jeschke & Tollrian, 2005, 2007; Jeschke, 2006; Krams et al., 2010; Vucic-Pestic et al., 2010). Fish in large groups have a reduced per capita risk of predation as a result of several mechanisms, including earlier predator detection, numerical dilution of risk and predator confusion during attacks (e.g. Neill & Cullen, 1974; Magurran et al., 1985; Morgan & Godin, 1985; Godin, 1986; Pitcher & Parrish, 1993; Krause & Godin, 1995; Hoare et al., 2004). One main way that the school reduces a predator's chance of making a successful kill is to confuse the predator as it makes its strike (Zheng et al., 2005). A predator facing a large number of fish quickly moving together has difficulty in singling out and tracking individual fish in a group. This confusion effect has been studied by many researchers (e.g. Major, 1978; Pitcher & Parrish, 1993). Neil and Cullen (1974) demonstrated by observing the hunting behavior of cephalopods and fish predators that for all species the increasing size of prey fish group decreased the success of the predators' attacks per encounter with a prey. A much greater success rate per attack has been achieved if single preys are targeted (Zheng et al., 2005).

### **17.2 Fortress defense**

Evolution of sociality in colonial invertebrates, social insects, and nonhuman mammals is likely to have often been driven by the adaptive nature of fortress defense. The fortress providing shelter from predation, a favorable microclimate, and sometimes food, is a life insurance (Foster & Northcott, 1994; Choe & Crespi, 1997; Queller & Strassmann, 1998; Pike & Foster, 2004; Wilson, 2008). Nest architectures obtained by simulations show that the complexity of the structures that are built by social insects is based on simple probabilistic stimulus-response behaviors but does not require sophisticated individual behavioral rules (Garnier et al., 2007). Property in the form of a private nest is an important preadaptation for eusociality (Alexander, 1974). One of the most familiar features of vertebrate or invertebrate social cooperation is a burrow, nest, hive or gall (e.g. ant, termite or bird nests, rodent burrows, beehives or aphid galls), usually made by the animals (Choe & Crespi, 1997). All of the clades known with primitively eusocial species surviving (in aculeate wasps, halictine and xylocopine

bees, sponge-nesting shrimp, termopsid termites, colonial aphids and thrips, ambrosia beetles, and naked mole rats) have colonies that have built and occupied defensible nests (Wilson, 2008). The nest functions not only as a shelter for the queen and the brood, but may buffer individuals from temperature changes and enables the storage of food as an insurance against the vagaries of nature. In a sequence of events, the first stage and causative agent is the advantage of a defensible nest, especially one both expensive to make and within reach of adequate food (Nowak et al., 2010). Nowak et al. (2010) further argued: "In a few cases, unrelated individuals join forces to create the little fortresses. Unrelated colonies of *Zootermopsis angusticollis*, for example, fuse to form a supercolony with a single royal pair through repeated episodes of combat (Johns et al., 2009). In most cases of animal eusociality, the colony is begun by a single inseminated queen (Hymenoptera) or pair (others). In all cases, however, regardless of its manner of founding, the colony grows by the addition of offspring that serve as non-reproductive workers. Inclusive fitness theorists have pointed to the resulting close pedigree relatedness as evidence for the key role of kin selection in the origin of eusociality, but as argued here and elsewhere (Wilson & Wilson, 2007, 2008), relatedness is better explained as the consequence rather than the cause of eusociality." Group living among kin (who might come together merely by virtue of being neighbors) will evolve more easily (West-Eberhard, 1978; Schwarz, 1988). Grouping by family can hasten the spread of eusocial alleles, but it is not the causative agent of eusociality (Nowak et al., 2010).

Sexually reproducing organisms should carry at least a twofold disadvantage with regard to the evolution of altruism since the benefits are at least multiplied by 0.5 while in clonal and parthenogenetic organisms with  $r = 1$ , altruism should arise much more easily. Clonality is often cited as a fundamental pillar of the evolution of the extreme aphid altruism that is sometimes observed (e.g., Krebs & Davies, 1993) and it has been claimed that the relatedness value of 1 often seen in aphids is the ultimate predisposition to altruism. However, the rarity of social aphid species (which represent just 1% of aphids) provides a clear demonstration that clonality alone is not sufficient to produce altruism (Stern & Foster, 1996; Pike & Foster, 2008). In a number of aphid species, kin recognition was sought, but not found (Aoki et al., 1991; Foster & Benton, 1992; Carlin et al., 1994; Miller, 1998a; 2004; Shibao, 1999). Clonal mixing may be facilitated by this inability. In a *Pemphigus* species, which is highly

social, *P. obesinymphae*, the average level of clonal mixing is 41% with a range of 21–71% (Abbot et al., 2001). In *P. spyrothecae*, a species which is also highly social, microsatellite genotyping has been used to demonstrate that the average level of clonal contamination was 10%, albeit with a great range that varied from 0–59% (Johnson PCD et al., 2002). Abbot et al. (2001) were also able to confirm theoretical predictions by demonstrating that the invaders had (i) a vastly reduced propensity to defend and (ii) developmental rates that were accelerated such that they reached the reproductive stage more quickly than individuals of the host clone. One of the key correlates of aphid sociality is the galling habit. Whereas not all gall-forming aphids are social, all of the approximately 60 aphid species that are known to be social do form galls on a host plant at some point in their life cycle (Foster & Northcott, 1994). It thus follows that galling life must convey crucial selective predispositions to sociality, over and above its more general selective advantages such as protection from hygrothermal stress and enemies and improved nutrition (Price et al., 1987). Because galls are a rich and truly invaluable resource to the aphids which create and inhabit them, they are ideal examples of defense-worthy fortresses (Queller & Strassman, 1998). The implications that the galling habit holds for the evolution of sociality have been reviewed by Foster and Northcott (1994) and Pike and Foster (2008).

### 17.3 Social queuing as lottery

Traditionally mainly indirect benefits have been considered to explain cooperative behavior like cooperative breeding. The group augmentation hypothesis (Woolfenden, 1975; Rood, 1978; Brown, 1987; Kokko et al., 2001) states that if helpers in cooperatively breeding animals raise the reproductive success of the group, the benefits of living in a resulting larger group favor the evolution of helping behavior. Kingma et al. (2014) illustrated that direct benefits of group augmentation can accrue via different evolutionary mechanisms that relate closely to well-supported general concepts of group living and cooperation (Kokko et al., 2001; Dierkes et al., 2005; Bergmüller et al., 2007; Clutton-Brock, 2009a; Heg & Taborsky, 2010; Sumner et al., 2010; Kingma et al., 2011; Wong & Balshine, 2011; Zöttl et al., 2013a). Helping might increase survivorship, or the possibility of eventually obtaining reproductive dominance in that group (Reyer, 1980; Wiley & Rabenold, 1984; Courchamp et al., 1999; Kokko & Johnstone, 1999; Pen & Weissing, 2000; Griffin & West, 2002).

Queuing processes, i.e. waiting peacefully in line to

acquire dominant status in the future, seem to occur in a wide variety of taxa (birds, fish, mammals, and invertebrates) and life histories (van de Pol et al., 2007; Field & Cant, 2009; Kingma et al., 2011; Sharp & Clutton-Brock, 2011; Wong & Balshine, 2011). Queue-like systems range from queues for mating opportunities (Schwagmeyer & Parker, 1987), social and breeding position in group-living and cooperative breeding species (Wiley & Rabenold, 1984; East & Hofer, 2000; Heg et al., 2005; Mitchell, 2005), positions on the lek (Kokko et al., 1998), or access to harems or colonies (Poston, 1997; Voigt & Streich, 2003) to queues for high-quality territories (Stacey & Ligon, 1991; Zack & Stutchbury, 1992; Ens et al., 1995; Ekman et al., 2001b). The queue hypothesis suggests that individuals maximize lifetime fitness by strategically waiting (queuing) for high quality breeding opportunities to become available, instead of immediately accepting a low-quality breeding opportunity (Zack & Stutchbury, 1992; Ens et al., 1995). In most cooperative vertebrates and many primitively social insects, subordinates apparently remain in or join groups as nonbreeders in expectation of inheriting a breeding position in the future (in Hymenoptera: e.g., Strassmann & Meyer, 1983; Samuel, 1987; Hughes & Strassmann, 1988; Field et al., 1999; Monnin & Ratnieks, 1999; Cant & Field, 2001; and in vertebrates: Wiley & Rabenold, 1984; Stacey & Koenig, 1990; Emlen, 1991; Creel & Waser, 1994; Poston, 1997; East & Hofer, 2001; Buston, 2003b, 2004).

Queuing can be regarded as conservative behavior compared to the risky alternative, dispersal. In a range of queuing species, offspring that delay dispersal and wait on their natal territory either gain better quality territories or are more likely to breed than their siblings that disperse as juveniles (Woolfenden & Fitzpatrick, 1984; Strickland, 1991; Walters et al., 1992; Ekman et al., 2001b; Green & Cockburn, 2001; Komdeur & Edelaar, 2001). Studies that measure bird survivorship and fecundity across a range of habitats reveal that individuals using the poorest measured habitats have lifetime fitnesses of less than one (Stacey & Ligon, 1987; Ligon & Ligon, 1990; Rabenold, 1990; Fitzpatrick et al., 1991; Komdeur, 1992; Ekman et al., 1999; Ridley & Sutherland, 2002). The decision to queue instead of leaving their natal nests and pursue other strategies may be a bet-hedging strategy (Yuan et al., 2006; Field, 2008). Subordinates can inherit dominance if they outlive those above them in the hierarchy (Strassmann & Meyer, 1983; Wiley & Rabenold, 1984; Field et al., 1999, 2006; Monnin & Peeters, 1999; Monnin & Ratnieks, 1999; Cant & Field, 2001). In many cooperative breeders, a proportion of

helpers can inherit their home territory (Woolfenden, 1975; Rood, 1978, 1990; Wiley & Rabenold, 1984; Dierkes et al., 2005; Hawn et al., 2007; Field & Cant, 2009; Sumner et al., 2010; Kingma et al., 2011, 2014; Leadbeater et al., 2011; Sharp & Clutton-Brock, 2011; Marino et al., 2012). Ragsdale (1999) defined the resource inheritance, a form of future direct benefit, as the probability of inheriting valuable resources multiplied by the expected number of offspring that an individual would produce after it inherits the resources (relative to a lone breeder). With resource inheritance, stable associations will form over a greater range of conditions, thus reducing the need for a 'social contract'. Inclusion of resource inheritance in reproductive skew theory generates predictions that are relevant to many social systems, including (under some conditions) parental facilitation, 'lazy workers', helping for 'payment', and complete skew when relatedness is zero or cooperative benefits are absent (Ragsdale, 1999). In green woodhoopoes (Hawn et al., 2007) and female dwarf mongooses (Rood, 1990), 58% and 43% of breeding positions, respectively, are obtained by inheritance. The scheme that individuals form a strict queue and move up in rank only when one of those ahead of them in the queue dies fits some species well (e.g., primitively social wasps: Field et al., 1999; Cant & Field, 2001, 2005; Sumner et al., 2002; vertebrates: Wiley & Rabenold, 1984; East & Hofer, 2001; Buston, 2003b, 2004). Alternative possibilities exist, however (Monnin & Ratnieks, 1999; Cant & Johnstone, 2000; Cant et al., 2006b). For example, in some termites, ants, mole-rats, and many primates, nonbreeders engage in vicious contests for any breeding vacancy that may arise (Pollock & Rissing, 1985; Pusey & Packer, 1987b; Myles, 1988; Clarke & Faulkes, 1997; Thorne, 1997). Even in the absence of a breeding vacancy, low rankers may jump the queue by attacking those of higher rank (e.g., groove-billed anis, Vehrencamp et al., 1986; dunnocks, Davies, 1992; hyenas, East & Hofer, 2001; many primates, Walters & Seyfarth, 1987).

Stable queues will select for the production of new recruits by helpers because the latter eventually will not only inherit a breeding position but also a group of helpers (the former recruits), and this exemplifies the benefits of group augmentation by delayed reciprocity (Wiley & Rabenold, 1984; Kokko et al., 2001a). An important feature of queuing decisions is their frequency-dependent nature, i.e. how many other individuals are queuing for the same opportunity (Shreeves & Field, 2002). Queuing is probably favored by selection because it confers a higher probability of ascending in rank than either dispersing or contesting. When ecological constraints are harsh and there is a

real threat of eviction, individuals may tolerate non-breeding positions in a society purely because of their potential to realize benefits in the future (Emlen, 1991; Kokko & Johnstone, 1999; Ragsdale, 1999; Buston, 2004). In queuing systems where joining decisions are based on inheritance prospects, egalitarian groups may be less attractive to a potential joiner than despotic groups. This is because the huge payoff of becoming the sole breeder in a despotic group may more than make up for the relatively low probability of reaching that position. By contrast, a subordinate joining an egalitarian group has a relatively high chance of inheriting one of the many breeding positions, but on doing so its offspring will face competition from those of other breeders for access to group resources (Cant & English, 2006).

Analysing models according to whether or not helpers can inherit their parents' territory, Pen and Weissing (2000) concluded that (i) territory inheritance always promotes cooperative breeding; (ii) if territories are not inherited, neither ecological constraints nor variation in life-history traits predict interspecific variation in cooperative breeding; and (iii) if territories are inherited, the mechanism of density regulation is crucial in determining which factors promote cooperative breeding. If density dependence acts on the probability to obtain a free territory or on the survival of dispersers, variation in ecological constraints cannot explain variation in cooperative breeding. Lower adult mortality favors helping, not because it reduces the availability of free territories, but because it enhances the direct benefits of helpers. If density dependence acts on fecundity, lower probability of obtaining a free territory and lower survival of dispersers promote cooperative breeding. In this case, lower adult mortality works against the evolution of helping. Pen and Weissing (2000) suggest that the difference between birds and social insects in the covariance between cooperative breeding and life-history traits is due to different mechanisms of density regulation that operate in these taxa, and explain how natural selection on habitat choice might have caused these different mechanisms to operate.

Nest inheritance can explain the presence of unrelated helpers in a classic social insect model, the primitively eusocial wasp *Polistes dominulus*. Leadbeater et al. (2011) found that subordinate helpers produced more direct offspring than lone breeders, some while still subordinate but most after inheriting the dominant position: about 32% of the reproduction of subordinates came from sneaking in eggs while the dominant was still alive and 68% came from inheriting the position of the dominant in the nest after the latter

had died. Toyoizumi and Field (2014) analyzed queues formed by social hover wasps to inherit the dominant position in the nest. The analysis of various potential strategies of hover wasps (lone breeding, simple social queuing and social queuing with division of labor) shows that lone breeding and simple social queuing that includes extended parental care fail to maintain a viable population with realistic parameter values. On the other hand, division of labor, which extends queen lifespan, will significantly increase the productivity of a simple social queue. The numerical analysis shows that the impact of division of labor on nest productivity is slightly greater than the impact of simple social queuing itself. Thus, division of labor might be one of the main benefits of social queues. If helping roles within groups are assigned through a lottery rather than being genetically determined, maximum degrees of "altruism" can evolve in groups of nonrelatives of any size (Gadagkar, 1991a; Wilson, 2001; Avilés et al., 2004).

Frequency-dependent queuing processes have been used to explain the logic of delayed breeding (Ens et al., 1995), territory choice (Kokko & Sutherland, 1998; Kokko et al., 2001b; Pen & Weissing, 2001), reproductive skew (Kokko & Johnstone, 1999), and cooperative breeding (Pen & Weissing, 2000; Kokko & Ekman, 2002). Natal philopatry characterizes the social dynamics in some communally breeding birds (Brown, 1987; Mumme, 1997), carnivores (Moehlman, 1986; Rood, 1986), cetaceans (Connor, 2000), primates (Pusey & Packer, 1987b), proboscideans (Archie et al., 2006b), rodents (Michener, 1983; Solomon, 2003; Armitage, 2007; Lacey & Sherman, 2007; Ebensperger & Hayes, 2008; Lucia et al., 2008), or mammals in general (Waser, 1988; Lefebvre et al., 2003). Experiments that manipulated resource levels in western bluebirds and carrion crows (Dickinson & McGowan, 2005; Baglione et al., 2006) indicate that predictable access to resources promotes offspring philopatry and helping. In evolutionary equilibrium, the competition, and thereby queuing time, for high-quality breeding positions increases up to a point at which it pays to accept low-quality breeding positions at a young age (Ens et al., 1995). Queuing models that take into account even the smallest individual quality differences, which are probably plentiful in nature, result in individuals using queuing strategies completely different from those in models that assume qualitatively equal competitors (van de Pol et al., 2007). Under most ecological scenarios, queuing is obviously more favored than dispersing. Since there are benefits to be gained from remaining in the natal territory, larger and socially dominant siblings within broods are more likely to stay and to expel siblings

from natal territories (Strickland, 1991; Ekman et al., 2002).

#### 17.4 Parental care and assured fitness returns

In many taxa, the survival of offspring is dependent on parental care, which is defined as any trait that enhances the fitness of offspring and originated/is maintained for this function (Smiseth et al., 2012). Parental care is common across animal taxa and increases offspring survival and/or quality in a range of species (Clutton-Brock, 1991). Parental care tends to increase the current reproductive success of the parent, but providing care is physically costly and decreases the amount of resources an individual can invest into future reproduction (Williams, 1966a; Trivers, 1972). A variable environment that affects adult or egg death rates can either increase or decrease the fitness of parental care relative to that in a constant environment, depending on the specific costs of care. Ecological factors such as harsh environments, ephemeral food sources or predation pressure are broadly accepted as evolutionary drivers of parental care (Wong et al., 2013). Increasing parental care across different life-history stages can increase fitness gains in variable environments. Wilson (1975) and Clutton-Brock (1991) suggested that care is most likely to evolve when environmental conditions are harsh and competition for resources is intense, as these are the conditions under which the benefits of care are likely to be large. Klug and Bonsall (2010) showed that parental care can evolve from an ancestral state of no care under a range of combinations of ecological conditions and life histories (e.g. egg, juvenile, and adult mortality rates, adult reproductive rate, egg maturation rate, and the duration of the juvenile stage). Costly investment in care is expected to affect the overall fitness benefits, the fitness optimum and rate of evolution of parental care. The authors compared the evolution of parental care in a constant versus a variable environment. They found that in a variable environment, the selection of parental care depends on the interaction between environmental variability, the life-history traits affected by such variability, and the specific costs of care (Bonsall & Klug, 2011). For example, environmental variability reduces selection for parental care when the costs of care are associated with both reduced parental survival and reproductive rate, but favors parental care if the only cost of care is a reduced parental survival rate. Whereas recent theoretical developments support the idea that ecological agents of selection in combination with preexisting life histories are important, they also revealed that ecological agents on their own are

usually not sufficient for the emergence of parental care (Klug & Bonsall, 2010; Klug et al., 2012), leaving scope for other important factors (Wong et al., 2013). One of them is the social environment, which results from interactions between the two parents (Smiseth & Moore, 2004), between parents and offspring (Mas et al., 2009) or among siblings (Ohba et al., 2006). Such social interactions are indeed known to shape the benefits/costs ratio of care and, hence, possibly to influence the strength of natural selection on parental care once a basic level of care has evolved (Royle et al., 2002; Smiseth et al., 2012). Extended parental care (Stubblefield & Charnov, 1986; Queller, 1994b; Queller & Strassmann, 1998) has been associated with the evolution of eusociality in Hymenoptera. The role of maternal behavior in the evolution of eusociality was supported by wasp brain gene expression that, in workers, was more similar to that in foundresses, which show maternal care, than to that in queens and gynes, which do not (Toth et al., 2007). Insulin-related genes were among the differentially regulated genes, suggesting that the evolution of eusociality involved major nutritional and reproductive pathways (Toth et al., 2007).

One factor that may promote group living is the idea of assured/delayed fitness returns (Gadagkar, 1990c). The key preadaptation for eusociality in the social Hymenoptera is progressive provisioning, a behavior that in solitary species arises by individual direct selection (Wilson, 2008). Most nonsocial wasps and bees are mass provisioners, sealing each egg into its own cell containing all of the food required to reach maturity. Other species instead provision progressively, feeding their offspring only gradually as they develop and usually provisioning more than one offspring simultaneously (Field, 2005). In order to obtain a return on its reproductive investments, an individual progressive provisioner that nests solitarily must survive until its offspring are no longer dependent on it for their survival. If the individual dies before its offspring have become independent, the offspring will also die and the individual's fitness will be zero. In contrast, an individual that contributes only partially to raising young in a social group will not have wasted its investments when it dies, provided the surviving adults can complete rearing the offspring through to independence. This safeguard reduces the fitness cost of death, and therefore also allows individuals to engage in more risky, but potentially more rewarding, strategies (Clark & Dukas, 1994). The longer the brood is dependent on the continued presence of the adult for survival, the greater the potential advantages of this insurance. In progressive provisioning species, which have an extended period of brood dependence,

assured fitness returns may therefore be especially important (Field, 2005). Assured fitness returns models argue that patterns of adult mortality combine with offspring dependence on parental care to select for group living (Queller 1989, 1994b, 1996; Strassmann & Queller, 1989; Gadagkar, 1990c, 1991; Bull & Schwarz, 2001; Field & Brace, 2004). Studies of progressive provisioning species (those species that must feed offspring repeatedly throughout larval development) such as paper wasps and hover wasps (Vespidae), and allodapine bees (Apidae) support assured fitness returns models (Queller, 1989; Gadagkar, 1990c; Bull & Schwarz, 1996, 1997; Schwarz et al., 1997, 1998; Field et al., 2000; Hogendoorn et al., 2001). There are well-supported examples of assured fitness returns in social groups with dedicated workers, such as the hover wasp *Liostenogaster flavolineata* (Field et al., 2000), the paper wasp *Polistes dominulus* (Shreeves et al., 2003), but also in species without workers/helpers such as the apoid wasp *Microstigmus nigrophthalmus* (Lucas & Field, 2011) and the social spider *Anelosimus studiosus* (Jones et al., 2007).

In a mass provisioner, females provide all necessary food for offspring development before laying an egg (Wilson, 1971; Michener, 1974). Although offspring could potentially reach maturity even if the parent died immediately after oviposition, they may be dependent on other forms of parental care, such as defense against nest predation and parasitism (Queller, 1994a; Eickwort et al., 1996; Kukuk et al., 1998; Forbes et al., 2002b; Smith et al., 2003). Nests of solitary females are unattended for a greater portion of each day than are nests with multiple females. One benefit of shared nests may be increased vigilance against predators and parasites (Lin & Michener, 1972; Alexander, 1974; Abrams & Eickwort, 1981; Rehan et al., 2011). In the mass provisioner sweat bee *Megalopta genalis*, ant predation selects for group living not because the brood is safer when defended by more than one bee, but because having two or more bees cohabiting increases the likelihood that at least one bee will remain to defend the nest (Smith et al., 2003). Group-nesting females have lower per capita reproductive output than solitary females (Soucy et al., 2003), a paradox noted already by Michener (1964) for many hymenopterans. Assured fitness returns models represent a type of conservative bet-hedging strategy in a general sense, because a solitary female that survives the period of her brood's dependence would have the highest reproductive success, but brooding females in multifemale colonies trade the possibility for maximum reproductive success for a greater mean reproductive success (Soucy et al., 2003; Jones &

Riechert, 2008; Rehan et al., 2011).

## 19. Prosocial intent and anthropocentric arguments

### Summary

**Sociobiology is burdened by a multitude of teleological, anthropocentric and moralizing concepts. Intentional wording like altruism, spite, selfish, cheating, and sacrifice abound. George C. Williams argued vigorously against the use of terms “burdened with value judgment and emotional flavour,” such as altruism, and proposed a value-neutral terminology.**

Evolution is far-sighted (Altenberg, 2005; Heininger, 2015) but it has no foresight. Evolution is not teleological in the sense that its processes or actions are for the sake of an end, i.e., the Greek “telo” or final cause. Clearly, once an organism has survived and/or reproduced one can point to its various attributes and say “yes, that attribute appears to have contributed to the organism’s survival/reproduction”. However, that is no more evidence of “foresightedness” than a lottery winner saying “I chose these lottery numbers (or bought those particular scratch-off tickets) because I knew they would be winners”. This is known as the “fallacy of affirming the consequent” (also called post hoc, ergo propter hoc argumentation) and is logically inadmissible in the natural sciences (MacNeill, 2009). ‘Backwards causation’, by which some future state or event influences (‘causes’) an action in the present or past, is often characteristic of teleological arguments. The Modern Synthesis took pride in having discouraged such thinking (Mayr, 1992). The literature on social interactions, however, is replete with teleological arguments. A good deal of concepts in sociobiology are anthropocentric post hoc statements, biased by theory, misguided by moral prejudices: they judge the intentions of the agents by the final outcome irrespective of the underlying processes. Earlier (Heininger, 2012), I have emphasized that a lively style of writing cannot do without teleological wording. However, this wording should clarify issues but not distort and misrepresent them. Anthropocentric moral judgments should altogether be banned from discussions of animal social interactions.

Studying the structure of an atom is not personal, and neither is studying, for example, night vision in mammals. Studying altruism can be personal, however, because we all want to understand the origins of goodness (Dugatkin, 2007). Sociobiology is burdened by a multitude of anthropocentric and

moralizing concepts. In a discussion of social adaptations, George C. Williams argued vigorously against the use of terms “burdened with value judgment and emotional flavour,” such as altruism, and proposed a value-neutral terminology (Williams & Williams, 1957, p. 32–33). “Altruist” and “cooperator” were to be replaced with “social donor” or, simply, “donor.” Noncooperators—now routinely labeled as selfish or “cheaters”—were “nondonors.” (Lyon, 2011). I fully support this attitude and argue that the moralizing concepts have blocked, or at least distorted, the awareness for evolutionary patterns, patterns that are general and have easily been recognized in other areas of evolutionary biology that are less biased by value judgments.

## 20. Kin selection and inclusive fitness: the fall of Hamilton

*...that an opinion has been widely held is no evidence whatever that it is not utterly absurd....*

Bertrand Russell (1929)

*Inclusive fitness theory, often called kin selection theory, is both mathematically and biologically incorrect.*

Edward O. Wilson, 2012

### Summary

**From a systems biology perspective, Hamilton’s rule is simplistic, biased by observation selection, static, and parochial. Both Einstein’s relativity theory and Hamilton’s rule are hypothetico-deductive models. For this type of models applies what Einstein said: “No amount of experimentation can ever prove me right; a single experiment can prove me wrong.” Hamilton’s rule and its predictions have been disproved repeatedly. Several of the basic, often implicit, assumptions of Hamilton’s rule are flawed: linearity, egalitarian society, deterministic reproductive success in stochastic environments, haplodiploidy as cause of eusociality. An alternative theory of eusociality was advanced 40 years ago (Alexander, 1974; Michener & Brothers, 1974): The worker caste has arisen by individual selection on mothers resulting in their control of the activities of their female offspring. The queen is somehow able to keep them in the nest and diminish their reproductivity, and in a sense is parasitic upon her daughters. The theory was virtually ignored.**

**In response to the increasingly restricted scope of the kin selection theory, advocates of the theory**

**tried to broaden the definitions of the behavior/outcome of altruism and inclusive fitness, and use the highly speculative greenbeard argument as an argumentative red herring. That the plausible alternative theory was widely ignored but the highly speculative greenbeard argument is often discussed is a telling witness to the biased scientific climate in which Hamilton’s rule flourished.**

From a systems biology perspective, Hamilton’s rule is simplistic, biased by observation selection, static, and parochial. Hamilton’s rule is hypothetico-deductive. The hypothetico-deductive model or method proceeds by formulating a hypothesis in a form that could conceivably be falsified by a test on observable data. A test that could and does run contrary to predictions of the hypothesis is taken as a falsification of the hypothesis. This method can never absolutely verify (prove the truth of) the hypothesis but can only falsify it (Hempel, 1966). This is what Einstein meant when he said, “No amount of experimentation can ever prove me right; a single experiment can prove me wrong.” Hamilton’s rule and its predictions have been disproved repeatedly, e.g. disproval of the haplodiploidy hypothesis, disproval that inclusive fitness is the reason for eusociality (in fact, it is force and chemical manipulation). Kin selection theory in sociobiology is the result of silo thinking, silo education, and silo research. Those using silo thinking and analysis seek to simplify, to reduce complexity (Waldman, 2007). Advocates of the inclusive fitness theory prefer to live in a state of self-imposed blindness maintaining that the tail of the elephant is a snake (see chapter 2). For example Wild et al. (2010) wrote: “The inclusive-fitness approach assumes within-individual selection is negligible (Grafen, 2006), which is justified by the huge empirical success of the theory (Krebs & Davies, 1993).” The sentence was written after within-individual selection had been demonstrated conclusively for 35 years (see chapter 4.1.1). Moreover, the insights of complexity theory identifying cooperation as emergent behavior of complex systems, and neurobiology emphasizing the context-dependency and pleiotropy of social behavior, have been widely ignored.

According to West et al. (2007a), “the importance of Hamilton’s work cannot be overstated—it is one of the few truly fundamental advances since Darwin in our understanding of natural selection.” The advocates of the theory maintain that there is no doubt that kin selection theory has been very successful in explaining a wide range of phenomena and that many empirical studies support their theory. But often the

connection that is made between data and theory is superficial, and as argued in chapter 4.2.3.2 is spurious due to a common “confounding factor”. Behavioral studies demonstrate that individuals in small-scale societies preferentially aid close kin over more distant kin and nonkin (e.g., Chagnon & Bugos, 1979; Chagnon, 1981; Hawkes, 1983; Betzig & Turke, 1986; Hames, 1987; Betzig, 1988; Flinn, 1988; Gurven et al., 2000; Patton, 2005). Such nepotistic biases are often cited as evidence that indirect fitness payoffs (Hamilton, 1964; Maynard Smith, 1964) have shaped human social interactions. Allen-Arave et al. (2008) considered the roles of kin selection and reciprocal altruism in maintaining nepotistic food transfers on an Ache reservation in northeastern Paraguay. Households do not primarily direct aid to related households that receive larger comparative marginal gains from food intake as would be predicted under kin selection theory. Instead, (i) food transfers favor households characterized by lower relative net energy production values irrespective of kinship ties, (ii) households display significant positive correlations in amounts exchanged with each other, suggesting contingency in food transfers, and (iii) kinship interacts with these positive correlations in amounts households exchange with each other, indicating even stronger contingency in sharing among related households than among unrelated households. While kin are preferred recipients of food aid, food distributions favor kin that have given more to the distributing household in the past rather than kin that would benefit more from the aid. Such discrimination among kin accords better with reciprocal altruism theory than with kin selection theory (Allen-Arave et al., 2008).

“For testing the usefulness of inclusive fitness theory it is not enough to obtain data on genetic relatedness and then look for correlations with social behavior. Instead one has to perform an inclusive fitness type calculation for the scenario that is being considered and then measure each quantity that appears in the inclusive fitness formula. Such a test has never been performed” (Nowak et al., 2010). Edward O. Wilson, famous for his work on insect societies and sociobiology and once a forceful advocate of kin selection, now argues that kinship plays a minor part in the evolution of ant, bee, termite and other social insect colonies (Wilson, 2005; Wilson & Hölldobler, 2005; Wilson & Wilson, 2007; Nowak et al., 2010). More important, he says, are the ecological factors that make social living so successful. Cautioning against an excessive concentration on the role of genetic relatedness in driving social evolution, Lin and Michener (1972) drew attention to a large number of social insect species where sterility is absent or

incomplete and suggested the possibility that individuals in such groups may be selected to come together for mutual benefit (Gadagkar & Bonner, 1994). This theory of mutualism has often been dismissed as incapable, by definition, of explaining the evolution of a sterile worker caste because the term mutualism suggests that both or all participants benefit. In contrast, the sterile worker caste and the fertile queen are not usually thought of as benefiting equally from the associations (e.g., Crozier, 1977; Itô, 1989). The insight (since more than 25 years) that the help of the workers is enforced (remember, punishment can select for any behavior [Boyd & Richerson, 1992]) should have led to a rethinking of this argument but only few were able to do this.

The flawed track on which evolution theory embarked was not initiated by Hamilton. In fact, it dates back to Darwin with his assumption of constant environments. Yet, in 1876 in a letter to Moritz Wagner he wrote: “In my opinion, the greatest error which I have committed has been not allowing sufficient weight to the direct action of the environment, for example, food and climate, independently of natural selection. When I wrote *The Origin*, and for some years afterwards, I could find little good evidence of the direct action of the environment; now there is a large body of evidence”. This late insight, however, was widely ignored. Plausible as it is, Hamilton’s rule was instrumental in paving this flawed track and stifling any attempt to look for alternative explanations. Apart from being “a decades-long distraction in the field that is theoretically unsound, unnecessarily focused on genetic relatedness and poorly supported by the empirical evidence” (Bourke, 2011a), two highly contentious issues originate from this hypothesis: the individual selection-group selection controversy and the kin selection-group selection controversy.

The theory of kin selection was criticized in two studies, one published in 1998 (Alonso, 1998) and another in 2002 in PNAS (Alonso & Schuck-Paim, 2002). Alonso and Schuck-Paim argued that the behaviors which kin selection attempts to explain are not altruistic (in pure Darwinian terms) because: (i) they may directly favor the performer as an individual aiming to maximize its progeny (so the behaviors can be explained as ordinary individual selection); (ii) these behaviors benefit the group (so they can be explained as group selection); or (iii) they are by-products of a developmental system of many “individuals” performing different tasks (like a colony of bees, or the cells of multicellular organisms, which are the focus of selection). They also argued that the genes involved in sex ratio conflicts could be treated as “parasites” of

(already established) social colonies, not as their “promoters”, and, therefore the sex ratio in colonies would be irrelevant to the transition to eusociality. Those papers were mostly ignored until they were re-edited by Martin Nowak, Corina Tarnita, and Edward O. Wilson. These latter authors argue that “Inclusive fitness theory is not a simplification over the standard approach. It is an alternative accounting method, but one that works only in a very limited domain. Whenever inclusive fitness does work, the results are identical to those of the standard approach. Inclusive fitness theory is an unnecessary detour, which does not provide additional insight or information.” A mathematically meaningful approach to inclusive fitness cannot be performed for the majority of evolutionary processes (Nowak et al., 2010), and the linear regression method (Hamilton, 1970; Queller, 1992c; Gardner et al., 2011) does not provide meaningful insights and cannot make empirical predictions (Allen et al., 2013; Wilson & Hölldobler, 2014). Hamilton’s rule is a linear regression to generally non-linear data (Damore & Gore, 2012). Van Dyken et al. (2011) wrote: “If doubling the number of altruists in a group always exactly doubles the total benefit of altruism, then social interactions are said to be linear. However, if the total benefit is more than doubled (or less than doubled) or if it is doubled only when altruists are at a specific frequency within the group, then social interactions are nonlinear. A disadvantage of this approach is that the number of possible nonlinear fitness functions is vast, making it difficult to extract general predictions.” The last sentence provides in a nutshell the dilemma of mathematical models: the trade-off between the degree of abstraction from reality and the mathematical tractability. The development of systems of equations, however sophisticated, may well have very little to tell us about the social world. Nonlinearity challenges the universalism of the Newtonian conception at the level of the real world which we inhabit and experience (Byrne & Callaghan, 2014).

In conventional quantitative accounts of causality, change in the value of an effect is proportionate to changes in causal elements. The simplest expression of this is through a linear equation (Byrne & Callaghan, 2014). In a world of nonlinearity of biological processes and social interactions (Avilés, 1999; Avilés et al., 2002; Chuang et al., 2010; smith et al., 2010) caused by a variety of nonlinear processes such as density- and frequency-dependent selection (Mueller et al., 1991; de Mazancourt & Dieckmann, 2004), diminishing returns (Orr, 2005; Barrick et al., 2009; MacLean et al., 2010b; Chou et al., 2011; Khan et al., 2011; Flynn et al., 2013), pleiotropic trade-offs (see

chapter 9.3), plastic genotype-phenotype maps (Müller, 2007; Gjuvsland et al., 2013; Badyaev & Walsh, 2014), epistasis (MacLean et al., 2010b; Flynn et al., 2013; Anholt & Mackay, 2015) and degeneracy (Edelman & Gally, 2001; Whitacre & Bender, 2010; Heining, 2013) it is simplistic to think that such a complex trait like social behavior should (in addition to ecological cost-benefit ratio) be regulated by linear genetic kinship. For instance, epistasis dominates the genetic architecture of complex traits, including behaviors (Yamamoto et al., 2009; Huang et al., 2012; Swarup et al., 2012, 2013). Wright (1931, 1969) considered epistasis to be ‘ubiquitous’ and stated that “The inadequacy of any evolutionary theory that treats genes as if they had constant effects, favourable or unfavourable, irrespective of the rest of the genome, seems clear” (Wright, 1969, p. 88). He emphasized that the “...existence [of epistasis] must be taken as a major premise in any serious discussion of population genetics and evolution” (Wright, 1969, p. 105). Degeneracy is the ability of elements that are structurally different or of molecular tools to perform the same function or yield the same output. It is a prominent property of gene networks, neural networks, and evolution itself. Edelman and Gally (2001) proposed that degeneracy may act both as a source of robustness and evolvability in biological systems (Whitacre & Bender, 2010). Due to the degeneracy of molecular tools in addition to the stochasticity of the genotype-phenotype mapping no certain molecular process can be assigned to a phenotypic effect (Heining, 2013). Taking the nonlinearity of social interactions (Avilés, 1999; Avilés et al., 2002; Chuang et al., 2010; smith et al., 2010; Byrne & Callaghan, 2014) into account, inclusive fitness in a nonlinear public goods game points in the wrong direction (van Veelen, 2009). In addition, while a two-player situation still allows for (adjusted) formula’s that do use relatedness, a slightly less simple example shows that with groups larger than two, relatedness can be the wrong population characteristic to look at. This implies that the prediction of the model cannot be given in a formula with costs, benefits and relatedness only (van Veelen, 2009).

Hamilton’s rule was (and many mathematical models still are) shaped by an egalitarian worldview in which autonomous individuals “decide” to forego their reproduction and help their kin to ensure the representation of their genes in the next generation. In nature, however, the vast majority of cooperative systems are characterized by asymmetric conflicts between dominants and subordinates over limited resources/reproductive opportunities. The “decision” of subordinates to help is not self-determined but

enforced by despotic dominants and the prevailing environmental conditions that limit the subordinates' options for independent reproduction. As soon as the ecological conditions favor their own reproductive activity they "vote with their feet and hope for the best" (Betzig, 2004).

Nowak et al. (2010) wrote: "For many models we find that cooperators are favoured over defectors for weak selection, if a condition holds that is of the form (Nowak, 2006a; Ohtsuki et al., 2006; Traulsen & Nowak, 2006; Taylor et al., 2007; Antal et al., 2009; Tarnita et al., 2009a): 'something' > c/b. This result is a straightforward consequence of the linearity introduced by weak selection (Tarnita et al., 2009b) and has nothing to do with inclusive fitness considerations." As Nowak et al. (2011) pointed out, even in simple models, if cost and benefit are parameters of individual actions then Hamilton's rule almost never holds (Cavalli-Sforza & Feldman, 1978; Karlin & Matessi, 1983; Nowak et al., 2010; Smith et al., 2010; Damore & Gore, 2012). Since reproduction per definition produces kin-structured populations (Blouin, 2003) this 'something' could be reproduction. Another 'something' may be delayed dispersal (see chapter 4.2.3). The vast majority of multicellular organisms develop clonally via 'staying together' after mitotic reproduction. Evolutionary theory predicts that cells' staying together provides several key advantages over multicellular construction via cells 'coming together', a prediction that has been recently corroborated experimentally in *Saccharomyces cerevisiae* (Pentz et al., 2014). On the other hand, Goodnight (2005) showed that what Hamilton called relatedness is more generally interpreted as the proportion for variance among groups, and that many processes in addition to relatedness can increase the variance among groups.

An alternative theory of eusociality was advanced 40 years ago (Alexander, 1974; Michener & Brothers, 1974): The worker caste has arisen by individual selection on mothers resulting in their control of the activities of their female offspring. The influence that even a solitary mother hymenopteron exercises on her immature progeny by feeding and protecting them continues, in eusocial species, past maturation of the daughters. The queen is somehow able to keep them in the nest and diminish their reproductivity, and in a sense is parasitic upon her daughters (Michener & Brothers, 1974). The theories were virtually ignored (as of 02-20-2015, according to Google Scholar 150 citations for Michener & Brothers [1974] vs. 12,151 for Hamilton [1964]).

### 20.1 Attempts to save Hamilton's rule

The "survival kit" of Hamilton's rule is: (i) ignore all types of cooperation that are not compatible with your framework (e.g. cooperation among nonkin, mutualisms, symbioses representing the vast majority of cooperative behaviors); (ii) call acts of fitness transfer "altruistic" (e.g. "reciprocal altruism", "enforced altruism", "coin-flipping altruism") that are not "altruistic"; (iii) ignore or downplay the fact that game theoretic models are indifferent to the degree of relatedness between the cooperators; (iv) ignore the fact that dominance hierarchies in eusociality have both an "altruistic" (worker) and exploitative/parasitic (queen) side making Hamilton's rule a zero-sum game; (v) ignore the fact that reproductive success in uncertain, unpredictable environments is highly stochastic and future inclusive fitness gains should be heavily discounted.

When a theory comes under critique, the range of conditions under which it applies often has to be restricted (e.g., see Doebeli & Hauert, 2006; Nowak et al., 2010). Conversely, the advocates of the kin selection theory try to broaden the definitions of the outcome/behavior that the theory putatively describes, presumably in the attempt to maintain the theory any meaningful area of scope. I will illustrate the latter attempts by means of three examples:

1. Altruism is defined as self-sacrifice with no apparent personal reward (Bryan & Test, 1967; Bar-Tal, 1976; Hoffman, 1981). In addition, altruism is commonly expected to be voluntary (Unger, 1991; Smith et al., 1995; Ziemek, 2006; Carpenter & Myers, 2010; Linardi & McConnell, 2011). The insight that helping in eusocial colonies is coerced by queen pheromones and worker policing (Ratnieks, 1988; Ratnieks & Visscher, 1989; Liebig et al., 1999; Ratnieks & Wenseleers, 2005; Smith AA et al., 2009), even in a clonal ant without genetic conflicts (Hartmann et al., 2003), led scientists to create the semantic monster "enforced altruism" (e.g. Wenseleers & Ratnieks, 2006b; Ratnieks & Wenseleers, 2008; Ratnieks & Helanterä, 2009). In a similar vein of thought, a putative gene for queen pheromone production that must be expressed by termite queens to suppress worker reproduction (Korb et al., 2009) was dubbed "altruism gene" (Thompson et al., 2013). Obviously, enforced altruism is not voluntary but with benefit to the "giver", i.e. the avoidance of punishment. Punishment is such a strong evolutionary force that it allows the evolution of anything (Boyd & Richerson, 1992). Within the conceptual framework of "enforced altruism", the tithes payed to feudal lords and payments of tribute of former times although enforced, were acts of altruism. Obviously for this type of

“coerced altruism” no kinship ties are necessary. Within this logic, robbery is also “enforced altruism”: the enforced transfer of assets that lower the fitness of the “benefactor” and increase the fitness of the “beneficiary”. Even prey-predator dyads can be characterized as “enforced altruism”. All of these “transfers” are enforced and no one, except some adherents of the kin selection theory, would call them altruistic. Random fates in the lotteries of life (see chapter 5.4) have been termed “coin-flipping altruism” by Cooper and Kaplan (1982). According to this logic every participant of a lottery, by buying a lottery ticket, commits an act of altruism towards the eventual winner(s) of the lottery. Likewise, the clients of insurance companies in which the insured event does not occur would act altruistically versus the ones in which the insured event occurs. And are gamblers at the casino and/or stock traders (Statman, 2002; Gao and Lin, 2011; Liao, 2013) when they lose altruists towards the winners? In the same vein of thought the winner of a lottery should be deemed to be selfish. Likewise, the term “reciprocal altruism” is misleading because this type of interaction is not altruistic but mutually beneficial (e.g. West et al., 2007a, 2007c; Douglas, 2008; Davies et al., 2012).

2. Another example concerns recently extended definitions of inclusive fitness. Since current concepts of fitness put much emphasis on the representation of the individual's genes in the next generation, expected fitness is defined by reproduction rather than survival of the individual (the latter is only evolutionarily relevant in the tautological sense of “survive to reproduce”). The definition of fitness as expected number of offspring has a one-generation time-scale (Sober, 2001). In principle, however, there is no a priori limit on the size of the time frame over which the concept of fitness may have to be stretched (Beatty & Finsen, 1989; Sober, 2001; Abrams, 2009). Grafen (1999) defines “reproductive value” as “a measure of the contribution made by an individual to the gene pool in distant generations.” Long-term concepts of fitness (Thoday 1953; Cooper, 1984; Beatty & Finsen, 1989; Sober, 2001; Abrams, 2009; McNamara et al., 2011) suggested that fitness should be defined as the probability of leaving descendants in the very long run. Traditionally, inclusive fitness theory partitioned fitness components into direct fitness effects of the focal individual's own reproduction and indirect fitness effects due to reproduction of the focal individual's non-offspring relatives (Hamilton, 1964; Price, 2007). “Parents helping children is not an example of kin selection, but rather straightforward selection-maximizing direct fitness” (Rand & Nowak, 2013). The basic idea of inclusive fitness theory was

purportedly enunciated by JBS Haldane in a pub when he quipped that he would sacrifice himself by jumping into a river to save two brothers or eight cousins, a view he only expressed in print at a much later date (Haldane, 1955). Recently, however, this traditional concept was extended by some authors to the focal individual's own reproduction and parental care. They considered parental care a prime example for an altruistic trait that evolved to enhance the fitness of the recipients of care (offspring) at the expense to the donor of care (parents) (Ekman et al., 1994; Royle et al., 2012; Smiseth et al., 2012; Wong et al., 2013). “Parental care is beneficial to the offspring because it increases their direct fitness. From the perspective of the parent (or a parental care gene), the offspring fitness benefit is an indirect fitness benefit because the fitness of the genetically related recipient of care (i.e. the offspring) is enhanced, not that of the donor of care (i.e. the parent). Similarly, parents may pay a direct fitness cost of care in terms of their fecundity” (Wong et al., 2013).

The issue of parent-offspring conflict has been analysed in detail by Alexander (1974). He argued that any behavior by the parent which can prevent offspring selfishness will be selected for. But in addition, he and also Williams (1966b) have suggested that this kind of selfish behavior cannot even spread because although the offspring may temporarily gain by being selfish as a juvenile, this gain will be more than offset by the loss in reproduction incurred when the juvenile becomes a parent. This loss in reproduction is due to the fact that as a parent the selfish individual can expect to produce broods with an increased proportion of selfish members. Thus, even though as a juvenile a selfish individual may gain, as a parent it will on average produce fewer descendants such that in the long run it loses. Hence, selfish behavior will be selected against (Blick, 1977).

In resource-limited habitats (the vast majority of habitats; Heininger, 2012), quality of offspring is more important than quantity and individuals that invest into more competitive individuals are selectively favored (Heininger, 2013). Extended parental investment is an important factor that has been suggested to facilitate family formation (Brown, 1987; Ekman et al., 2001a; Ekman, 2006) and increases the reproductive success of parents and survival of offspring, both direct fitness benefits (Royle et al., 2012). For many species of birds and mammals, much of the variance in lifetime reproductive success among females can be attributed to differences in the survival of their offspring until recruitment (Clutton-Brock, 1988).

3. Another quite popular rescue strategy for a theory under pressure is the advancement of highly speculative arguments that are backed by no evidence whatsoever. The first to speculate on a tag for altruism was Hamilton (1964). He conceived what he called a supergene, able to produce (i) a distinctive phenotypic trait, (ii) the faculty to recognize the trait in others, and (iii) the propensity to direct benefits toward bearers of that trait, even though this entails a fitness cost. Soon afterwards, Dawkins (1976) described Hamilton's thought experiment by using as phenotypic trait the catchy example of a greenbeard. The supergene was now termed "greenbeard gene," in part to acknowledge its inherent unlikelihood. "Too good to be true," were Dawkins' words: for the gene would have to be able to program for 3 effects, namely the feature, its recognition, and the altruistic propensity. The greenbeard argument has been used as an argumentative red herring. The 'greenbeard effect' has often been dismissed as implausible because it is unlikely that a single gene can code for altruism and a recognizable tag (Hamilton, 1964; Dawkins, 1976; Blaustein, 1983; West & Gardner, 2010). The second reason greenbeard traits have been thought implausible is that they can be "cheated". In a population of greenbeard altruists, a mutant capable of producing a greenbeard effect but without the costly tendency to be altruistic, would spread (Guilford, 1988; Okasha, 2002; Henrich, 2004; Gardner & West, 2010). Consequently, this model works only if we allow a mutational constraint. Moreover, Henrich (2004) argued that the common practice should be unacceptable of simply assuming that individuals know the strategies of other individuals and assort accordingly, without providing any justification (theoretical or empirical) as to why this should be so (e.g., Wilson & Dugatkin, 1997). This is tantamount to assuming the answer (Henrich, 2004).

According to a suggestion already made by Fisher (1918) most complex traits such as social behavior are products of a large number of loci with individually small effects (Lynch & Lande, 1993). This premise has stood up to a substantial body of empirical work (Falconer, 1989). For example, mutations generally have small effects on social tendencies in animals, and the resulting effects of these mutations on social tendencies have been considered to be too small for selection to act strongly (Sinervo & Lively, 1996; Sinervo & Calsbeek, 2006; Sinervo et al., 2006; Ross-Gillespie et al., 2007; Wild & Traulsen, 2007). In budding yeast, non-sexual cell aggregation has a polygenic molecular architecture (Li et al., 2013). The complex genetic programming of cooperation even in a relatively "primitive" amoeba (Santorelli et al., 2008)

(providing manifold opportunities to cheat) implies that any genetic kin recognition system would require a highly complex network to ensure cooperation with kin. Recent evidence shows that the distribution of allelic effects of quantitative traits is exponential (Mackay, 2001). A few loci with large effects (major genes) influence most of the genetic variation and an increasingly large number of loci with increasingly smaller effects (minor genes) influence the remaining variation. Numerous genes with large effects on behavior have been identified by mutation (Sokolowski, 2001), Mendelian analysis of behavioral variants (Sokolowski, 2001), QTL mapping (Anholt & Mackay, 2004) and the identification of differences in RNA or protein expression between behavioral variants (Insel & Young, 2000). These are all candidate genes for natural variation in behavior (Fitzpatrick et al., 2005).

Repeatedly, the demonstration of greenbeard genes has been claimed (Haig, 1996; Keller & Ross, 1998; Krieger & Ross, 2002; Queller et al., 2003; Summers & Crespi, 2005; Sinervo et al., 2006; Smukalla et al., 2008; West & Gardner, 2010). Taking into account the polygenic nature of cell adhesion systems, the selective data collection results in an observation selection, *sensu* Bostrom (2003, see chapter 2). In fact, a variety of the reported "greenbeard effects" are dependent on polygenic prokaryotic and eukaryotic cell adhesion and self/non-self recognition systems (Haig, 1996; Queller et al., 2003; Summers & Crespi, 2005; Smukalla et al., 2008). Another one, reported by Keller, Krieger and Ross (1998, 2002), rather than controlling an altruistic greenbeard effect, is a locus that encodes a pheromone-binding protein and may be closely involved in maintaining monogyny and polygyny, and genetic separation of subpopulations (Grafen, 1998). That a highly speculative argument such as the greenbeard has been widely discussed (as of 20-02-2015 according to Google Scholar 1600 citations) while more plausible alternative models have been almost ignored (e.g. 150 citations for Michener & Brothers [1974]) offers eloquent testimony to the biased scientific climate in which the kin selection theory flourishes.

4. Aldous Huxley is said to have stated (Preston, 1981): "The tragedy of science is that frequently a beautiful hypothesis is slain by an ugly fact." A huge amount of "ugly" data so far was not able to "slain" Hamilton's rule. The adherents of this "beautiful hypothesis" go at lengths to rescue their favorite topic of scientific investigation, an undertaking that results in twisted logic and misrepresentation.

In its last consequence, kin selection theory is a fascistoid concept, emphasizing the cohesive value of

genetic homogeneity for a population tied together by parochial altruism. Nature holds many examples of kin-structured societies that solve their conflicts in an Orwellian society by policing and oppression (Whitfield, 2002, see chapter 9). "Worker policing is a mechanism by which a society resolves its conflicts," says Ratnieks. "I think it's the best example of conflict resolution in nature." (Whitfield, 2002). Parochialism results in hostility toward individuals not of one's kin or own ethnic, racial, or other group (Choi & Bowles, 2007). Parochial altruism promotes group conflict and may coevolve with warfare (Choi & Bowles, 2007). Consistently, it has been shown that kin and tag-based selection are a theoretical basis for parochialism, war, and other attempts to damage nonkin, because those behaviors lead to enhanced survival of kin (Hamilton, 1964; Bernhard et al., 2006; Choi & Bowles, 2007; Efferson et al., 2008). On the other hand, mutualism causes partners to become increasingly dependent on each other as a basis for peaceful coexistence in societies (Clutton-Brock, 2002). In promoting peaceful coexistence, mutualism would be antagonized by kin selection (Zahavi, 1995; Clutton-Brock, 2002).

Andrew Bourke's (2011a) rhetorically intended statement "If the analysis of these authors [*i.e.*, Nowak et al. 2010, KH] is correct, inclusive fitness theory has been a decades-long distraction in the field that is theoretically unsound, unnecessarily focused on genetic relatedness and poorly supported by the empirical evidence" has been revealed in this work as a factual statement. It hit the nail on the head.

Occam's razor, one of the fundamental tenets of modern science, was formulated in the late Middle Ages and states that "Entities should not be multiplied beyond necessity". According to Sir William of Occam's notion of "parsimony of explanations", given two models, the simpler one should be preferred because simplicity is desirable in itself. In fact, the focus on genetic relatedness is unnecessary to explain the evolution of cooperation in stochastic environments and should be abandoned altogether.

## 21. Does altruism exist?

### Summary

**The claim that altruism does not exist has a long tradition in philosophical political, economic and biological thought. In humans, the most widely assumed autonomous motivation for altruism is thought to be empathy, which has also been proposed for other mammals. Behind the "veil of ignorance", the fair lottery-social insurance interplay may be the common denominator that**

**regulates such diverse phenomena as stochastic cell fate decisions and acts of "altruistic" sacrifice. Oxytocin may be the neuro-endocrinological agent linking altruism and psychosomatic health. In this way, altruism might have an intrinsic positive component, calling for reconsideration of the emphasis placed on its cost.**

In sociobiology, altruism is defined (West et al., 2007c): (i) with respect to the lifetime consequences of a behavior; (ii) on absolute fitness effects (*i.e.* does it increase or decrease the actor's fitness, and not relative to just some subset of the population). A fundamental flaw in the sociobiological definition of altruism is that it does not define how the fitness effects of the alleged altruistic act occur. This leads to strange concepts such as "enforced altruism" and "coin-flipping altruism" (see chapter 20.1). On the other hand, if a cooperative behavior was costly in the short term, but provided some long-term (future) benefit, which outweighed that, it would be mutually beneficial and not altruistic. Determining whether and how a cooperative behavior provides short- or long-term direct fitness benefits remains a major problem (Clutton-Brock, 2002; Griffin & West, 2002). It is presumably for this reason that Hamilton (1996, p. 263) thought that reciprocal altruism was misnamed, and that he and others have used alternative terms such as 'reciprocity' (Alexander, 1974), or 'reciprocal cooperation' (Axelrod & Hamilton, 1981). The literature often attributes non-human primate altruism and cooperation to kin selection, thus calling human cooperation with non-relatives a 'huge anomaly' in the animal kingdom (Fehr & Fischbacher, 2003; Gintis et al., 2003; Boyd, 2006; Melis & Semmann, 2010).

The claim that altruism does not exist has a long tradition in philosophical political, economic and biological thought (Wilson, 2015). Those who challenge the existence of altruism do not deny that there are seemingly altruistic acts but question whether they are based upon altruistic motives (Wilson, 2015). In humans, the most widely assumed autonomous motivation for altruism is thought to be empathy (Batson et al., 1988, 2002; Batson, 1991, 2012; Batson & Shaw, 1991a; Batson & Moran, 1999; Van Lange, 2008; Rumble et al., 2010; Lozada et al., 2011; Silk & House, 2011), which has also been proposed for other mammals (de Waal, 1996, 2008). Empathy is the capacity to (i) be affected by and share the emotional state of another (*e.g.* emotional contagion), (ii) assess the reasons for the other's state and/or (iii) identify with the other, adopting his or her perspective (Eisenberg & Fabes, 1998; Hinde, 2002; de Waal, 2008; de Waal & Suchak, 2010). Research

indicates that empathy is a multicomponent process that includes affect sharing, cognitive perspective taking, and cognitive appraisal (Decety & Jackson, 2004; Lamm et al., 2007; Hein & Singer, 2008; Olsson & Ochsner, 2008). Experiments where empathic concern was induced showed that high empathic conditions increased altruistic responses (Van Lange, 2008). Studies suggested that the experience of empathy has been shown to motivate prosocial behaviors, such as volunteering and donating to charities (Brooks, 2006; Dovidio et al., 2006). Willingness to help others has been correlated with brain activation patterns similar to those activated during empathic states (e.g. Singer & Lamm, 2009; Lutz et al., 2008). Empathy is biased the way one would predict from evolutionary theories of cooperation (i.e. by kinship, social closeness and reciprocation) (Batson & Shaw, 1991b; de Waal & Suchak, 2010).

A simple form of empathy—not retaliating after being punished for involuntary defection—is a prerequisite for evolutionarily stable cooperation. Furthermore, the stability of this, empathic retaliator, strategy increases with the number of opportunities for cooperative exchanges in the life of an average individual (Fishman, 2006). Not all altruistic behavior requires empathy, though. When animals alert others to an outside threat, sacrifice themselves by stinging an intruder or vocally attract others to discovered food, biologists may speak of altruism or cooperation, yet such behavior is unlikely to be based on empathy with the beneficiary. The traditional example of the dangerous rescue of another's child seems to go beyond cooperation to demand strong altruism, that is, valuing another's welfare. However, even this stronger sort of altruism alone will not produce stable cooperation in social dilemmas; reciprocity is also necessary (Levine, 1998; Sethi & Somanathan, 2001; Danielson, 2002). Indeed, these behaviors are probably inborn responses to certain stimuli performed with little consideration for the exact situation of the recipients. The fair lottery-social insurance interplay may be the common denominator that regulates such diverse phenomena as stochastic cell fate decisions (see chapter 5.4) and acts of "altruistic" sacrifice. The role of empathy is limited to so-called directed altruism, defined as helping or comforting behavior directed at an individual in need, pain or distress. It has been proposed that empathy relies on automatically activated state-matching that produces shared representations and similar emotions (Preston & de Waal, 2002; Decety & Jackson, 2006). Empathy may promote prosocial behavior, whereas a sense of fairness may play a role as a stabilizer, but not as a

promoter of prosocial behavior in non-human animals. Yamamoto and Takimoto (2012) argued that prosocial behavior motivated by sympathetic concerns can survive only with a sense of fairness, the inhibitory system for unnecessarily excessive expression of prosocial behavior. Without a sense of fairness, empathic animals might be exploited by free-riders, which might lead to the extinction of cooperation. Therefore, the interplay of a sense of fairness and empathy are both important to maintaining prosocial behavior and cooperation (Silk & House, 2011). However, these concepts do not seem to account for the pro-social behavior observed when players know that reputation building is not possible (Hilbe & Sigmund, 2010). The evidence that altruism and social support can be beneficial for health (Brown et al., 2005; Cohen & Janicki-Deverts, 2009; Lozada et al., 2011; Thoits, 2011) could partly explain its frequent incidence among unrelated individuals and in situations not involving reciprocity. In this way, altruism might have an intrinsic positive component, calling for reconsideration of the emphasis placed on its cost.

Oxytocin promotes emotional and cognitive aspects of empathy, by exogenous administration as well as at the gene level (Domes et al., 2007b; Rodrigues et al., 2009; DeDreu, 2012; Wu et al., 2012). Empathy towards strangers triggers oxytocin release and subsequent generosity (Barraza & Zak, 2009). On the other hand, consistent with a potential to disrupt social collaboration (see chapter 12), administering exogenous testosterone decreases a variety of empathic processes (Hermans et al., 2006; van Honk et al., 2011; Ronay & Carney, 2013). Oxytocin has potent and long-term physiological antistress effects (Uvnäs-Moberg, 1998) and has been implicated in both immune competence, mental and somatic health, and well-being (Uvnäs-Moberg, 1998; Neumann, 2009; Tom & Assinder, 2010; IsHak et al., 2011; Norman et al., 2012; Smith & Wang, 2012). Thus, oxytocin may be the common neuro-endocrinological agent linking altruism and psychosomatic health.

## 22. Conclusions

At its 125th anniversary the Science journal asked 125 questions that scientists should have a good shot at answering over the next 25 years, or they should at least know how to go about answering them (Kennedy & Norman, 2005). Questions 93 and 94 were:

93 How Did Cooperative Behavior Evolve?

94 How Will Big Pictures Emerge From a Sea of Biological Data?

I think, with this work I provide some clues how the answers to questions 93 and 94 may look like. The answer to question 93 is given on the preceding pages. I think that the answer to question 94 is implicitly given in my 4 recent papers, including this one. All of these papers (Heininger, 2012, 2013, 2015) that contain a total of more than 18,500 references, deal with evolutionary/ecological conundrums and controversies using a systems biology approach.

As Thomas Kuhn (1970) said, science is puzzle solving. Each of the millions of publications in the biomedical literature can be considered as a piece in the puzzle of the Big Picture. There is a good chance to drown in this sea of biological data. Where could be a lighthouse that may lead the castaway in this huge sea and guide her/him to safe ground? Fortunately, nature provides clues in which direction to move. During its almost 4 billion years, evolution has left traces that can be detected. Darwin's "descent with modification" has left a trail of genetic, physiological and procedural continuity, that can be used like Ariadne's string for the way out of the labyrinth. It has been advocated previously that a deeper understanding of biological and pathological processes can only be achieved by "unearthing" the "fossil record" of the genome (Runnegar, 1986; Buss, 1987). But this approach, at least to my knowledge, never has been followed rigorously, possibly because it requires the integration of virtually the complete biomedical sciences into a coherent concept. Concerning question 94, my work is based on information retrieved from more than 500,000 papers and a plethora of books from evolutionary biology, ecology, microbiology, epidemiology, paleontology, molecular biology, botany, endocrinology, immunology, and neurobiology that were read over approx. 25 years. Its early stages date back to my occupation with Alzheimer's disease (Heininger, 1999a, b, 2000a, b), when I realized that metabolically stressed neurons use stress response tools that evolved in microorganisms (Storz & Hengge-Aronis, 2000) and are rooted deep in evolutionary time (Heininger, 2001). A fundamental feature of the "start from the scratch" approach is that it should be an open-ended process, not guided by any preconceived opinion. Previously, holistic concepts have been based on *a priori* plausibility assumptions. All evolutionary theories were informed by population genetics, the dominant paradigm of evolutionary biology. But population genetics "is not an empirically sufficient theory" (Lewontin, 1974 p. 267) and failed gloriously to provide consistent and generally accepted answers to the conundrums of evolutionary biology: aging, sexual reproduction, the level of selection, and social

behavior. My evidence-based hypotheses to these conundrums and controversies represent a unique, in their scope unprecedented approach that provides revolutionary (*sensu* Kuhn) paradigm shifts (see Heininger 2012, 2013, 2015, this work). Importantly, these papers sketch a coherent and consistent Big Picture of ecological and evolutionary processes, defining evolution as cybernetic automaton orchestrated by Ross Ashby's "Law of Requisite Variety". And, as corollary, give explanations for other biomedical phenomena: the Cambrian explosion, the different bauplans of modular and unitary organisms, Francis Crick's Central Dogma as closed circle with stochastic environmental-genetic feedback, the relationship between sexual reproduction and cancerogenesis (cancer as evolutionary cost of evolvability), apoptosis as fair lottery, and the rebuttal of Motoo Kimura's Neutral Theory.

## 23. Abbreviations

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AVP: arginine vasopressin  
 CA: corpora allata  
 CBP: conspecific brood parasitism  
 CRF: corticotropin-releasing factor  
 DA: dopamine  
 DIFs: differentiation-inducing factors  
 GC: glucocorticosteroids  
 HC: hydrocarbons  
 HPA: hypothalamic-pituitary-adrenal  
 IGF: insulin-like growth factor  
 JH: juvenile hormone  
 IIS: insulin/IGF-like signaling  
 MHC: major histocompatibility complex  
 OT: oxytocin  
 OTR: oxytocin receptor  
 PHB: poly-3-hydroxybutyrate  
 QTL: quantitative trait loci  
 V1aR: vasopressin 1a receptor

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