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6 The Unit of Adaptation, the Emergence of Individuality, and the Loss of Evolutionary Sovereignty

Minus van Baalen

Associations Rule the World

In the course of evolution, originally independently functioning units may merge to form new, persistent associations. This is not a new insight: the symbiont theory for lichens was proposed in 1867 by the Swiss botanist Simon Schwendener, while the Russian Konstantin Mereschkowsky suggested that chloroplasts were derived from bacteria in 1905 (Sapp 1994). However, when Margulis (1970) suggested that all eukaryotic cells were the result of an association of different kinds of bacteria, she met with widespread skepticism. Nonetheless a large body of evidence in favor of the symbiotic origin of many structures has been amassed, and the hypothesis is now generally accepted, at least regarding the bacterial origins of mitochondria, chloroplasts, and some other organelles (Bosch & McFall-Ngai 2011). The creative potential of symbiosis is thus no longer contested. Indeed, many of the major evolutionary transitions listed by Maynard Smith and Szathmáry (1995), such as the evolution of eukaryotes, diploidy, multicellularity, and symbiosis, to name a few, result from the formation of coherent associations of smaller subunits (Strassmann & Queller 2010). Thus, the emergence of individuality in the course of evolution is strongly linked to the question of what selective pressures favor individuals (be it of different or of the same species) to associate and to reproduce together (Law & Dieckmann 1998).

In this chapter I will give a short overview of what is known about the selective pressures that act on partners and their associations and discuss why complete merging is difficult to explain, the consequences of the conflict that results when merging is incomplete, and why we need to review the role of information in the emergence of new units of adaptation.

Why Associate?

That long-lasting associations are common was recognized in the previous century, when Frank and De Bary invented the term "symbiosis" to refer to these

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interactions, ranging from parasitism to mutualism (see Richardson 1999). Why such associations have formed repeatedly in the course of evolution, however, is an issue still surrounded by a nebula of difficult questions (Buss 1987; Frank 1997; Law & Dieckmann 1998; Michod 2005). It is usually assumed that some form of cooperation lies at the basis of association, but that cooperators often expose themselves to cheating has long been recognized (Hardin 1968; Axelrod 1984). Nonetheless, evolutionary game theory suggests that the conditions for cooperation are quite broad (Taylor & Nowak 2007). Individuals may help each other to defend themselves against predators, exchange nutrients or services, divide tasks to raise young more efficiently, and so on—the list is endless.

However, the persistence of the association of cooperating partners is rarely considered in evolutionary game theory. Yet the duration of these associations is highly variable, and obviously important. Even highly profitable interactions sometimes only result in fleeting encounters (e.g., plant-pollinator interactions), while in other cases partners engage in long-lasting associations that do not seem so profitable to some of the partners, such as infections by commensalistic organisms. In some such associations the participating partners retain their independence (e.g., germinating plants need to re-establish interactions with rhizosphere organisms in every generation), while in others the associations have become truly obligatory and persistent, such that partners can no longer persist on their own (for instance, the overwhelming majority of eukaryotic cells cannot function without mitochondria, while mitochondria have long lost the ability to survive independently).

Evolutionary Sovereignty

What is it that makes lineages completely give up their evolutionary sovereignty in some cases (such as mitochondria seem to have done, for instance)? Why is it that in other associations the participating partners hold fast to their individuality? These are central questions to which no satisfactory answers exist to date.

Though hypotheses abound for how and why associations form, a general perspective is still largely lacking. In a sense this is surprising, since the question has been around at least since the late nineteenth century, when it was discovered that lichens are actually associations of fungi and algae or photosynthetic bacteria (for a historical overview, see Sapp 1994 or Richardson 1999). The earliest attempt at a theoretical analysis of the evolutionary consequences of symbiosis dates from 1934! In order to investigate the hypothesis that host-parasite interactions can evolve into mutualistic symbioses, Kostitzin (1934) may have formulated the very first model to study the interplay between ecology and evolution. Unfortunately for Kostitzin, in his time the mathematical toolbox for analyzing the resulting highly nonlinear model was not yet as well-filled as it is now, preventing him from reaching clear conclusions, and today his work seems largely forgotten.

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Common Good Versus Selfish Interest

More sophisticated mathematical methods than those available in the 1930s have now been applied to Kostitzin's (1934) model, and this has generated new insights into the selective pressures on partnership formation. Among the first to take up the challenge posed by Kostitzin's framework were Law and Dieckmann (1998). They have shown that, in order to defend themselves against overexploitation by the stronger partner, weaker partners may have to give up the capacity to survive in isolation—so that, for these weaker partners, symbiosis has become effectively obligatory. Natural selection may then act on both lineages so as to synchronize their reproductive effort to such an extent that both lineages effectively merge into a single one. However, Law and Dieckmann (1998)'s result rests on the assumption that there exists a trade-off between independent existence and defense against more powerful partners. This may indeed be a realistic assumption for the amoeba-bacteria interactions that Law and Dieckmann considered, but is not necessarily self-evident for other systems.

Using a similar but less detailed model, Van Baalen and Jansen (2001) have shown that whenever individuals associate they share a common good that favors cooperation. But at the same time, the partners retain a selfish interest strongly acting against further integration. For instance, plants and rhizosphere organisms are selected to cooperate to increase their mutual survival, but not to increase their partner's fecundity. The only way for complete alignment of interest to result is when partners totally couple their reproductive effort. Only then will natural selection favor partners to invest all in the common good, survival, and reproduction of the partnership. In all other conditions, partners will have to strike a balance between common good and selfish interest (figure 6.1), which is generally suboptimal for the association as a whole.

The notion that associates experience a tension between common good and selfish interest has of course been around for a long time in evolutionary theory (Hardin 1968; Leigh 1991), to the extent that this dilemma is built in right from the start into many game theoretical models for the emergence of cooperation among humans, such as the Prisoner's Dilemma game (Axelrod 1984). But to my knowledge, we still lack a general approach or method to extract these quantities from an arbitrary interaction. Indeed, whenever one encounters these notions in studies of cooperation, they tend to appear in the discussion to make sense of findings. Presumably everybody "knows" from personal experience what these concepts entail, but a precise mathematical definition is surprisingly hard to come by.

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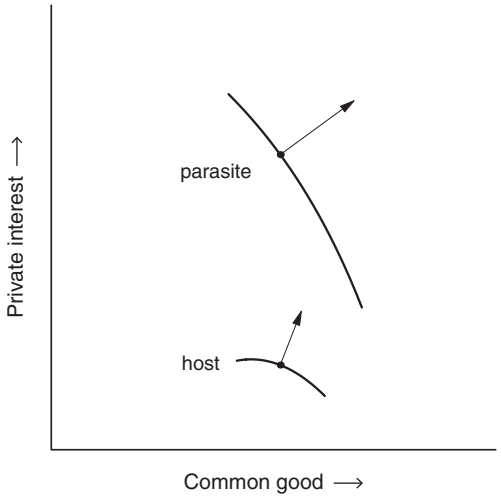

Figure 6.1
Example of how selection affects the balance between private interests and common good in a host-parasite association. The curves represent trade-offs for each partner (tracing the consequences of changes in strategy on the two components, where the common good is shared by both partners and the private interests are not), the arrows represent the gradient of selection, so that the two points on the trade-off represent the co-evolutionarily stable strategies (Van Baalen 1998). Note that the arrows point in different directions: contrary to what intuition would probably suggest, improving the common good is relatively more important to the parasite than it is to its host. A full evolutionary merger would require both vectors to align with the horizontal axis. (This figure is adapted from Van Baalen & Jansen 2001 and full model details can be found there.)

What Is Involved?

Various mechanisms are thought to play a key role in symbiotic mutualism and the emergence of compound individuals, but to date no such mechanism has been shown to be the sole factor responsible. I will briefly discuss the most important ones below.

Vertical Transmission

It is often thought that vertical transmission plays a crucial role in aligning the interests of partners, promoting the transition from host-parasite relationship to mutualism (Yamamura 1993; Lipsitch, Nowak, Ebert, & May 1995; Yamamura 1996; Turner, Cooper, & Lenski 1998). However, this can only be a partial explanation. While it is true that with vertical transmission parasites are selected to better preserve their hosts and thus to be less virulent, as long as there is horizontal transmission parasites will remain parasites and continue to cause damage. Now if there is vertical transmission, not only will the infected host itself incur the cost of infection, but its offspring will as well (Van Baalen & Jansen 2001)! The entire lineage founded

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by an individual may become compromised. Selection on the host to get rid of its parasite will therefore be even stronger than in the absence of vertical transmission. Promoting vertical transmission is definitely no failsafe mechanism for creating mutualistic symbiosis (Van Baalen & Jansen 2001).

Full-blown symbiotic mutualism only results when vertical transmission becomes the exclusive mode of reproduction of both partners, so that they effectively cease to be independent partners. As it is difficult to think of conditions that impel any partner to ignore opportunities for independent reproduction (i.e., not pursue its selfish interests), it becomes a question whether true, full-blown symbiotic mutualism (merging of lineages) actually does exist!

Genetic Conflict

Indeed, wherever one looks closer into purportedly mutualistic interactions, one finds evidence for many forms of strife and conflict (Herre, Knowlton, Mueller, & Rehner 1999; Burt & Trivers 2008). For instance, genes are usually thought of as working together to create a well-adapted phenotype. Yet since Hamilton's (1967) early insights and most notably Dawkins' (1976) notion of the "selfish gene" (which is actually a popularization of views already expressed in the 1960s by Williams 1966), the idea that the genome is an area of potential conflict has become almost universally accepted (Werren 2011 and references therein). The enormous amount of noncoding ("junk") DNA present in almost all eukaryotic organisms is difficult to explain otherwise (Burt & Trivers 2008).

Chromosomal structure and diploidy add further levels of mutualistic association (of genes and of chromosomes) with further scope for interest alignment. Yet each extra level also introduces new potential for conflict. The detrimental consequences (to the compound organism) of such genetic conflict are difficult to assess but they may be spectacular, as witnessed by the effects of sex-ratio distorters and meiotic drive elements (Burt & Trivers 2008).

The Germ Line

Similarly, the organization and unity of purpose expressed by a typical multicellular organism may be only apparent. It is now thought (Buss 1987) that the separation in soma and germ line recognized as fundamental by Weismann is there to undercut the incentives for selfish behavior of components of the organism. The idea is that, since the soma is a reproductive dead end, the components that form it can only increase their (inclusive) fitness by helping the related elements in the germ line. This thus encourages the soma to unselfishly cooperate: their evolutionary interests are completely aligned through the success of the germ line. Organisms without a clear soma–germ line distinction (such as in multicellular algae like many *Volvox*

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species) have much more trouble suppressing selfish behavior (Herron & Michod 2008).

However, even the soma–germ line separation may not create a complete alignment of interest within the soma, as there are many indications that the soma does not always harmoniously cooperate—the occurrence of cancer being perhaps the most conspicuous example of the individual being harmed by its own parts. But on a more general level, wherever one scrutinizes the functioning of complex organisms, indications of selfishness and cheating invariably emerge, spoiling the picture of harmonious cooperation for a common purpose (Burt & Trivers 2008; Strassmann & Queller 2010).

The first and most basic selective factor limiting the evolution of somatic cohesion is that some cell lineages can escape from the soma and spread through some form of horizontal transmission (Dingli & Nowak 2006). A notorious example is that of the facial tumor currently decimating the Tasmanian Devil because it spreads by biting (McCallum & Jones 2006). Another example may be the occurrence of so called "genetic mosaics" that can result from somatic mutation but also occur when cells from a sibling (or even the mother) invade a developing embryo in the womb (Pearson 2002). Whatever the causes, within-soma genetic heterogeneity is much more common than originally thought (Gottlieb, Beitel, Alvarado, & Trifiro 2010). Finally, it is highly suggestive, though to my knowledge no thorough study exists (but see Dingli and Nowak 2006, Welsh 2011), that cancers seem to occur more often in or near organs that create a potential for transmission (such as sexual organs, the skin, or mammae). As discussed by Buss (1987), the development of schemes to suppress or regulate within-soma diversity (such as policing; see Michod 1996) was a key step in the evolution of multicellular organisms.

Kin Selection

Another reason for the existence of an upper limit to integration is that "the" germ line is not a monolithic entity, but actually also a more or less loose association of a hierarchy of smaller parts (chromosome sets, chromosomes, gene complexes, genes, exon/intron structures) that each may have differential options for spreading, which, representing only a private interest, reduces the incentive for cooperation. When parts of the germ line will not cooperate, neither should their soma counterparts. This insight underlines the importance of kin selection as a fundamental evolutionary mechanism. Kin selection has come under fire (Nowak, Tarnita, & Wilson 2010); primarily attacked was its capacity to explain features observed in social insects. This criticism completely ignores, however, its essential role in explaining the emergence of multicellularity. However, in the multicellular way of organizing life, cells have no long-term descendants unless they are in the germ line, and as Buss (1987) points out, the fact that they play no other role in creating a

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phenotype (individual) is essential to avoid conflict. Cells in a multicellular organism cooperate to produce gametes for exactly the same reasons that workers in an ant colony cooperate to produce dispersing, sexual progeny.

Darwin already had the hunch that under some conditions adaptation may occur at a higher level than that of the individual: worker bees do not themselves reproduce, but their mothers do, so one can explain worker traits by assuming that adaptation occurs at the hive level. This idea was largely ignored until it was put on a concrete footing by Hamilton (1963, 1964). In a similar fashion, soma cells do not usually make it into a next generation of soma but their relatives in the germ line do, creating a strong incentive for cooperation. However, even worker bees within a hive may compete with one another: so called "cheater lineages" have been described (Châline, Ratnieks, & Burke 2002). Likewise, components may compete to the detriment of the soma as a whole.

Non-Genetic Inheritance

Yet another cause for an upper limit of integration may be that, as is becoming more and more clear, the genome does not contain all the information necessary to fully characterize an individual. To start with, it seems that epigenetic mechanisms play a much more important role in adaptation than previously thought (Jablonka & Lamb 2005). Epigenetic mechanisms include well-known and well-studied systems such as methylation of DNA and maternal effects on development of the embryo. It is not at all obvious whether epigenetic inheritance is affected by a soma–germ line separation, and even if it is, its germ line may function differently, thus engendering potential conflict between genetic and epigenetic information.

Distributed Genomes

Finally, many of the traits that define adaptations are not coded into the main individual's own genome, but in that of one of its symbionts. For instance, a cow can digest cellulose because it harbors bacteria that can degrade it. The ability to digest grass is therefore not an adaptation of the cow, but rather of the cow-symbiont association. I will return to this notion of adaptation in the discussion, below. The ability to digest cellulose is but one spectacular example. Even we depend on our gut microflora to fully digest some types of food and extract all resources (MacFarlane & Gibson 1997). That symbionts can provide useful services is not surprising when one realizes that their combined DNA contains 150 times as many genes as our own genome (Qin, Li, Raes, Arumugam et al. 2010)!

Even though the notion that the "microbiome" can encode adaptations in addition to the classical genome is rather new (the term is attributed to the Nobel prize–winning microbiologist Joshua Lederberg by Hooper & Gordon 2001), and it is not obvious yet how to assess its precise scope and importance, it is now obvious that

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classical genetics provide only part of the explanatory power for evolution. That is, following the population dynamics of a given gene pool (species) is not enough: one must consider its coevolution with a potentially very large number of other gene pools. Moreover, it must be considered how alleles from what might be called "meta-gene-pools" construct compound phenotypes. Thus, in order to render the theory of evolution more complete, more insight is needed into the population (and functional) genetics of multispecies associations.

Behavior

What makes partners associate? What prevents them from favoring their private interests (which, by definition, do not benefit their partners Van Baalen & Jansen 2001)? The continued persistence (and functioning) of associations may often crucially depend on behavioral flexibility and communication, as this allows partners to synchronize their actions and to respond to eventual acts of cheating by their associates. For instance, Michod and co-workers have found that multicellular associations of volvocine function better if cheats can be punished (Herron & Michod 2008). Similarly, plants that harbor nitrogen-fixating bacteria in root nodules can encourage their cooperation by "punishing" them (by stopping the carbohydrate reward; West, Kiers, Pen, & Denison 2002). It is not often realized that humans and other mammals have a dedicated immune system in their digestive system, one of whose functions probably is to detect and respond to cheaters among the gut microflora (Walter, Britton, & Roos 2011). Similarly, it is now widely acknowledged that the regular immune system plays an important role in suppressing cancer (i.e., eradicating cell lines that escape central control and no longer contribute to the common good; Dingli & Nowak 2006, Welsh 2011).

From partners that respond to each other's behavior to communication is but a small step: if partners benefit from adjusting their behavior to that of their partners, they have a lot to gain by transferring information. A communication system arises when cues that are used by partners are amplified. Indeed some forms of interspecific cooperation are facilitated by an elaborate system of communication. Plants, for instance, that are attacked by arthropod herbivores can emit airborne signals ("synomones") to inform predators of the herbivores of the presence of prey (Vet & Dicke 1999). And what else are hormones than a physiological system that allows components of a multicellular organism to communicate and adjust their behavior to achieve a common goal (Smith 2010)?

Information and Adaptation

Adaptation requires information of various kinds. Genetic information, of course, but also epigenetic switches, bacterial genomes, and, why not, memes (Dawkins 1976;

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Blackmore 1999) play a role. Not all these kinds of information are equivalent, and in particular memes are rather difficult to define (Claidière & André 2012). Whatever its carrier, information is often transferred. Obviously, such transfer is often vertical—that is, from one generation to the next—to help descendants in the struggle for existence (mainly genes, of course, but also epigenetic information, immunity, and behavioral experiences can be transferred vertically). Information transfer may also be horizontal, since we have seen that communication (sometimes in a strict but often in a more loose sense, such as individuals of a population copying each other's behaviors) may play an important role. This indicates that information is a key concept necessary to understand adaptation in compound organisms. Genetic information obviously is an important component, but other types of information may play important and even crucial roles, too, in the interplay between evolution and ecology (Hogeweg 2009).

As different kinds of information may be encoded and transferred by different means, with different fidelities and different dynamics, it is important that evolutionary theory should try to develop a more general concept than the gene as the sole carrier of evolutionary information (Danchin, Charmantier, Champagne, Mesoudi et al. 2011).

At this stage it is not very clear what such a more general information-based theory of evolution should look like, but at least we can be sure that standard approaches from information theory will not suffice. The latter theory is derived from thermodynamical principles and, at its origin, tried to assess how much useful information can be carried by a signal that also contains random noise (Shannon 1948). The problem, as was pointed out by Bateson in the 1960s and 1970s (Bateson 1963, 1972), is that this theory uses a purely syntactical definition of information. Using the arbitrary "bit" as a unit of information might suit radio engineers and computer scientists, but for applications in ecology and evolution we have to know what particular bits refer to—that is, what the information they encode actually means. After all, even if a gene is just a particular sequence of bases, it may have a whole suite of phenotypic (hence physical) effects, which can be interpreted as the gene's meaning (Maynard Smith 2000). This "meaning" can be highly context-dependent, however, as the expression of genes is typically strongly regulated by other genes and by physiological and environmental conditions.

The Information-Based View of Adaptation

Maynard Smith (2000) argued that information plays a central role in evolutionary biology: the genome contains the information necessary to produce a phenotype. In a similar vein, Williams (1992) argued that evolution takes place in what he called the "codical domain," in which resides the information stored in genes (rather than in their physical avatars). Such an information-based approach produces the insight

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that being adapted is equivalent to having the right (genetic) information to produce the optimum phenotype for a given environment (Maynard Smith 2000).

I propose to extend this definition so as to include any kind of information: being adapted implies being in the possession of the information necessary to solve a given life-history problem. This information is of course very often genetic (that is, encoded in a focus individual's DNA) but may have other origins too. For instance, the cow's ability to digest plant matter is an adaptation because the cow–gut flora association disposes of all the information needed to construct a physiological system that can degrade and convert the cellulose contained in hard-to-digest silicium-rich plant material. In contrast, a hypothetical "axenic" (that is, symbiont-free) cow is not adapted to grass, even if it were viable on a carefully prepared artificial diet: the ability to digest grass is not encoded by the cow's own genes but by what is now called the microbiome. For humans, it is estimated that about 10% of fatty acids can be digested only with the assistance of the microbiome (Walter et al. 2011).

Epigenetic inheritance, in this view, is not so very different: it is just another source of information that helps individuals to adapt to given conditions. Methylation patterns modify the expression of genes so they are tightly linked to genetic information. Other epigenetic mechanisms function more independently. Prions, for instance, were probably invented by microorganisms to pass on information about (that is, allow adaptation to) environmental changes that are slow on the individual (cellular, in this case) level but nevertheless too fast for selection to "track" (Shorter & Lindquist 2005). This is but one example; the list of epigenetic mechanisms able to transfer information is endless (Jablonka & Lamb 2005).

Whose Information?

The conceptual consequences of this information-based perspective will be explored in more detail elsewhere (M. van Baalen, A. Chaine, J. Clobert, E. Danchin & T. Monnin, in preparation.). One of the important consequences here is that an adaptation is not always associated with an easily recognizable individual. Adaptation is often linked to function: that is, an adaptation maximizes an entity's fitness. As Gardner points out in his contribution to this book, these entities may be individuals in the classical sense but they may also be groups, as long as the entities have a fitness that can be maximized. Shifting the focus to information requires us to identify what structure actually benefits from an adaptation. This is far from a trivial task! Symbiotic mutualisms like lichens or cows (if we accept that an axenic cow is not a true cow!) seem clear enough, but what of host-parasite relationships, in which the parasite exploits its host while at the same time conferring it some benefits (e.g., bacteria and resistance-conferring plasmids)? Adaptations affecting plant-rhizosphere interactions are even fuzzier, as there exist no clear physical boundaries delimiting the association. Plants and fungi may form continuous

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networks that spread across entire ecosystems: who or what is benefitting from a given adaptation in such a network?

Hamilton (1967) supposed that the mechanism of kin selection also operates in what he termed "viscous populations," or spatially extended populations with limited and local dispersal. That it may indeed do so is not immediately obvious, however: individuals in such populations are not only likely to be related to their neighbors, they also tend to compete with them, and in some models these effects indeed exactly cancel out (Taylor 1992). However, Van Baalen and Rand (1998) and Lion and Van Baalen (2007, 2009) found that in a broad class of models kin selection does indeed work as Hamilton supposed. What happens is that when a mutant appears in the population, it will create a local cluster (as depicted in figure 6.2), and it is the properties of this cluster that determine the fate of an invasion attempt. Altruistic individuals can indeed invade a population of selfish individuals, as clustering allows them to direct the benefits of altruism to other altruists rather than to the average egoist. Although Taylor and Nowak (2007) classify cluster-mediated altruism as a different mechanism from kin-selection mediated altruism, it is actually the same phenomenon, as Hamilton already surmised.

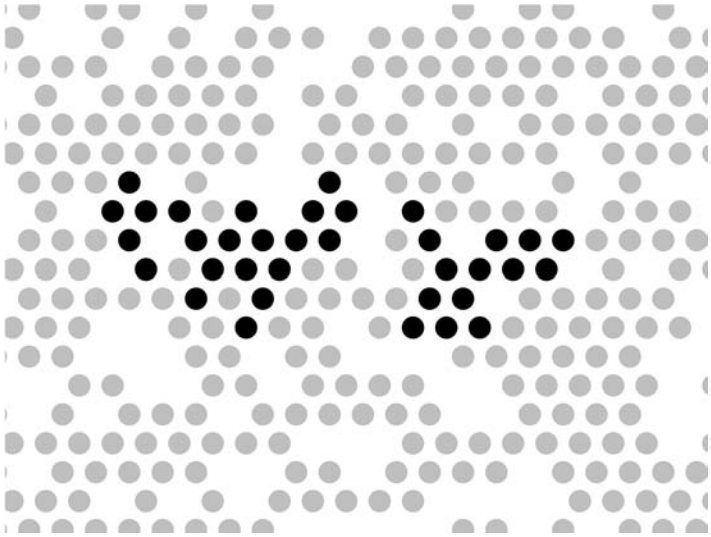

Figure 6.2
Example of a cluster of related individuals (black) spreading in a viscous population (white). Even though the black individuals may be extremely rare globally, because they cluster, they experience a significant density of other (related) black individuals in their neighborhood. This allows the cluster to benefit from altruistic acts or cooperative behaviour (Van Baalen & Rand 1998).

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Credibility

When partners need to coordinate their actions in order to successfully cooperate, they may need to communicate either explicitly or implicitly in a series of actions and counteractions (much as players in the Iterated Prisoner's Dilemma game provide information about their intentions by their moves, or players of the contract bridge card game through their bidding schemes). For partners engaged in such interactions, a problem is to assess the credibility of the information they acquire. Of course, if the interests of all partners completely overlap, everyone has an interest in providing useful and thus credible information. However, as we have seen, interests are rarely (if ever) completely aligned, which means that some members of an association may let their private interests prevail and cheat on their partners. Under such conditions it may become very tempting to provide false information.

There has been a long discussion among evolutionary biologists over what mechanisms can favor honest signaling in communication interactions (Dall, Giraldeau, Olsson, McNamara et al. 2005). One way to convince receivers is by using costly signals. This strategy often seems to be used to advertise mate quality for attracting sexual partners (Grafen 1990), but very often signals are relatively cheap (Bergstrom & Lachmann 1998). It has now become clear that individuals may have to assess the credibility of the information: signaling is very often tied to a cooperative interaction that can be exploited by cheaters (Van Baalen & Jansen 2003). The pattern that emerges is that communication among partners that have sufficiently aligned interests leads to a universally adopted signaling system (Nowak & Krakauer 1999), whereas evolution leads to much more diverse and dynamically unstable outcomes when conflict becomes more important (Jansen & Van Baalen 2006; Rousset & Roze 2007). The as-yet untested hypothesis that results is that diversity in a communication system reflects the underlying balance of cooperation and conflict among partners.

The Unit of Adaptation

A fundamental question in evolution is how life could have started at all. One popular hypothesis is that, somehow, freely floating molecules with catalytic action spontaneously organized themselves into "catalytic networks," and that these were the precursors of more compartmentalized cells. Eigen and Schuster (1979) showed that a catalytic network organized in a circle (a "hypercycle") can indeed grow and dominate the primeval soup. However, Maynard Smith (1979) was quick to point out that such hypercycles were susceptible to "cheater" molecules, molecules that are catalyzed by members of the hypercycle but without catalytic capacity themselves. Boerlijst and Hogeweg (1991) showed later that if the system is spatially

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extended and limited by diffusion, hypercycles could maintain themselves even in the presence of cheater molecules, because they tend to organize themselves (at least in a two-dimensional world) in rotating spirals. There are regions in a spiral where a cheat will do well, but because the spirals rotate, the cheats tend to get swept outward until they end up in the no-man's land between spirals and go extinct for lack of catalytic support (figure 6.3). Boerlijst and Hogeweg argued that such self-organizing structures can become the new unit of selection: they showed that rotation speed of the spirals is strongly linked to their evolutionary success, a trait that cannot be attributed to the component parts in isolation (1991). Van Baalen and Rand's (1998) analysis lent further support to the idea that self-structuring can have important consequences for evolution, as I will discuss in some detail below.

Ever since Williams (1966, 1971) pointed out that many evolutionary theories were based on group selectionist ideas without a proper theoretical foundation (phrases like "individuals are selected so as to ensure the persistence of the species" can still occasionally be heard in nature documentaries, for instance), a debate has raged over whether the relevant units of selection are individuals, groups of individuals, or even entire species. This debate was further deepened when genes were added to the list of potential units of selection, after Dawkins (1976) popularized the idea that "selfish genes" may pursue their own interest to the detriment of their carrier. It has been argued that genes are the most relevant level, because it is they that carry the necessary information from one generation to the next. However, individualists argue that it is not the genes that directly feel selection, it is the phenotype they construct that is tested by natural selection. On top of this came the discussion about the extent to which larger structures, such as groups and families, can also form such units. This debate has given the notion of unit of selection so many meanings that it has become difficult to use it without creating confusion. I therefore propose to use the concept of "unit of adaptation" to refer to those structures that benefit from an adaptation.

It should be kept in mind that units of adaptation are fundamentally emergent structures. It is not at all easy to predict their scale and extent, which can vary quite dramatically depending on the conditions and traits considered. For instance, the unit of adaptation of a selfish element may indeed be a stretch of DNA, while the unit of adaptation of a neighboring altruism gene may be a cluster of related individuals across space. In principle, any structure can function as a unit of adaptation.

This definition allows us to generalize the classical notion of the individual to other levels of organization. However, it forces us to rethink the notion of "fitness" too. One can state that an adaptation allows the unit of adaptation to increase its fitness, but what is fitness at levels other than that of the individual?

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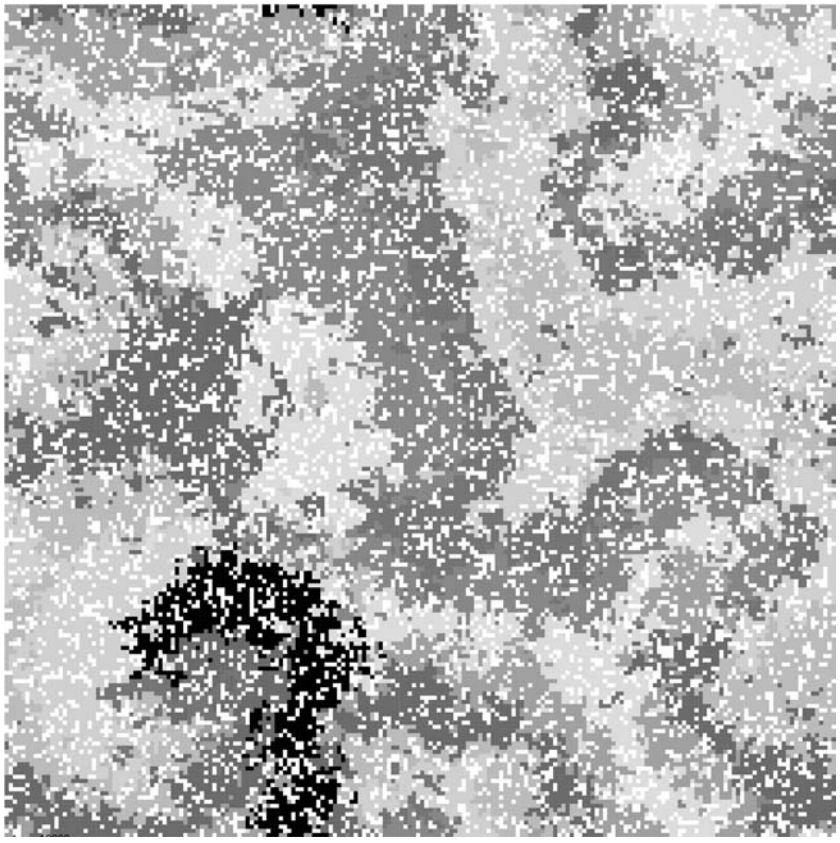

Figure 6.3
Example of a spatial structure generated by a diffusion-limited seven-species hypercycle (the different species are represented by different levels of grey). A number of centers can be discerned around which spirals rotate. These spirals rotate in such a way that a parasite (black) is always expelled from the center of the spirals. These spirals are emergent units of adaptation because, as Boerlijst and Hogeweg (1991) have shown, one decisive trait in determining which spiral type will outcompete the others is its rotation rate, which is decidedly an emergent property. Boerlijst and Hogeweg (1991) modeled a discrete-time probabilistic cellular automaton (PCA), but this snapshot comes from an asynchronous PCA with a 4-cell Moore neighborhood, harboring a 7-species hypercycle and one parasite; birth rate 1, mortality rate 0.2 exp(–25 #helpers); all rates are per capita per unit of time. Mutations occur with a probability of 10^{-4} per unit of time and occur with a probability of 10 per reproduction event. See Van Baalen and Rand (1998) and Van Baalen (2000) for details on how such cellular automata can be constructed and analyzed.

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Invasion Fitness

As already noted by Dawkins (1982), the word "fitness" has acquired a multitude of meanings in biology, mostly overlapping but sometimes contradictory. The most robust definition of fitness is perhaps the notion of lifetime reproductive success. If one can easily distinguish individuals (at some precise and standardized physiological state), one can count the number of offspring (in precisely the same state) produced by the focal individual over its entire life. This is the realized lifetime reproductive success of this individual, and it is often used (or estimated) in experimental studies. But in evolutionary theory what counts is the expected lifetime reproductive success, and this necessitates some form of averaging over time and environmental conditions. Standard population genetics theory defines the problem away by only considering relative fitness and supposing that selection coefficients are constants. Adaptive dynamics theory has provided a method that allows the assessment of fitness in general ecological scenarios (Metz, Nisbet, & Geritz 1992). The problem for our application is that it requires calculating the average growth rate of a rare mutant gene: since a so-called "resident" gene has an expected growth rate of zero, a positive expected growth rate implies that the mutant gene can invade. This approach poses no conceptual problems if applied to clonal (haploid, nonsexual) organisms. Once diploidy and sexual reproduction come into play, adaptive dynamics becomes technically more challenging, but nothing changes in principle: fitness is associated with the long-term (expected) growth rate of a rare gene. The conceptual issue here is that most biologists link fitness with individuals, whereas fitness in adaptive dynamics requires following lineages rather than individuals.

Indeed, our definition of adaptation only exacerbates this problem: how should we define the fitness of a (potentially short-lived) association? A lichen propagule contains both partners, so we can easily define its fitness by the number of propagules produced by the association. But this cannot be done for the association of a plant and its root symbionts: all partners in this system typically reproduce independently (plant seeds are unlikely to contain the spores of its symbionts). Can such an association be said to have a fitness? If not, saying that an adaptation benefits a given structure because it increases its fitness makes no sense.

Emergent Structures

There may be a way out of this conundrum, however, when one considers the unit of adaptation and fitness as linked emergent properties. Perhaps the easiest way to understand this is to consider the cluster of invading mutants in figure 6.2. As Van Baalen and Rand (1998) show, the dynamics of this cluster can be described by a set of differential equations (rather than by a single equation, as in non-structured

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populations). This implies that the mutant's capacity to increase is given by the dominant Lyapunov exponent of this set of equations. (The dominant Lyapunov exponent is a mathematical concept that tells us whether something increases or decreases in the long run.) This gives us a recipe for calculating fitness (easy in principle, even though in practice the method quickly becomes unwieldy). What Van Baalen and Rand (1998) also note is that because this dominant Lyapunov exponent is an eigenvalue of the system of equations describing mutant dynamics, it is also associated with an eigenvector, and they show that this eigenvector describes the characteristic structure of the invading cluster. Thus, altruism can be selected because it increases the fitness (Lyapunov exponent) of the unit of adaptation (the cluster, described by the corresponding eigenvector).

In spatial settings, the eigenvector describes the average structure of an invading cluster. In stage- or age-structured populations, the eigenvector describes the characteristic distribution (in terms of stage or age, as the case may be; see Caswell 2001). In populations that have both spatial and stage structure, the eigenvector is a mixture of both. If one adds diploid genetics with sexual reproduction, the eigenvector would also incorporate the effects of recombination. In all of these cases, the vector describes the characteristic structure a rare mutant creates when it tries to invade the system. Thus, the couple eigenvalue/eigenvector tells us not only how quickly a mutant invades, but also in what spatial structure. In other words, the notion of fitness is tightly coupled with that of the unit of adaptation, such that one cannot be considered without simultaneously considering the other. With the development of the theory of adaptive dynamics, great advances have been made with respect to the understanding of the former, but our understanding of the latter is lagging behind.

Unit of Adaptation versus Unit of Selection

That individuals are not always the relevant unit when considering evolutionary phenomena has long been recognized: sometimes it seems that one has to follow the evolutionary fate of individual genes, whereas in other cases one needs to consider larger structures (kin selection, group selection; Keller 1999). This has led to an ongoing debate about the relative importance of levels of selection other than that of the standard individual. In discussions of group selection, it is often argued that selection at a particular level requires that (1) there is heritable variation among the units involved, and (2) that this variation affects the replication of these units (see, for instance, Williams 1992, and Gardner in this volume). An important consequence of this definition is that without replication there cannot be selection at a given level. This is an important restriction: a plant-rhizosphere complex cannot be considered a level of selection, since plants and microorganisms do not spread together.

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However, as I argue here, even without replication a nonpersistent association can function as a unit of adaptation. It is therefore important to realize that the unit of selection and the unit of adaptation are not necessarily the same thing. In order for evolution to work, discreteness is necessary (evolution cannot occur if there are no persistent heritable variations can be selected), but in order to understand (and predict) the consequences of evolution, one needs to incorporate the fact that these units may be embedded in larger and less persistent structures: even if they do not replicate as such, they affect the fates of their constituent parts that do. As noted by Buss (1987), this hierarchical view was already adopted by Weismann (1893), who is normally considered to be a founder of the theory that the individual is the relevant unit of selection. Thus, although the unit of selection can be identical to the unit of adaptation, it need not be. A unit of adaptation may also be an embedding structure (for instance, a group of kin or a symbiotic association) but also something that is embedded within a classical individual (such as a group of genes that encode a particular trait).

Given that some authors use the notion of unit of selection in the classical sense (that which varies and which is selected) and others use it more in terms of the unit of adaptation, it is no surprise that a great confusion results, with a debate that goes on to this day. For instance, if group selection is interpreted in terms of units of selection sensu stricto, it is indeed not the same as kin selection, as argued by Dawkins (1979). However, interpreted in terms of unit adaptation, kin selection is just another way of formulating group selection (where adaptations benefit groups of related individuals; Grafen 1984; Leigh 2010).

Discussion

Even though it is now abundantly clear that the formation of associations is an important creative process in evolution, the ecological and evolutionary conditions that favor this process are still poorly understood. Perhaps one reason for this is the fact that many evolutionary biologists focus more on the process of speciation; that is, on the splitting of lineages, rather than on their merging. Whatever the reason, however, this is an unfortunate state of affairs, the more so if one realizes that the problem has been recognized since the nineteenth century, when it was realized that organisms such as lichens are actually associations.

The current state of affairs is that we do have many insights into why individuals may cooperate (Taylor & Nowak 2007). We do have lots of ideas about how such interactions can be exploited by parasites and cheaters (Ferrière, Bronstein, Rinaldi, Law et al. 2002; Burt & Trivers 2008; Jones, Ferrière, & Bronstein 2009). We have ideas about why individuals may associate to form larger structures (Buss 1987;

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Herron & Michod 2008). We may even begin to have some grasp of how members should balance their private interest with that of a larger structure they are part of (see figure 1 in Van Baalen and Jansen 2001). What we hardly have a clue about is under what conditions—if they exist at all—individuals should completely give up their evolutionary sovereignty and go up into some larger whole.

To my knowledge, the only theoretical study that explicitly addresses this issue is that of Law and Dieckmann (1998). They concluded that such a merger can occur if the weaker party can only defend itself against exploitation by the stronger one by giving up its capacity for independent existence. This outcome necessitates two things. First, the existence of a pronounced asymmetry between partners (which applies to many, but certainly not all, symbioses). Second, the weaker partner has to be subject to a rather specific trade-off (costs and benefits are expressed in different environments). The model certainly predicts an evolutionary merger, but the conditions seem rather specific.

So either we have to conclude that some crucial aspects still escape us, or that full mergers are much rarer than we think. The latter conclusion implies that partners even in an apparently persistent and coherent association have not completely given up their evolutionary sovereignty. This means that, under some conditions, possibly rare, partners may all of a sudden start to pursue their private interests, to the detriment of the larger whole they are part of. This could provide a general evolutionary explanation for diseases like cancer and some forms of autoimmune disorders.

If we accept that individuals are almost always associations of subunits without fully aligned interests, as argued by Buss (1987), it becomes all the more important to understand what maintains the apparent cohesion of recognizable "individuals." It seems that flexible behavior and communication may play central roles here, for instance by allowing the recognition and "punishment" of components that behave too selfishly.

Heritability

Another cherished concept that may have to go (or at least must be revised thoroughly) if we allow individuals to be composites is that of heritability. It is textbook knowledge that heritability of traits is one of the prime conditions necessary for evolution to occur. Usually, heritability is defined as the regression between offspring and their parents, and is thus linked to entities that may form lineages. However, as I have argued, very often partners in an association reproduce independently, so that it becomes difficult to work out who are the "parents" of a given association, and who will be its offspring. This criticism is not so serious, because in diploid sexual populations as well, offspring are genetically often very different from

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their parents: the formation of a multipartner association is (in a fundamental sense) not very different from fusion of a pair of gametes. So as soon as the unit of adaptation is sufficiently well described, it should not be so difficult to work out measures of heritability if one wishes to do so: it suffices to assign "parent" and "offspring" structures (which may entail a rather arbitrary choice) and measure correlations between these structures. It should not be forgotten that heritability, even in the classical sense, may depend on the transmission of multiple kinds of information (Danchin & Wagner 2010; Danchin et al. 2011).

Finally, we have to be aware that even when we observe "individuals" in the sense of independently operating entities, these may not be the relevant units of adaptation. This is less controversial, since for social insects this insight was already obvious to Darwin and is now generally accepted (Keller 1999). Nevertheless, in many cases the identification of the unit of adaptation is a far from trivial matter. Think, for instance, of the complex network of above-ground and below-ground interactions in a continuous vegetation. Such networks are a mixture of mutualistic and parasitic interactions (Van der Heijden, Klironomos, Ursic, Moutoglis et al. 1998), but the associations they create are far from neatly delineated. Much work is still needed before we can work out the units of adaptation in such systems.

Kin Selection Revisited

Andy Garder (in this volume; but see also Gardner and Grafen 2009) discusses how group selection and kin selection change the agenda (the "things to be done") of individuals in the system: instead of trying to maximize their own fitness (lifetime reproductive success), they strive to maximize their inclusive fitness (Hamilton 1963, 1964); that is, their individual fitness plus the fitness of the individuals affected by their actions, weighted according to their relatedness (Rousset & Billiard 2000). Any adaptations that result are in some sense "good for the group," and compatible with Williams' principle (see Gardner's contribution to this volume), which states that for group adaptations to arise there should be competition among groups. Calculating inclusive fitness is nothing but a way of calibrating the two processes (individual and group selection) at the level of the individual. I have no intention of entering this debate here, but in the context of this volume, I want to point out that, for either interpretation, one should be able to recognize and characterize groups, and doing so is not always obvious. Group selection theory usually assumes two neatly delineated levels (individuals and groups), but often the higher levels are not so well characterized. More seriously, group size is often not an externally imposed constraint but results from the participants' behaviors (Gadagkar 2001; Garcia & De Monte, unpublished data, 2012). And, as I've argued here, higher-level units of adaptation are often composed of members of more than one species, and are thus

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difficult to capture using traditional approaches, which focus on single populations, such as partitioning the Price equation. In any of those more complicated cases, it may be difficult to identify adaptations by trying to assess function and purpose, because we may not know where to look! It is only after we have identified the unit of adaptation that we can try to understand function and purpose, and establish what agenda its constituent parts should have.

Recently, there has been debate around the explanatory capacity of kin selection (Nowak et al. 2010; Abbot, Abe, Alcock, Alizon et al. 2011; Ferrière & Michod 2011). Nowak et al. (2010) argue that kin selection theory is not even relevant to understanding the evolution of sociality because, they claim, it is based on a much more restrictive set of assumptions than warrants its broad application. While I agree that simplifying assumptions underlying its usual formulation (for instance, Price's famous equation for the change of allele frequencies; Price 1970) sometimes limits its application, I think that Hamilton's original insight has gloriously stood the test of time. I would even argue that kin selection theory is actually the only revolutionary breakthrough in evolutionary theory since Darwin! Thus, in sharp contrast to Nowak and colleagues (2010), I think that without kin selection theory we cannot even begin to understand why the most fundamental major transitions in evolution occurred, such as the evolution of multicellular organisms and, indeed, possibly even life itself. While there can be disagreement about methodological aspects—such as whether the Price equation (Price 1970) is the best tool to understand kin selection and predict its consequences (I do not think so)—there should be no doubt that kin selection stood at the basis of many fundamental evolutionary inventions. One of the potential shortcomings of many kin selection models is their focus on the evolution of single populations, making it difficult to assess to what extent the evolution of multispecies associations are governed by similar principles (Herre et al. 1999). There is no doubt that the Price-equation approach can be used to capture selection at other levels than that of the individual (Gardner & Grafen 2009), but it is not well-suited to study coevolution in independent gene pools, as would be necessary to adopt the approach to study symbiotic mutualisms. However, as I have argued here, and as others have argued previously (Frank 1994; Fletcher & Doebeli 2009), between- and within-species cooperation is often governed by similar principles, and rather than abolishing kin selection, we should try to generalize the phenomenon to multispecies interactions in their ecological contexts. For this, the single-species point of view needs to be abolished, and more general methods—such as, for instance, Szathmáry's "stochastic corrector" approach (Zintzaras, Santos, & Szathmáry 2002) or Fletcher and Doebeli's (2009) assortment-based approach—need to be developed. Only then can we start to understand why life evolved the way it has, with its incredible diversity and structure.

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References

Abbot P, Abe J, Alcock J, Alizon S, Alpedrinha JAC, Andersson M, et al. 2011. Inclusive fitness theory and eusociality. *Nature* 471: E1–E4.

Axelrod RR. *The Evolution of Cooperation.* Basic Books: New York, NY; 1984.

Bateson G. 1963. The role of somatic change in evolution. *Evolution* 17: 529–539.

Bateson G. *Steps to an Ecology of Mind.* Chandler: San Francisco, CA; 1972.

Bergstrom CT, Lachmann M. 1998. Signaling among relatives. III. Talk is cheap. *Proc Natl Acad Sci USA* 95: 5100–5105.

Blackmore S. *The Meme Machine.* Oxford, UK: Oxford University Press; 1999.

Boerlijst M, Hogeweg P. 1991. Spiral wave structure in pre-biotic evolution: Hypercycles stable against parasites. *Physica D* 48: 17–28.

Bosch TG, McFall-Ngai MJ. 2011. Metaorganisms as the new frontier. *Zoology* 114: 185–190.

Burt A, Trivers RL. *Genes in Conflict: The Biology of Selfish Genetic Elements.* Cambridge, MA: Belknap Press; 2008.

Buss LW. *The Evolution of Individuality.* Princeton, NJ: Princeton University Press; 1987.

Caswell H. *Matrix Population Models. Construction, Analysis, and Interpretation.* 2nd ed. Sunderland, MA: Sinauer; 2001.

Châline N, Ratnieks FWL, Burke T. 2002. Anarchy in the UK: Detailed genetic analysis of worker reproduction in a naturally occurring British anarchistic honeybee, *Apis mellifera*, colony using DNA microsatellites. *Mol Ecol* 11: 1795–1803.

Claidière N, André J-B. 2012. The transmission of genes and culture: A questionable analogy. *Evol Biol*. In press: 39: 12–24.

Dall SRX, Giraldeau L-A, Olsson O, McNamara JM, Stephens DW. 2005. Information and its use by animals in evolutionary ecology. *Trends Ecol Evol* 20: 187–193.

Danchin E, Charmantier A, Champagne FA, Mesoudi A, Pujol B, Blanchet S. 2011. Beyond DNA: Integrating inclusive inheritance into an extended theory of evolution. *Nat Rev Genet* 12: 475–486.

Danchin E, Wagner RH. 2010. Inclusive heritability: Combining genetic and non-genetic information to study animal behavior and culture. *Oikos* 119: 210–218.

Dawkins R. *The Selfish Gene.* Oxford, UK: Oxford University Press; 1976.

Dawkins R. 1979. Twelve misunderstandings of kin selection. *Z Psychol Z Angew Psychol* 51: 184–200.

Dawkins R. *The Extended Phenotype.* Oxford, UK: Freeman; 1982.

Dingli D, Nowak MA. 2006. Infectious tumour cells. *Nature* 443: 35–36.

Eigen M, Schuster P. *The Hypercycle: A Principle of Natural Self-Organization.* Berlin: Springer; 1979.

Ferrière R, Bronstein JL, Rinaldi S, Law R, Gauduchon M. 2002. Cheating and the evolutionary stability of mutualisms. *Proc Biol Sci* 269: 773–780.

Ferrière R, Michod RE. 2011. Inclusive fitness in evolution. *Nature* 471: E6–E8.

Fletcher JA, Doebeli M. 2009. A simple and general explanation for the evolution of altruism. *Proc Biol Sci* 276: 13–19.

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Frank SA. 1994. Genetics of mutualism: The evolution of altruism between species. *J Theor Biol* 170: 393–400.

Frank SA. 1997. Models of symbiosis. *Am Nat* 150: S80–S99.

Gadagkar R. *The Social Biology of* Ropalidia marginata. Cambridge, MA: Harvard University Press; 2001.

Gardner A, Grafen A. 2009. Capturing the superorganism: A formal theory of group adaptation. *J Evol Biol* 22: 659–671.

Gottlieb B, Beitel LK, Alvarado C, Trifiro MA. 2010. Selection and mutation in the "new" genetics: An emerging hypothesis. *Hum Genet* 127: 491–501.

Grafen A. Natural selection, group selection and kin selection. In Krebs JR, Davies NB, eds. *Behavioural Ecology: An Evolutionary Approach*. 2nd ed. Oxford, UK: Blackwell; 1984: pp. 62–84.

Grafen A. 1990. Biological signals as handicaps. *J Theor Biol* 144: 517–546.

Hamilton WD. 1963. The evolution of altruistic behaviour. *Am Nat* 97: 354–356.

Hamilton WD. 1964. The genetical evolution of social behaviour. I and II. *J Theor Biol* 7: 1–16, 17–52.

Hamilton WD. 1967. Extraordinary sex ratios. *Science* 156: 477–488.

Hardin G. 1968. The tragedy of the commons. *Science* 162: 1243–1247.

Herre EA, Knowlton N, Mueller UG, Rehner SA. 1999. The evolution of mutualisms: exploring the paths between conflict and cooperation. *Trends Ecol Evol* 14: 49–53.

Herron MD, Michod RE. 2008. Evolution of complexity in the volvocine algae: Transitions in individuality through Darwin's eye. *Evolution* 62: 436–451.

Hogeweg P. 2009. From population dynamics to ecoinformatics: Ecosystems as multilevel information processing systems. *Ecol Inform* 2: 103–111.

Hooper LV, Gordon JI. 2001. Commensal host-bacterial relationships in the gut. *Science* 292: 1115–1118.

Jablonka E, Lamb MJ. *Evolution in Four Dimensions.* Cambridge, MA: MIT Press; 2005.

Jansen VAA, Van Baalen M. 2006. Altruism through beard chromodynamics. *Nature* 440: 663–666.

Jones EI, Ferrière R, Bronstein JL. 2009. Eco-evolutionary dynamics of mutualists and exploiters. *Am Nat* 174: 780–794.

Keller L. *Levels of Selection in Evolution.* Princeton, NJ: Princeton University Press; 1999.

Kostitzin VA. *Symbiose, Parasitisme et Évolution (Étude Mathématique).* Paris, France: Hermann et Cie; 1934.

Law R, Dieckmann U. 1998. Symbiosis through exploitation and the merger of lineages in evolution. *Proc Biol Sci* 265: 1245–1253.

Leigh EG. 1991. Genes, bees and ecosystem: The evolution of common interest among individuals. *Trends Ecol Evol* 6: 257–262.

Leigh EG. 2010. The group selection controversy. *J Evol Biol* 23: 6–19.

Lion S, Van Baalen M. 2007. From infanticide to parental care: Why spatial structure can help adults be good parents. *Am Nat* 170: E26–E46.

Lion S, Van Baalen M. 2009. The evolution of juvenile-adult interactions in populations structured in age and space. *Theor Popul Biol* 76: 132–145.

Lipsitch M, Nowak MA, Ebert D, May RM. 1995. The population-dynamics of vertically and horizontally transmitted parasites. *Proc Biol Sci* 260: 321–327.

MacFarlane GT, Gibson GR. Carbohydrate fermentation, energy transduction and gas metabolism in the human large intestine. In: Mackie R, White B, eds. *Gastrointestinal Microbiology.* New York, NY: Chapman and Hall; 1997:269–317.

Margulis L. *The Origin of Eucaryotic Cells.* New Haven, CT: Yale University Press; 1970.

Maynard Smith J. 1979. Hypercycles and the origin of life. *Nature* 280: 445–446.

Maynard Smith J. 2000. The concept of information in biology. *Philos Sci* 67: 177–194.

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Maynard Smith J, Szathmáry E. *The Major Transitions in Evolution.* Oxford, UK: Freeman; 1995.

McCallum H, Jones M. 2006. To lose both would look like carelessness: Tasmanian devil facial tumour disease. *PLoS Biol* 4: e342–e432.

Metz JAJ, Nisbet RM, Geritz SAH. 1992. How should we define "fitness" for general ecological scenarios? *Trends Ecol Evol* 7: 198–202.

Michod RE. 1996. Cooperation and conflict in the evolution of individuality. II. Conflict mediation. *Proc Biol Sci* 263: 813–822.

Michod RE. 2005. On the transfer of fitness from the cell to the multicellular organism. *Biol Philos* 20: 967–987.

Nowak M, Krakauer DC. 1999. The evolution of language. *Proc Natl Acad Sci USA* 96: 8028–8033.

Nowak MA, Tarnita C, Wilson E. 2010. The evolution of eusociality. *Nature* 466: 1057–1062.

Pearson H. 2002. Human genetics: Dual identities. *Nature* 417: 10–11.

Price GR. 1970. Selection and covariance. *Nature* 227: 520–521.

Qin J, Li R, Raes J, Arumugam M, Burgdorf KS, Manichanh C, et al. 2010. A human gut microbial gene catalogue established by metagenomic sequencing. *Nature* 464: 59–65.

Richardson DHS. War in the world of lichens: Parasitism and symbiosis as exemplified by lichens and lichenous fungi. Mycol Res 1999;103:641–650.

Rousset F, Billiard S. 2000. A theoretical basis for measures of kin selection in subdivided populations: Finite populations and localized dispersal. *J Evol Biol* 13: 814–825.

Rousset F, Roze D. 2007. Constraints on the origin and maintenance of genetic kin recognition. *Evolution* 61: 2320–2330.

Sapp J. *Evolution by Association: A History of Symbiosis.* New York, NY: Oxford University Press; 1994.

Shannon CE. 1948. A mathematical theory of communication. *Bell Syst Tech J* 27: 379–423, 623–656.

Shorter J, Lindquist S. 2005. Prions as adaptive conduits of memory and inheritance. *Nat Genet* 6: 435–450.

Smith EA. 2010. Communication and collective action: Language and the evolution of human cooperation. *Evol Hum Behav* 31: 231–245.

Strassmann JE, Queller DC. 2010. The social organism: Congresses, parties and committees. *Evolution* 64: 605–616.

Taylor C, Nowak MA. 2007. Transforming the dilemma. *Evolution* 61: 2281–2292.

Taylor PD. 1992. Inclusive fitness in a homogeneous environment. *Proc Biol Sci* 249: 299–302.

Turner PE, Cooper VS, Lenski RE. 1998. Tradeoff between horizontal and vertical modes of transmission in bacterial plasmids. *Evolution* 52: 315–329.

Van Baalen M. 1998. Coevolution of recovery ability and virulence. *Proc Biol Sci* 265: 317–325.

Van Baalen M. Pair approximations for different spatial geometries. In: Dieckmann U, Law R, Metz JAJ, eds. *The Geometry of Ecological Interactions: Simplifying Spatial Complexity.* Cambridge, MA: Cambridge University Press; 2000: 359–387.

Van Baalen M, Jansen VAA. 2001. Dangerous liaisons: the ecology of private interest and common good. *Oikos* 95: 211–224.

Van Baalen M, Jansen VAA. 2003. Common language or Tower of Babel? On the evolutionary dynamics of signals and their meaning. *Proc Biol Sci* 270: 69–76.

Van Baalen M, Rand DA. 1998. The unit of selection in viscous populations and the evolution of altruism. *J Theor Biol* 143: 631–648.

Van der Heijden MA, Klironomos JN, Ursic M, Moutoglis P, Streitwolf-Engel R, Boller T, et al. 1998. Mycorrhizal fungal diversity determines plant biodiversity, ecosystem variability and productivity. *Nature* 396: 69–72.

PROPERTY OF MIT PRESS: FOR PROOFREADING AND INDEXING PURPOSES ONLY

Vet LEM, Dicke M. Plant-carnivore interactions: evolutionary and ecological consequences for plant, herbivore and carnivore. In: Olff H, Brown VK, Drenth RH, eds. *Herbivores: Between Plants and Predators.* Oxford, UK: Blackwell Science; 1999:483–520.

Walter J, Britton RA, Roos S. 2011. Host-microbial symbiosis in the vertebrate gastrointestinal tract and the *Lactobacillus reuteri* paradigm. *Proc Natl Acad Sci USA* 108: 4645–4652.

Weismann A. *The Germ Plasm: A Theory of Heredity.* New York, NY: Charles Scribner; 1893.

Welsh JS. 2011. Contagious cancer. *Oncologist* 16: 1–4.

Werren JH. 2011. Selfish genetic elements, genetic conflict, and evolutionary innovation. *Proc Natl Acad Sci USA* 108: 10863–10870.

West SA, Kiers TE, Pen I, Denison RF. 2002. Sanctions and mutualism stability: When should less beneficial mutualists be tolerated? *J Evol Biol* 15: 830–837.

Williams GC. *Adaptation and Natural Selection.* Princeton, NJ: Princeton University Press; 1966.

Williams GC. *Group Selection.* Chicago, IL: Aldine; 1971.

Williams GC. *Natural Selection. Domains, Levels, and Challenges*. Oxford, UK: Oxford University Press; 1992.

Yamamura N. 1993. Vertical transmission and evolution of mutualism from parasitism. *Theor Popul Biol* 44: 95–109.

Yamamura N. 1996. Evolution of mutualistic symbiosis: A differential equation model. *Res Popul Ecol (Kyoto)* 38: 211–218.

Zintzaras E, Santos M, Szathmáry E. 2002. "Living" under the challenge of information decay: The stochastic corrector model vs. hypercycles. *J Theor Biol* 217: 167–181.

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