



TOWARD AN EVOLUTIONARY DEFINITION OF CHEATING

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The term “cheating” is used in the evolutionary and ecological literature to describe a wide range of exploitative or deceitful traits. Although many find this a useful short hand, others have suggested that it implies cognitive intent in a misleading way, and is used inconsistently. We provide a formal justification of the use of the term “cheat” from the perspective of an individual as a maximizing agent. We provide a definition for cheating that can be applied widely, and show that cheats can be broadly classified on the basis of four distinctions: (i) whether cooperation is an option; (ii) whether deception is involved; (iii) whether members of the same or different species are cheated; and (iv) whether the cheat is facultative or obligate. Our formal definition and classification provide a framework that allow us to resolve and clarify a number of issues, regarding the detection and evolutionary consequences of cheating, as well as illuminating common principles and similarities in the underlying selection pressures.

KEY WORDS: Cheat, cooperation, deception, exploitation, intentional language, social evolution.

The problem of explaining the evolution of cooperative behavior is commonly framed in terms of the need to explain the selective forces that resist invasions by “cheats” but there is a lack of consensus about what a “cheat” actually is. The terms “cheat” or “cheating” are employed to describe a variety of traits and behaviors across a wide range of systems, from dishonest signalers to exploiters of mutualisms (Table 1). This suggests that many workers find the terminology a useful way to convey information about behavior. In addition, the need to explain why cheating does not lead to the breakdown of social systems is frequently posed as a major research challenge (Yu and Pierce 1998; Bronstein 2001; Kiers et al. 2003; Trivisano and Velicer 2004).

In contrast, it has also been argued that the term cheat is misleading and should be avoided in the biological context. First, it has been suggested that the term “cheat” is anthropomorphic and implies a cognitive intent that may not be appropriate in the majority of organisms (Bronstein 2001; Noe 2006; Douglas 2008). In some cases, alternative terms have been suggested or used such as “exploiter” or “greedy.” Second, although other intentional terms such as altruism and spite are defined purely in terms of fitness costs and benefits (Hamilton 1964), the term “cheat” also implies

something about how the fitness consequences arise. Third, the term “cheat” has been used inconsistently across a diversity of biological systems (Table 1). It is not always clear what exactly a cheat is, whether a cheat is always a cheat, how selection favors individuals that cheat, or how we would expect others to respond to cheating. If different researchers use the term cheat in different ways, then this will impede attempts to unify our understanding of both the evolutionary biology of cheats, and the subsequent implications.

We aim to resolve these points of contention and the potential confusion arising from the use of “cheating” in the evolutionary and ecological literature. We first examine general arguments for when intentional language can be used in biology, and provide a definition for cheating that can be applied widely. We use this definition as a framework to point out potential problems when empirically testing for cheats and for classifying the different forms of cheating, which have been observed in nature. Finally, we consider how and when selection is expected to lead to an effective counter-strategy to being cheated, and whether examining social behaviors from the perspective of cheats is always necessary or the most useful way forward.

Table 1. Examples of traits that have been classified as cheating.

Term	Organism
Nectar robbers ¹	Birds and insects
Non-hoarders ²	Birds and mammals
Mutualism exploiters ³	Insects, birds, plants, fishes
Mimics ^{3,4}	Insects, plants, arachnids
Social parasites ^{5,6}	Microbes
Hyperparasites ⁷	–
Brood parasites ⁸	Birds and insects
Aprovechados ^{3,9,10}	Plants and Insects
Kleptoparasites ¹¹	Insects, birds, plants, mammals, reptiles, amphibians, fishes
Scroungers ¹¹	Insects, birds, plants, mammals, reptiles, amphibians, fishes
Free loaders ^{12,13}	Insects and microbes
Defectors ^{10,14,15}	Fishes, insects, microbes, humans
Non-cooperators ^{14,16}	Microbes and humans
Non-producers ¹⁶	Microbes
Cancer cells ¹⁷	–
Illegitimate emitters ⁴	Arachnids, insects, and plants
Dishonest signaler ¹⁸	Insects
Somatic parasites ¹⁹	Microbes
Beneficiary mutant ²⁰	Microbes

¹Maloof and Inouye (2000).

²Andersson and Krebs (1978).

³Bronstein (2001).

⁴Dicke and Sabelis (1992).

⁵Strassmann and Queller (2011).

⁶Fiegna and Velicer (2003).

⁷Hochberg et al. (2000).

⁸Davies (1992, 2000) and Kilner and Langmore (2011).

⁹Tyre and Addicott (1993) and Addicott and Tyre (1995).

¹⁰Yu and Pierce (1998).

¹¹Barnard (1984).

¹²West et al. (2006).

¹³Bronstein et al. (2006).

¹⁴West et al. (2007c).

¹⁵Bshary (2002).

¹⁶Xavier (2011).

¹⁷Nunney (1999).

¹⁸Tibbetts and Dale (2004).

¹⁹Matapurkar and Watve (1997).

²⁰Morris et al. (2012).

Can the Use of Intentional Terms Like Cheat be Justified?

Biologists often borrow terms from everyday speech to describe phenomena. The advantage of this is that it can provide a shorthand that conveys meaning in an efficient way. One of the clearest examples of this is how the term “selfish” was used to help explain the “gene’s eye” view by Dawkin’s (1976) in *The Selfish Gene*. Another example is how the term “altruism” is used to describe helping behaviors that are costly to perform, but provide a ben-

efit to another individual (Hamilton 1964). Confusion can arise when terms are poorly defined or used inconsistently, as previously shown in relation to terms such as altruism and eusociality (Crespi and Yanega 1995; West et al. 2007c).

Cheat and cheating are usually used in ways that suggest an intention or purpose to deceive or exploit others, in line with dictionary definitions. The Oxford dictionary (2010) definition of a “cheat” is: “a person who behaves dishonestly in order to gain an advantage.” The definition of the verb to “cheat” is: “gain an advantage over or deprive of something by using unfair or deceitful methods.” A potential problem with the term cheat is that it is anthropomorphic and implies cognitive intent where there is not (Bronstein 2001; Bshary and Bronstein 2004). In particular, individuals are often referred to as cheats, in cases where they lack the cognitive ability to intentionally cheat and gain fitness, such as bacteria, slime molds, plants, and many animals.

However, evolutionary theory provides a formal justification for the use of intentional language. Natural selection will lead to organisms that appear to be designed to maximize their fitness, with our most general definition of fitness being inclusive fitness (Fisher 1930; Hamilton 1964; Grafen 2006; West and Gardner 2013). Another way of saying this is that natural selection will lead to organisms that act with the appearance of intention, as if they are trying to maximize their fitness. This does not mean that any or all intentional language is justified, but rather that intentional language is justified when it can be linked to an individual acting as a maximizing agent analogy, in terms of its fitness or reproductive success (Grafen 1999).

The advantage of using intentional language in this way is that it provides an useful shorthand that describes classes of traits, in a way that provides information about fitness consequences and gene dynamics (West et al. 2007c). For example, if we know that a behavior is “altruistic,” then this tells us that both: (a) the behavior is costly to perform, but benefits others; and (b) natural selection will have favored this behavior because it is directed toward relatives (Hamilton 1964, 1970). We would want the term cheat to provide analogously useful information. Other examples of justified and useful intentional language include the terms cooperation, selfish, signal, and deception (Maynard Smith and Harper 2003; West et al. 2007c).

What is a Cheat?

We define cheating as: (i) a trait that is beneficial to a cheat and costly to a cooperator in terms of inclusive fitness (ii) when these benefits and costs arise from the actor directing a cooperative behavior toward the cheat, rather than the intended recipient.

The distinction between “cheat” and “recipient” is key to our definition. Confusion can arise because both are individuals

that benefit from a cooperative act but they differ in the fitness consequences of that benefit to the actor that performs the cooperative act, and, therefore, in their effect on selection for cooperation. This follows from the formal definition of cooperation as a behavior that is favored by selection, at least in part, from its beneficial effect on the recipient (West et al. 2007c). If the benefit of cooperation goes to the intended recipient, then this provides a direct or indirect benefit to the actor that can favor cooperation. If the benefit goes to the cheat, then it decreases the fitness of the cooperator, potentially selecting against cooperation.

It is important to note that not every individual that benefits from a cooperative act is either a recipient or a cheat: a fringe-lipped bat (*Trachops cirrhosis*) that uses the mating calls of male frogs to locate and prey on them, or a parasitoid fly (*Euphasiopteryx ochracea*) that uses the songs of male crickets to locate a host on which to lay eggs (Cade 1975; Zuk and Kolluru 1998; Page and Ryan 2008) are not the “recipient” of the cooperative act of signaling. Other examples include nectar robbers, which steal a flower’s nectar, but are not the recipients that fulfill the flower’s pollination services (Richardson 1995; Maloof and Inouye 2000), or a man who raids a beehive is not the “recipient” of the cooperative act of producing honey. In all of these cases, the cooperative act is only favored by selection as a result of a benefit provided to the intended recipients—female frogs and crickets, pollinators, and colony mates. We suggest that it is not useful to include examples of eavesdropping or stealing in a definition of cheating, because the fitness consequences for cooperation in these examples are not driven by the fact that the behaviors being exploited are social.

Our requirement that the benefit and cost result from cooperation is required to distinguish cheating from other selfish behaviors. For example, consider when anglerfishes lure prey with the bioluminescent flesh growth on their head, or when chameleons camouflage themselves to hide from predators. In both cases, a cooperative interaction is not being exploited, and so we would not want to classify this as cheating—real prey do not want to be eaten, and uncamouflaged prey do not want to be found, respectively. This emphasizes that the problem of cooperation is to explain why cheating does not lead to the breakdown of cooperation (Sachs et al. 2004; West et al. 2007b; Bourke 2011).

Cheats require a mechanism for cheating others. Our definition of cheat includes individuals that intercept cooperation meant for someone else, and individuals that manipulate others to direct cooperation toward them. An example of interception would be an individual that did not perform, or performed less of, an indiscriminate cooperative behavior, but still benefited from the cooperation of others, such as a bacterial cell that did not produce iron scavenging siderophore molecules (Griffin et al. 2004). In this case, the mechanism of cheating is just to cooperate less, but specific exploitative traits are also possible.

An example of cheating by manipulation is when fork-tailed drongos (*Dicrurus adsimilis*) give false predator-warning alarm calls, to make pied babblers or meerkats flee, allowing the drongos to steal their food (Ridley et al. 2007; Flower 2011). In this case, the drongos are manipulating the babblers and the meerkats to perform what would normally be a cooperative response to an alarm call. A second example is when cleaner fish (*Labroides dimidiatus*) take a bite from the fish client, rather than eating/cleaning the parasites off them (Bshary and Grutter 2002). In this case, the cleaner fish are exploiting the cooperative behavior of the client fish to stay there and have its parasites eaten. Another example is when some firefly females of the genus *Photuris* mimic the light flash pattern of *Photinus* females of another species, to lure in males to what he perceives to be a receptive female, only to be preyed on by the *Photuris* female (Lloyd 1983).

Cooperation occurs at all levels of biological organization, and so we should also expect to see cheating at all levels of biological organization (Bourke 2011). Meiotic drivers, such as sex chromosome drivers, cheat other alleles at that locus (Burt and Trivers 2006). Cells within multicellular organisms can cheat other cells. For example, in the fruiting bodies of *Dictyostelium discoideum* slime molds, or *Myxooccus xanthus* bacteria, cells could increase their likelihood of being in the reproductive spore head, rather than the stalk that holds the spore head up (Strassmann et al. 2000; Velicer et al. 2000). Similarly, cancers can spread as cheats within a multicellular organism (Bourke 2011).

We distinguish between putative or potential cheats, which might not be favored by natural selection, and cheats that are maintained in populations as adaptations. Individuals can arise by mutation, or be experimentally created by genetic and phenotypic manipulations, that cooperate to a lesser extent and are therefore potential cheats (Foster et al. 2007; West et al. 2012). For example, bacteria mutants that produce less of an extracellular public good, such as iron-scavenging siderophore molecules, or rhizobia bacteria that are prevented from fixing nitrogen for their host plants (Kiers et al. 2003; Griffin et al. 2004). Whether this provides a fitness benefit, allowing them to be “successful” cheats that can spread and be maintained in the population is another matter. The success of such mutants will depend upon factors such as whether the population structure will allow them to exploit cooperators, or if their social partners have mechanisms to reduce cooperation with non-cooperators. This distinction allows us to have a formal definition for cheating adaptations that are maintained in the population, while also talking about how cooperation can be stable against potential cheats.

It is necessary to distinguish between the fitness consequences of being cheated and the fitness consequences of interacting with a cheat. Although the fitness effect of being cheated is costly (negative) to the recipient, this does not mean that interacting with a cheat will necessarily result in a net reduction

of fitness. For example, consider the cooperative interaction between legume plants (*Glycine max*) and their rhizobia bacteria (*Bradyrhizobium japonicum*), where rhizobia provide their plant hosts with nitrogen, and are given carbon in exchange. If a rhizobia strain were able to benefit by providing relatively less nitrogen to their host plant, while still receiving carbon, then it would be a successful cheat, at a (relative) cost to the fitness of their host plant (Kiers et al. 2003). Nonetheless, it could still be better for the plant to interact with this cheater strain than to not interact with it, when the smaller amount of nitrogen that it provides is better than getting no nitrogen at all.

How do We Find Cheats?

Consider a species of bacteria where individuals produce and release a molecule to acquire a resource from the environment. For example, the siderophore molecules produced by many bacteria to scavenge iron from the environment (West and Buckling 2003). If we detect individual variation in levels of production of this molecule, could we say that low producers are cheating? We suggest that there are three key questions that need to be considered when trying to determine whether individuals are cheats.

IS A COOPERATIVE TRAIT BEING EXPLOITED?

In the context of our bacterial example, is the production and release of the molecule a cooperative behavior? The first step in testing this is to grow two strains that differ in the amount of the molecule that they produce, either alone or in a mixed population. If the molecule is cooperative and individuals that produce less are acting as cheats, then we predict, when grown in an environment where the molecule is required for growth, that: (a) populations of cells that produce the molecule (the putative cooperators) should grow better than populations of cells that produce less of the molecule (the putative cheats); (b) when grown in mixed populations, the cells that produce less of the molecule (the putative cheat) should increase in frequency (Griffin et al. 2004). These results would show that the trait provides a benefit at the group level that can be exploited by individuals who do less. Put simply, the putative cheats are acting as cheats. A series of finer predictions can also be made, regarding how the fitness of putative cheats will also depend upon their frequency in the population, population density, and the relative extent to which they produce the molecule (West et al. 2006; Ross-Gillespie et al. 2007, 2009; Jiricny et al. 2010; West et al. 2012).

DOES VARIATION IN BEHAVIOR EVOLVE FROM SELECTION TO CHEAT?

The experiments described earlier can identify cheats, but this does not mean that they evolved or are being maintained in the population as cheats. For example, strains that produce less of the

molecule may have been isolated from environments where the molecule was not required to scavenge resources, and so they have just evolved a lower production for this reason. This can be a difficult problem to address. One option is to obtain multiple strains from an environment where you know that the strains can interact. Another option is to take a phylogenetic approach and examine the order in which different traits evolved. For example, Cordero et al. (2012) surveyed siderophore production across a large number of *Vibrio* populations, and showed that, although siderophore production is often lost, the ability to uptake siderophores is always retained. This suggests that there was selection to retain the ability to use siderophores produced by other strains, rather than just selection to lose the trait.

ARE THE STUDIES CARRIED OUT IN AN APPROPRIATE ENVIRONMENT?

Consider the scenario where we have a cooperator and a cheat strain, that evolved in a certain environment, but we carry out the growth assays in a different environment where there is an excess of resources such that the molecule provides no benefit. In this case, cheats avoids the cost of producing the molecule and grow better in both the mixed and monocultures. This could lead us to concluding that the trait was not social (e.g., Zhang and Rainey 2013), which would be an error, as it is social, just not in that particular environment. To give an analogy, this would be like testing whether lions foraged cooperatively, but doing the study in a zoo, where there was ad lib food and they did not do any actual foraging. Although it can be difficult to know the appropriate environment, it is very unlikely to be one where the molecule is not needed, because if that were the case, there would not have been selection to produce the molecule.

To give another possible scenario, imagine that we had two strains, neither of which were cheats. One strain produces a relatively large amount of the molecule (it came from a harsh environment where the molecule was required) and the other produces a relatively low amount of the molecule (it came from a rich environment where the molecule was less required). Now imagine that we carried out our growth assays in an intermediate environment, where only an intermediate amount of molecule was optimal. In this case, a mixed culture would produce the molecule at a rate closer to the optimal amount, and hence grow at a faster rate than the two monocultures. Although we might be tempted to conclude that this means “cheats” aid population growth, this would be misleading. Instead, what we have shown is that when some individuals are over-cooperating, this can be partially compensated for at the level of the population, by other individuals cooperating at lower levels (MacLean et al. 2010). Furthermore, the result in our thought experiment is an artifact of the conditions under which the experiment has been carried out in the laboratory. If we had used a strain that had evolved in the intermediate

environment, we would expect it to produce an intermediate level of the molecule, such that the addition of cheats would always decrease population growth.

It is important to distinguish cases of true cheating from cases of differential trait expression, because this distinction is key to understanding how cooperative groups resist the invasion of cheats and, therefore, ultimate questions about the evolution of cooperation. For example, if we accepted the low producers from the previous paragraph as “cheats,” we would get the wrong answers to these ultimate questions. Tolerance of being cheated is not favored as a result of population-level benefits and it is not favored because cheats may also cooperate to some extent. Cheating is bad for cooperators, by definition, and we can only understand how and why cooperation persists by understanding how cheating is resisted by direct or indirect (kin selected) benefits (Sachs et al. 2004; West et al. 2007b; Bourke 2011).

Another example of the need to recognize that cheating is bad for cooperation is provided by Rainey’s (2007; Rainey and Kerr 2010) suggestion that the germ line could have evolved by cheating in early multicellular organisms. If germ cells were cheats, then they would have imposed a cost on the soma cells, which would have led to a germ–soma conflict, and selection for the soma to suppress the germ (Bourke 2011). Instead, the germ line has evolved as a form of cooperation, which provided an inclusive fitness benefit to both germ and soma cells (Queller 2000; Bourke 2011), as supported by the fact that sterile cells are more likely to occur in species where the multicellular groups are clonal (Fisher et al. 2013).

We focused on a bacterial example in this section to illustrate general problems. We did this because, as illustrated earlier, we think that the term cheat is sometimes misapplied within the microbial literature, in a way that leads to the implications being overinterpreted. We provide other examples later, when discussing why cheats do not take over. This problem has arisen, in part, because of the extent to which both environmental condition and strain behavior can be experimentally manipulated in studies of microbes. In animals, such extreme manipulations are not possible, and the social fitness consequences of traits can be clearer, making such overinterpretation harder. For example, consider the parental behavior in a fictional species of bird where males and females form monogamous pairs, and raise one chick per breeding attempt. Now suppose a mother feeds at the optimal rate, but that the male feeds at a much higher rate, such that there is more food than the chick can eat. In this situation, we would conclude that the male is feeding at too high a rate, possibly due to an experimental manipulation. It is clearly incorrect to claim that the female is a cheat. However, analogous claims have been made in some microbial studies, by carrying out studies in environments where some strains are overperforming behaviors.

A Key to Cheating

Ideally, our definition of cheating can be applied to a diverse range of biological phenomena, ranging from molecular nutrient scavenging by bacteria to raising false alarm calls by drongos (Fig. 1). These behaviors have ostensibly little in common, with little overlap in the research that goes on between them. Our aim in this section is to categorize cheating behaviors in a way that illuminates common principles and similarities in the underlying selection pressures. We categorize cheats on the basis of four distinctions:

1. Is cooperation in the strategy set of the cheat?
2. Is deception involved?
3. Is the cheat of the same species as the cooperator?
4. Is the cheat facultative or obligate?

We chose these four distinctions because they divide cheats up in way that provides information about the evolutionary interaction between cooperators and cheats. Distinction (1) determines whether cheats could be selected to cooperate under certain conditions, and whether cheating has evolved from cooperation. Distinction (2) determines whether cheating occurs by exploiting a signaling system. Distinction (3) determines whether the cheats can replace cooperators, or just reduce the relative benefit of cooperation, potentially leading to its loss. Distinction (4) determines the consequences of the spread of cheating for cooperation—cooperation can be maintained with facultative cheats, but will be lost if obligate cheats spread to fixation.

IS COOPERATION IN THE STRATEGY SET OF THE CHEAT?

Our first distinction is whether the cooperative trait being exploited is in the potential strategy set of the cheat, in such a way that the cheat could potentially cooperate, or was a cooperator in its evolutionary past. Examples of when cooperation is in the strategy set include: (1) nonpollinating fig wasps in the family Agaonidae, which enter the fruit to lay their eggs, and which have evolved from pollinator species (van Noort and Compton 1996; Herre et al. 2008). (2) *Pseudomonas aeruginosa* strains that produce fewer siderophores (Griffin et al. 2004; Jiricny et al. 2010). (3) Fork-tailed drongos that give false predator-warning alarm calls, to make pied babblers or meerkats flee, allowing the drongos to steal their food (Ridley et al. 2007; Flower 2011). (4) Rhizobia strains that fix less nitrogen for their legume host, but still obtain the plant’s carbon resource in return (Kiers et al. 2003).

Examples of when cooperation is not in the strategy set, include: (1) common cuckoos (*Cuculus canorus*), which are obligate brood parasites, that lay their eggs in warbler’s nests, exploiting the warbler’s parent–offspring interaction (Davies 1992). (2) nonpollinating fig wasps in the family Torymidae, which lay

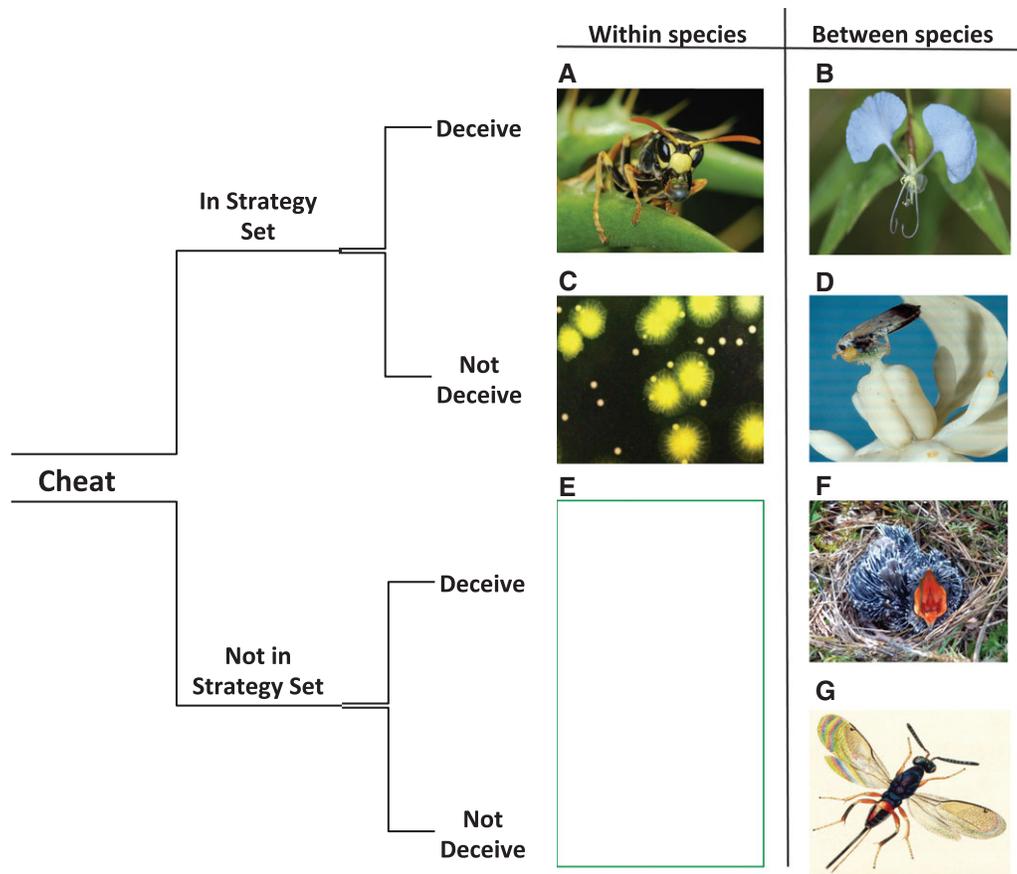


Figure 1. A key to cheating. The figure shows how different cheating behaviors can be categorized based on three distinctions: (i) whether cooperation is in the strategy of the cheat; (ii) whether deception is involved; and (iii) whether the cheat is of the same species as the cooperators. The examples given are: (A) *Polistes dominulus* wasp; (B) *Commelina mascarenica* flower with infertile stamens and false anthers (image courtesy of Rosie Treveylan); (C) *Pseudomonas aeruginosa* siderophore producers (yellow colonies) and nonproducers (white colonies); (D) *Tegeticula* moth on a *Yucca* plant; (E) we do not know of any examples—see main text; (F) a *Cuculus canorus* cuckoo in an *Acrocephalus scirpaceus* reed warbler nest; (G) *Torymidæ* fig wasp.

their eggs from outside the fruit, and compete with the pollinators for flowers in which to develop, but which have not evolved from pollinators (West and Herre 1994). (3) Bolas spiders (*Mastophora cornigera*) that mimic the sex pheromones of moths to attract and then prey on them, exploiting the cooperative communication between moths (Eberhard 1977; Stowe et al. 1987; Dicke and Sabelis 1992). (4) *Photuris* fireflies that make false signals of another species to lure in the males as prey (Lloyd 1983).

The above examples make clear that the definition of cheating we present includes cases where cheats have not evolved from cooperators. In contrast, within the mutualism literature, it is sometimes suggested that if an individual was a mutualist, it can then evolve to be a cheat, but if it was never a mutualist, its selfish behavior is simply parasitic (Kautz et al. 2009). We argue that it is useful to allow both these scenarios to be cheats because they both involve exploiting the cooperative behavior of others and, from an evolutionary perspective, both of these types of cheats could potentially lead to a breakdown in cooperation.

IS DECEPTION INVOLVED?

Our second distinction is whether deception is involved. Deception occurs when a signal is made under circumstances where the response is beneficial to the signaler and costly to the recipient. Recipients would only be expected to respond to deceptive signals if, under other circumstances, they gain a benefit from responding to the signal (Maynard Smith and Harper 2003).

Examples of cheats that use deception (deceitful signalers) include: (1) Subordinate *Polistes dominulus* wasps with facial patterns that alter their badge of status resembling that of a more dominant wasp (Tibbetts and Dale 2004). (2) The flowers of some plants, such as *Chilogottis* or *Ophrys* orchids, that mimic the morphology and pheromone odor of female wasps/bees, to lure in male wasps/bees, that then act as pollinators (Borgkarlson and Tengo 1986; Schiestl et al. 2003). (3) Fork-tailed drongos that make false alarm calls (Ridley et al. 2007; Flower 2011). (4) *Photuris* fireflies that make false signals to lure in males as prey (Lloyd 1983). (5) Male blennioid fish (*Salarias pavo*) that mimic

the color patterns and morphology of females, so that they can sneak into a harem nest to fertilize the spawned eggs (Goncalves et al. 1996). (6) Bolas spiders that mimic moth sex pheromones to lure them in as prey (Eberhard 1977; Stowe et al. 1987; Dicke and Sabelis 1992).

Examples of cheats that do not use deception include all the cases where individuals cheat by cooperating less. For example, *P. aeruginosa* LasR mutant strains that do not respond to quorum sensing signal but are able to exploit the cooperative public goods produced by other strains in response to quorum sensing (Diggle et al. 2007; Sandoz et al. 2007; Rumbaugh et al. 2009; Yang et al. 2010; Popat et al. 2012).

This distinction over whether deception is involved emphasizes that many of our cheating examples involve signaling systems. Signaling is open to cheating because all stable signaling systems are cooperative (Scott-Phillips et al. 2012). The reason for this is that signaling is only evolutionarily stable when it is, on average, beneficial to both the sender and the receiver of the signal (Maynard Smith and Harper 2003). If this were not the case, then the partner which did not benefit would be selected to either not signal or not respond, leading to the signaling system breaking down. Deception can also occur outside of signaling systems, and so not all cases of deception are cheats (Box 1). It remains to be seen whether signaling systems that are evolutionarily stable for different reasons, such as the cost (handicaps) or feasibility (indices) of dishonest signaling, or common interest, vary in their susceptibility to different types of cheating (Davies et al. 2012).

IS THE CHEAT OF THE SAME SPECIES AS THE COOPERATOR?

Our third distinction is whether cheats exploit individuals of their own species, or individuals of another species. Examples of cheating a member of the same species include: (1) male blennioid fish that mimic the color patterns and morphology of females, to sneak fertilize their eggs (Goncalves et al. 1996). (2) Fork-tailed drongos that make false alarm calls to their conspecifics (Ridley et al. 2007; Flower 2011). (3) LasR mutant strains of *P. aeruginosa*, that do not respond to quorum sensing signal (Diggle et al. 2007; Rumbaugh et al. 2009; Popat et al. 2012).

Examples of cheating a member of another species include: (1) Yucca moths that lay eggs in the developing yucca fruit that have already been pollinated, but do not pollinate the plant in return (Tyre and Addicott 1993; Pellmyr et al. 1996). (2) Arbuscular mycorrhizal fungi, of the subgenus *Glomus*, that supply less phosphorus to their host plant (Kiers et al. 2011). (3) Rhizobia bacteria that fix a low or negligible amount of nitrogen for their legume host (Kiers et al. 2003). (4) Plants, such as those of the Orchidaceae or honey mesquites (*Prosopis glandulosa*), that produce flowers without nectar, but which mimic the scent, morphology, and spectral color reflectance of flowers that do provide nec-

tar to pollinators (Lopez-portillo et al. 1993; Thakar et al. 2003; Anderson et al. 2005; Anand et al. 2007; Burkle et al. 2007; Brandenburg and Bshary 2011). (5) *Commelina mascarenica* flowers that have three false stamens that carry no pollen but are used to lure in pollinators. (6) Cleaner fishes that take a bite from the fish client, rather than eating/cleaning the parasites off them (Bshary 2002; Bshary and Grutter 2006).

Our first and third distinctions are not completely independent. Although cheating between species can occur when cooperation is in the strategy set or when cooperation is not in the strategy set, we do not know any examples of cheating within a species when cooperation is not in the strategy set (Fig. 1). We would expect such cheats to be rare or nonexistent, as it would require a cooperative behavior that could not be performed by a subset of the species.

IS THE CHEAT FACULTATIVE OR OBLIGATE?

Another biologically important distinction is whether the cheat is facultative (conditional) or obligate (Travisano and Velicer 2004; Santorelli et al. 2008; Buttery et al. 2009). A facultative strategy would be one in which the relevant trait is adjusted conditionally, dependent on the cheats social partners. For example, cooperate if with clone mates but cheat if with non-relatives. An obligate strategy would be one in which cheating is expressed unconditionally. For example, never perform a cooperative behavior.

Few studies have successfully determined whether cheats are facultative or obligate, and so we have not included it in our classification figure (Fig. 1). An important exception is studies of fruiting body production in the slime mold *D. discoideum*. When starved of food, individuals of this species aggregate together to form a motile slug that differentiates into a fruiting body with sterile stalk cells holding a viable spore head. Some strains have been shown to be cheats in that, when there are mixed genotype fruiting bodies, they contribute less than their proportional share to the dead stalk, and more to the reproductive spore head (Strassmann et al. 2000). It has also been shown that a number of strains are facultative cheats, which cheat when in mixed genotype fruiting bodies, but are able to produce a normal fruiting body when in single genotype (clonal) fruiting bodies (Fortunato et al. 2003; Santorelli et al. 2008; Buttery et al. 2009; Khare and Shaulsky 2010). Another important exception is the analogous fruiting body formation in the bacteria *M. xanthus*, where facultative cheating has also been observed (Velicer et al. 2000; Fiegna and Velicer 2005; Fiegna et al. 2006).

What is the Response to Cheating?

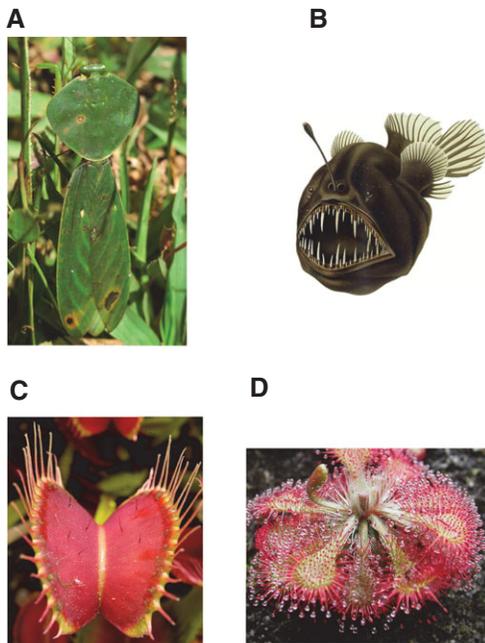
The presence of cheats imposes a fitness cost on cooperators such that this will favor mutations that confer resistance to cheating. The strategies available to cooperators will depend upon what

Box 1—Signaling systems, deception and cheating

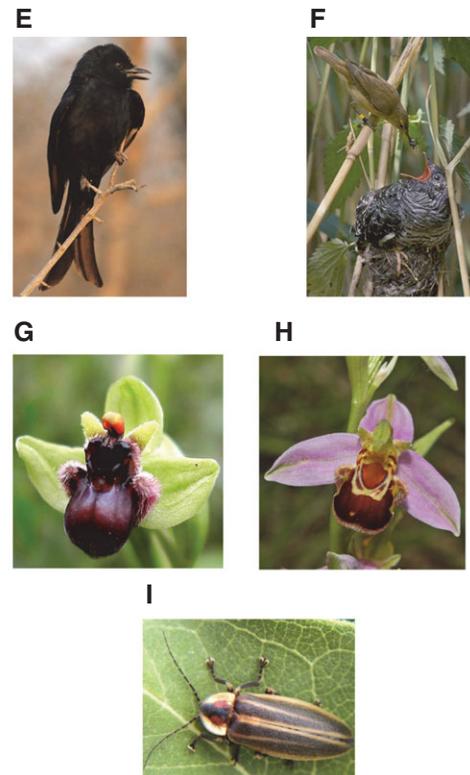
Although we have used deception as a characteristic to distinguish cheats, not all instances of deception will be cheating. Deception is cheating when it manipulates a cooperative signaling system. In contrast, deception will not be cheating when it is exploiting a feature of the world that can be used as a guide to action, termed a “cue” (Maynard Smith and Harper 2003). For example, when anglerfish lure in prey with bioluminescent “bulbs,” they are being deceptive, but they are not exploiting a cooperative signaling system, and so this is not cheating. An

illuminating example here is given by the carnivorous venus flytrap (*Dionaea muscipula*) and sundew plants (*Drosera anglica*). If these plants were mimicking flowers to attract in and eat pollinators, then they would be exploiting the cooperative plant–pollinator signaling, and so would be cheats. However, if they were just mimicking a cue of a food source, to attract in a range of insects, including nonpollinators, then they would not be exploiting a cooperative interaction, and so would not be cheats. Empirical data supports the latter (Ellison and Gotelli 2001; Murza et al. 2006; Ellison and Gotelli 2009; Gibson and Waller 2009).

Deception without cheats



Deceptive cheats



Deception without cheating and deceptive cheats. Not all deceptive behavior implies cheating. Deception can be divided into those that manipulate cooperative behaviors (cheats) and those that do not (deception without cheating). A common form of deception without cheating is deceptive predators such as: (A) *Choeradobis rhombicollis*, leaf-mimicking praying mantis; (B) anglerfish; (C) *Dionaea muscipula*, venus flytrap; (D) *Drosera* sundew plant. Examples of deceptive cheats include (E) *Dicrurus adsimilis*, fork-tailed drongo; (F) *Acrocephalus scirpaceus* reed warbler feeding a *Cuculus canorus* cuckoo chick; (G) *Ophrys bombyliflora*, bumblebee orchid; (H) *Ophrys apifera*, bee orchid; (I) *Photuris* firefly.

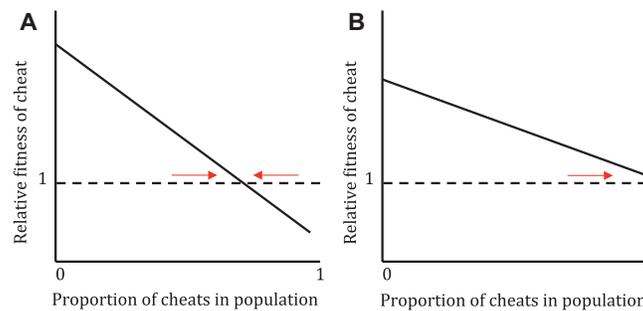
kind of cooperation is being cheated, and how it is being cheated. Cooperators could respond to cheats in at least four ways.

First, cooperators could adjust their behavior facultatively in response to cheats. Lindstrom et al. (1997) found that great tits were more likely to eat worms that honestly signaled distaste-

fulness, as the frequency of dishonest cheats (Batesian mimics) increased (Box 2). Ridley and Raihani (2007) showed that cooperatively breeding pied babblers respond more strongly to kleptoparasitic drongos alarm calls when in a small group size, where there are fewer guards to defend the group (more beneficial to

Box 2—Frequency dependence

Our definition of cheating suggests that because cheats can exploit the cooperation of others, they should be able to invade and spread into populations. Consequently, when we observe cheating, we might be looking at a stable equilibrium of cooperators and cheats, or at a form of cooperation that is breaking down and on its way out. A key factor here is whether the fitness of cheats is frequency dependent, such that the relative fitness of cheats decreases as they become more common in the system (Velicer et al. 2000; Fiegna and Velicer 2003; Ross-Gillespie et al. 2007). If such negative frequency dependence drives the relative fitness of the cheat below that of the cooperator, then a stable equilibrium is expected, where both cooperators and cheats will be maintained in the population (MacLean and Gudelj 2006; Gore et al. 2009; MacLean et al. 2010; (A). In contrast, if the relative fitness of the cheat does not go below that of the cooperators, then cooperation will be lost from the population (B).



The relative fitness of cheats as a function of the initial proportion of cheats in a mixed population with cooperators. A relative fitness >1.0 means that cheats have a higher fitness than cooperators, whereas a relative fitness <1.0 means that cheats have a lower fitness than cooperators. Part (A) shows when the relative fitness of cheats drops <1.0 , in which case we would expect a stable equilibrium with both cooperators and cheats in the population. Part (B) shows when the fitness of cheats is always greater than that of cooperators, in which case we would expect the cheats to go to fixation.

respond), but rarely respond to drongo alarm calls when in larger groups where more individuals participate in predator vigilance.

Second, cooperators could be selected to reduce the cooperative behavior that is being exploited, even leading to the loss of cooperation. For example, in the presence of bacterial cheats, who did not produce and release a cooperative nutrient-acquiring molecule (public good), there could be selection for the cooperative individuals to evolve to produce less of the molecule. An alternative could be to having phenotypic switching, with some proportion of individuals producing no public good (Diard et al. 2013; Frank 2013).

Third, cooperators could be selected to change the cooperative trait such that it is harder to exploit. For example, in the presence of bacterial cheats, who do not produce and release a cooperative nutrient-acquiring molecule (public good), there could

be selection for the cooperative individuals to evolve a receptor-specific molecule that is harder for cheats to exploit (West et al. 2007a). Empirical evidence for the evolution of cheater resistance comes from studies on both *D. discoideum* and *M. xanthus*. In both species it has been shown that the presence of cheater strains, which over contribute to the spores in fruiting bodies, selects for other strains to be less exploitable by these cheats (Fiegna et al. 2006; Khare et al. 2009). *Myxococcus xanthus* cheats re-evolve the ability to cooperate but in a way that they are immune to exploitation by the ancestral cheats from which they evolved (Fiegna et al. 2006). Although the presence of *D. discoideum* cheats selects for mutants that resist cheating but maintain cooperation (Khare et al. 2009).

At least three factors can lead to the fitness of cheats being negatively frequency dependent. First, if cheats are discriminated against, but less detected at low frequencies. This appears to be the case in cleaner fish, where the client's have an image scoring ability allowing them to interact more frequently with cleaners that mainly cooperate while avoiding cleaners that they observed cheated frequently (Bshary 2002). Second, if the presence of cheats impacts negatively on population growth, then the more cheats there are in a population, the less opportunity there will be for cheats to exploit cooperators, as has been found in bacteria (Ross-Gillespie et al. 2007; Frank 2010). Third, if cooperators are able to preferentially benefit from cooperative behaviors, such as when cooperators are clustered together, or if cooperation provides a direct as well as an indirect benefit, then this will lead to the fitness of cheats being negatively frequency dependent, as has been found in bacteria and yeast (Ross-Gillespie et al. 2007; Gore et al. 2009).

If cooperators evolve to become harder to exploit, this would in turn, select on cheats to improve their ability to exploit the

cooperators. Consequently, not only does the presence of cheats impose a selection pressure on cooperators, but this can lead to a coevolutionary arms race between cooperators and cheats. Possible examples of such coevolution include: (a) 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 and Stevens 2010; Langmore et al. 2011; Stoddard and Stevens 2011); (b) 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).

Do we Need to Talk About Cheating?

We emphasize that examining social behaviors from the perspective of cheats will not always be necessary or the most useful way forward. For example, the term cheat is used very little when discussing cooperation and conflict within the social insects, such as over the sex ratio or who produces male eggs (Ratnieks et al. 2006; West 2009). In these cases, it is often more useful to think about a conflict between partners with different interests, rather than one individual, or one class of individual, cheating another.

The analogous point that terminology and concepts can be extremely useful in some cases, but not others, has already been made for other intentional language such as altruism and cooperation (West et al. 2007c). For example, terms such as altruism or spite, and theoretical tools such as Hamilton's rule, are rarely used in studies of some social traits, such as sex allocation in response to population structure or relatedness asymmetries (West 2009). This does not alter the usefulness of either the term altruism or Hamilton's rule, when studying other issues. The general point here is that although clear and unambiguous terminology can facilitate the development of a conceptual overview, terms need only be used when useful.

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LITERATURE CITED

Anand, C., C. Umranikar, P. Shintre, A. Damle, J. Kale, J. Joshi, and M. Watve. 2007. Presence of two types of flowers with respect to nectar sugar in two gregariously flowering species. *J. Biosci.* 32:769–774.

Anderson, B., S. D. Johnson, and C. Carbutt. 2005. Exploitation of a specialized mutualism by a deceptive orchid. *Am. J. Bot.* 92:1342–1349.

Borgkarlson, A. K., and J. Tengö. 1986. Odor Mimicry—key substances in *Ophrys Lutea*-*Andrena* pollination relationship (Orchidaceae, Andrenidae). *J. Chem. Ecol.* 12:1927–1941.

Bourke, A. F. G. 2011. Principles of social evolution. Oxford Univ. Press, Oxford, U.K.

Brandenburg, A., and R. Bshary. 2011. Variable responses of hawkmoths to nectar-depleted plants in two native *Petunia axillaris* (Solanaceae) populations. *Arthropod-Plant Interact.* 5:141–148.

Bronstein, J. L. 2001. The exploitation of mutualisms. *Ecol. Lett.* 4:277–287.

Bshary, R. 2002. Biting cleaner fish use altruism to deceive image-scoring client reef fish. *Proc. R. Soc. Lond. B-Bio.* 269:2087–2093.

Bshary, R., and J. L. Bronstein. 2004. Game structures in mutualistic interactions: what can the evidence tell us about the kind of models we need? *Adv. Stud. Behav.* 34:59–101.

Bshary, R., and A. S. Grutter. 2002. Asymmetric cheating opportunities and partner control in a cleaner fish mutualism. *Anim. Behav.* 63:547–555.

———. 2006. Image scoring and cooperation in a cleaner fish mutualism. *Nature* 441:975–978.

Burkle, L. A., R. E. Irwin, and D. A. Newman. 2007. Predicting the effects of nectar robbing on plant reproduction: implications of pollen limitation and plant mating system. *Am. J. Bot.* 94:1935–1943.

Burt, A., and R. Trivers. 2006. Genes in conflict: the biology of selfish genetic elements. Belknap Press of Harvard Univ. Press, Cambridge, MA and Lond.

Buttery, N. J., D. E. Rozen, J. B. Wolf, and C. R. L. Thompson. 2009. Quantification of social behavior in *D. discoideum* reveals complex fixed and facultative strategies. *Curr. Biol.* 19:1373–1377.

Cade, W. 1975. Acoustically orienting parasitoids—fly phonotaxis to cricket song. *Science* 190:1312–1313.

Cordero, O. X., L. A. Ventouras, E. F. DeLong, and M. F. Polz. 2012. Public good dynamics drive evolution of iron acquisition strategies in natural bacterioplankton populations. *Proc. Natl. Acad. Sci. USA* 109:20059–20064.

Crespi, B. J., and D. Yanega. 1995. The definition of eusociality. *Behav. Ecol.* 6:109–115.

Davies, N. B. 1992. Dunnock behaviour and social evolution. Oxford Univ. Press, Oxford, U.K. and New York.

———. 2000. Cuckoos, cowbirds and other cheats. T & A.D. Poyser, Lond.

Davies, N. B., J. R. Krebs, and S. A. West. 2012. An introduction to behavioural ecology. Wiley-Blackwell, Oxford, U.K.

Diard, M., V. Garcia, L. Maier, M. N. P. Remus-Emsermann, R. R. Regoes, M. Ackermann, and W. D. Hardt. 2013. Stabilization of cooperative virulence by the expression of an avirulent phenotype. *Nature* 494:353–356.

Dicke, M., and M. W. Sabelis. 1992. Costs and benefits of chemical information conveyance: proximate and ultimate factors. Pp. 122–155 in B. Roitberg and M. Isman, eds. *Insect chemical ecology. An evolutionary approach.* Chapman & Hall, New York.

Diggle, S. P., A. S. Griffin, G. S. Campbell, and S. A. West. 2007. Cooperation and conflict in quorum-sensing bacterial populations. *Nature* 450:411–417.

Douglas, A. E. 2008. Conflict, cheats and the persistence of symbioses. *New Phytol.* 177:849–858.

Eberhard, W. G. 1977. Aggressive Chemical mimicry by a bolas spider. *Science* 198:1173–1175.

Ellison, A. M., and N. J. Gotelli. 2001. Evolutionary ecology of carnivorous plants. *Trends Ecol. Evol.* 16:623–629.

———. 2009. Energetics and the evolution of carnivorous plants—025EFDarwin's 'most wonderful plants in the world'. *J. Exp. Bot.* 60:19–42.

Fiegna, F., and G. J. Velicer. 2003. Competitive fates of bacterial social parasites: persistence and self-induced extinction of *Myxococcus xanthus* cheaters. *Proc. R. Soc. B* 270:1527–1534.

- . 2005. Exploitative and hierarchical antagonism in a cooperative bacterium. *PLoS Biol.* 3:1980–1987.
- Fiegna, F., Y. T. N. Yu, S. V. Kadam, and G. J. Velicer. 2006. Evolution of an obligate social cheater to a superior cooperator. *Nature* 441:310–314.
- Fisher, R. A. 1930. The genetical theory of natural selection. The Clarendon Press, Oxford, U.K.
- Fisher, R. M., C. K. Cornwallis, and S. A. West. 2013. Group formation, relatedness and the evolution of multicellularity. *Curr Biol.* 23:1120–1125.
- Flower, T. 2011. Fork-tailed drongos use deceptive mimicked alarm calls to steal food. *Proc. R. Soc. B* 278:1548–1555.
- Fortunato, A., D. C. Queller, and J. E. Strassmann. 2003. A linear dominance hierarchy among clones in chimeras of the social amoeba *Dictyostelium discoideum*. *J. Evol. Biol.* 16:438–445.
- Foster, K. R., K. Parkinson, and C. R. L. Thompson. 2007. What can microbial genetics teach sociobiology? *Trends Genet.* 23:74–80.
- Frank, S. A. 2010. Microbial secretor-cheater dynamics. *Philos. Trans. R. Soc. B* 365:2515–2522.
- . 2013. Microbial evolution: regulatory design prevents cancer-like overgrowths. *Curr Biol.* 23:R343–R346.
- Gibson, T. C., and D. M. Waller. 2009. Evolving Darwin's 'most wonderful' plant: ecological steps to a snap-trap. *New Phytol.* 183:575–587.
- Goncalves, E. J., V. C. Almada, R. F. Oliveira, and A. J. Santos. 1996. Female mimicry as a mating tactic in males of the blennioid fish *Salaria pavo*. *J. Mar. Biol. Assoc. U.K.* 76:529–538.
- Gore, J., H. Youk, and A. Van Oudenaarden. 2009. Snowdrift game dynamics and facultative cheating in yeast. *Nature* 459:253–256.
- Grafen, A. 1999. Formal Darwinism, the individual-as-maximizing-agent analogy and bet-hedging. *Proc. R. Soc. Lond. B-Bio.* 266:799–803.
- . 2006. Optimization of inclusive fitness. *J. Theor. Biol.* 238:541–563.
- Griffin, A. S., S. A. West, and A. Buckling. 2004. Cooperation and competition in pathogenic bacteria. *Nature* 430:1024–1027.
- Hamilton, W. D. 1964. Genetical evolution of social behaviour I & II. *J. Theor. Biol.* 7:1–52.
- . 1970. Selfish and spiteful behaviour in an evolutionary model. *Nature* 228:1218–1220.
- Herre, E. A., K. C. Jander, and C. A. Machado. 2008. Evolutionary ecology of figs and their associates: recent progress and outstanding puzzles. *Annu. Rev. Ecol. Evol. Syst.* 39:439–458.
- Jiricny, N., S. P. Diggle, S. A. West, B. A. Evans, G. Ballantyne, A. Ross-Gillespie, and A. S. Griffin. 2010. Fitness correlates with the extent of cheating in a bacterium. *J. Evol. Biol.* 23:738–747.
- Kautz, S., H. T. Lumsch, P. S. Ward, and M. Heil. 2009. How to prevent cheating: a digestive specialization ties mutualistic plant-ants to their ant-plant partners. *Evolution* 63:839–853.
- Khare, A., and G. Shaulsky. 2010. Cheating by exploitation of developmental prestalk patterning in *Dictyostelium discoideum*. *PLoS Genet.* 6: e1000854.
- Khare, A., L. A. Santorelli, J. E. Strassmann, D. C. Queller, A. Kuspa, and G. Shaulsky. 2009. Cheater-resistance is not futile. *Nature* 461: 980–982.
- Kiers, E. T., R. A. Rousseau, S. A. West, and R. F. Denison. 2003. Host sanctions and the legume-rhizobium mutualism. *Nature* 425:78–81.
- Kiers, E. T., M. Duhamel, Y. Beesetty, J. A. Mensah, O. Franken, E. Verbruggen, C. R. Fellbaum, G. A. Kowalchuk, M. M. Hart, A. Bago, et al. 2011. Reciprocal rewards stabilize cooperation in the mycorrhizal symbiosis. *Science* 333:880–882.
- Langmore, N. E., M. Stevens, G. Maurer, R. Heinsohn, M. L. Hall, A. Peters, and R. M. Kilner. 2011. Visual mimicry of host nestlings by cuckoos. *Proc. R. Soc. B* 278:2455–2463.
- Lindstrom, L., R. V. Alatalo, and J. Mappes. 1997. Imperfect Batesian mimicry—the effects of the frequency and the distastefulness of the model. *Proc. R. Soc. B* 264:149–153.
- Lloyd, J. E. 1983. Bioluminescence and communication in insects. *Annu. Rev. Entomol.* 28:131–160.
- Lopez-portillo, J., L. E. Eguiarte, and C. Montana. 1993. Nectarless honey mesquites. *Funct. Ecol.* 7:452–461.
- MacLean, R. C., and I. Gudelj. 2006. Resource competition and social conflict in experimental populations of yeast. *Nature* 441:498–501.
- MacLean, R. C., A. Fuentes-Hernandez, D. Greig, L. D. Hurst, and I. Gudelj. 2010. A mixture of “cheats” and “co-operators” can enable maximal group benefit. *PLoS Biol.* 8: e1000486.
- Maloof, J. E., and D. W. Inouye. 2000. Are nectar robbers cheaters or mutualists? *Ecology* 81:2651–2661.
- Maynard Smith, J., and D. Harper. 2003. *Animal signals*. Oxford Univ. Press, Oxford, U.K.
- Maynard Smith, J., and E. Szathmary. 1995. *The major transitions in evolution*. W.H. Freeman/Spektrum, Oxford, U.K.
- Murza, G. L., J. R. Heaver, and A. R. Davis. 2006. Minor pollinator-prey conflict in the carnivorous plant, *Drosera anglica*. *Plant Ecol.* 184:43–52.
- Noe, R. 2006. Cooperation experiments: coordination through communication versus acting apart together. *Anim. Behav.* 71:1–18.
- Page, R. A., and M. J. Ryan. 2008. The effect of signal complexity on localization performance in bats that localize frog calls. *Anim. Behav.* 76:761–769.
- Pellmyr, O., J. LeebensMack, and C. J. Huth. 1996. Non-mutualistic yucca moths and their evolutionary consequences. *Nature* 380:155–156.
- Popat, R., S. A. Crusz, M. Messina, P. Williams, S. A. West, and S. P. Diggle. 2012. Quorum-sensing and cheating in bacterial biofilms. *Proc. R. Soc. B* 279:4765–4771.
- Queller, D. C. 2000. Relatedness and the fraternal major transitions. *Philos. Trans. R. Soc. B* 355:1647–1655.
- Rainey, P. B. 2007. Unity from conflict. *Nature* 446:616–616.
- Rainey, P. B., and B. Kerr. 2010. Cheats as first propagules: a new hypothesis for the evolution of individuality during the transition from single cells to multicellularity. *Bioessays* 32:872–880.
- Ratnieks, F. L. W., K. R. Foster, and T. Wenseleers. 2006. Conflict resolution in insect societies. *Annu. Rev. Entomol.* 51:581–608.
- Richardson, S. C. 1995. Temporal variation in pollinator abundance and pollinator foraging behavior in response to robbed flowers. *USDA Rocky* 264:311–316.
- Ridley, A. R., and N. J. Raihani. 2007. Facultative response to a kleptoparasite by the cooperatively breeding pied babbler. *Behav. Ecol.* 18:324–330.
- Ridley, A. R., M. F. Child, and M. B. V. Bell. 2007. Interspecific audience effects on the alarm-calling behaviour of a kleptoparasitic bird. *Biol. Lett.* 3:589–591.
- Ross-Gillespie, A., A. Gardner, S. A. West, and A. S. Griffin. 2007. Frequency dependence and cooperation: theory and a test with bacteria. *Am. Nat.* 170:331–342.
- Ross-Gillespie, A., A. Gardner, A. Buckling, S. A. West, and A. S. Griffin. 2009. Density dependence and cooperation: theory and a test with bacteria. *Evolution* 63:2315–2325.
- Rumbaugh, K. P., S. P. Diggle, C. M. Watters, A. Ross-Gillespie, A. S. Griffin, and S. A. West. 2009. Quorum sensing and the social evolution of bacterial virulence. *Curr Biol.* 19:341–345.
- Sachs, J. L., U. G. Mueller, T. P. Wilcox, and J. J. Bull. 2004. The evolution of cooperation. *Q. Rev. Biol.* 79:135–160.
- Sandoz, K. M., S. M. Mitzimberg, and M. Schuster. 2007. Social cheating in *Pseudomonas aeruginosa* quorum sensing. *Proc. Natl. Acad. Sci. USA* 104:15876–15881.

- Santorelli, L. A., C. R. L. Thompson, E. Villegas, J. Svetz, C. Dinh, A. Parikh, R. Sucegang, A. Kuspa, J. E. Strassmann, D. C. Queller, et al. 2008. Facultative cheater mutants reveal the genetic complexity of cooperation in social amoebae. *Nature* 451:1107–1110.
- Schiestl, F. P., R. Peakall, J. G. Mant, F. Ibarra, C. Schulz, S. Franke, and W. Francke. 2003. The chemistry of sexual deception in an orchid-wasp pollination system. *Science* 302:437–438.
- Scott-Phillips, T. C., R. A. Blythe, A. Gardner, and S. A. West. 2012. How do communication systems emerge? *Proc. R. Soc. B* 279:1943–1949.
- Spottiswoode, C. N., and M. Stevens. 2010. Visual modeling shows that avian host parents use multiple visual cues in rejecting parasitic eggs. *Proc. Natl. Acad. Sci. USA* 107:8672–8676.
- Stoddard, M. C., and M. Stevens. 2011. Avian vision and the evolution of egg color mimicry in the common cuckoo. *Evolution* 65:2004–2013.
- Stowe, M. K., J. H. Tumlinson, and R. R. Heath. 1987. Chemical mimicry—bolas spiders emit components of moth prey species sex-pheromones. *Science* 236:964–967.
- Strassmann, J. E., Y. Zhu, and D. C. Queller. 2000. Altruism and social cheating in the social amoeba *Dictyostelium discoideum*. *Nature* 408:965–967.
- Thakar, J. D., K. Kunte, A. K. Chauhan, A. V. Watve, and M. G. Watve. 2003. Nectarless flowers: ecological correlates and evolutionary stability. *Oecologia* 136:565–570.
- Tibbetts, E. A., and J. Dale. 2004. A socially enforced signal of quality in a paper wasp. *Nature* 432:218–222.
- Travisano, M., and G. J. Velicer. 2004. Strategies of microbial cheater control. *Trends Microbiol.* 12:72–78.
- Tyre, A. J., and J. F. Addicott. 1993. Facultative non-mutualistic behavior by an obligate mutualist—cheating by yucca moths. *Oecologia* 94:173–175.
- van Noort, S., and S. G. Compton. 1996. Convergent evolution of agaonine and sycoecine (Agaonidae, Chalcidoidea) head shape in response to the constraints of host fig morphology. *J. Biogeogr.* 23:415–424.
- Velicer, G. J., L. Kroos, and R. E. Lenski. 2000. Developmental cheating in the social bacterium *Myxococcus xanthus*. *Nature* 404:598.
- West, S. A. 2009. Sex allocation. Princeton Univ. Press, Princeton, NJ.
- West, S. A., and A. Buckling. 2003. Cooperation, virulence and siderophore production in bacterial parasites. *Proc. R. Soc. Lond. B-Bio.* 270:37–44.
- West, S. A., and A. Gardner. 2013. Adaptation and inclusive fitness. *Curr. Biol.* 23:R577–R584.
- West, S. A., and E. A. Herre. 1994. The ecology of the new-world fig-parasitizing wasps idarnes and implications for the evolution of the fig-pollinator mutualism. *Proc. R. Soc. Lond. B-Bio.* 258:67–72.
- West, S. A., S. P. Diggle, A. Buckling, A. Gardner, and A. S. Griffins. 2007a. The social lives of microbes. *Annu. Rev. Ecol. Evol. Syst.* 38:53–77.
- West, S. A., A. S. Griffin, and A. Gardner. 2007b. Evolutionary explanations for cooperation. *Curr. Biol.* 17:R661–R672.
- . 2007c. Social semantics: altruism, cooperation, mutualism, strong reciprocity and group selection. *J. Evol. Biol.* 20:415–432.
- West, S. A., A. S. Griffin, A. Gardner, and S. P. Diggle. 2006. Social evolution theory for microorganisms. *Nat. Rev. Microbiol.* 4:597–607.
- West, S. A., K. Winzer, A. Gardner, and S. P. Diggle. 2012. Quorum sensing and the confusion about diffusion. *Trends Microbiol.* 20:586–594.
- Yang, J. W., B. A. Evans, and D. E. Rozen. 2010. Signal diffusion and the mitigation of social exploitation in pneumococcal competence signalling. *Proc. R. Soc. B* 277:2991–2999.
- Yu, D. W., and N. E. Pierce. 1998. A castration parasite of an ant-plant mutualism. *Proc. R. Soc. Lond. B-Bio.* 265:375–382.
- Zhang, Q. G., A. Buckling, R. J. Ellis, and H. C. J. Godfray. 2009. Coevolution between cooperators and cheats in a microbial system. *Evolution* 63:2248–2256.
- Zhang, X.-X., and P. B. Rainey. 2013. Exploring the sociobiology of pyoverdinin-producing *Pseudomonas*. *Evolution* 67. *In press*.
- Zuk, M., and G. R. Kolluru. 1998. Exploitation of sexual signals by predators and parasitoids. *Q. Rev. Biol.* 73:415–438.

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APPENDIX

Table A1. Examples of how cheating has been defined in various studies.

Cheat/cheating definitions	Reference
“cells that gain additional advantage from the cooperating type over and above that gained by avoiding the cost of cooperation”	(Rainey and Rainey 2003)
“individuals that have access to group benefits without contributing their fair share”	(Gilbert et al. 2007)
“We partition facultative cheating into two forms: (1) promotion of individual fitness through selfish behavior (“self-promotion”) and (2) coercion of other genotypes to act cooperatively.”	(Buttery et al. 2009)
<i>S. cerevisiae</i> “cheat by stealing the sugar digested by their neighbors without contributing the enzyme themselves”.	(Greig and Travisano 2004)
“cheaters—strains that make more than their fair share of spores in chimerae.”	(Khare and Shaulsky 2010)
“Genetic mutants that fail to perform a group-beneficial function but that reap the benefits of belonging to the group should have a withing-group selective advantage, provided that the mutants are not too common.”	(Velicer et al. 2000)
“As with any system depending on coordination, this transition is vulnerable to cheaters that do not perform a typical response (e.g., cells that fail to respond to cell-cell signals or cells that fail to halt cell division) but profit in some way from the fact that other members of the population still respond.”	(Vulic and Kolter 2001)
“Those strains that secrete invertase are considered “co-operators”, while non-producers are regarded as selfish “cheats”.”	(MacLean et al. 2010)

Continued.

Table A1. Continued.

Cheat/cheating definitions	Reference
“In the case of multicellularity, these cheats are cancer cells.”	(Nunney 1999)
“There is strong variation between cleaners with respect to cheating of clients (i.e. feeding on client tissue instead of parasites)”	(Bshary 2002)
“Cheaters are illegitimate emitters that mimic infochemicals of other organisms to exploit a communicative system.”	(Roitberg and Isman 1992)
““producers”- who secrete a substance that breaks down antibiotic- and nonproducers (“cheats”) who do not secrete, or carry the machinery associated with secretion.”	(Dugatkin et al. 2008)
“subdivisions of signal interception includes: “spies”, “stowaways”, “boasters”; we do not go into the semantic distinctions here. The metaphors virtually always involve dishonesty and cheating”	(Zuk and McKean 2000)
“We use the term “cheater” only for individuals that belong to the mutualist species under investigation. They may either be individuals who always cheat (designated by Bronstein, 2001, as “pure exploiters”), or individuals that cooperate under some defined range of conditions (“conditional exploiters”).”	(Bshary and Bronstein 2004)
“A Proportion of nectarless flowers are known to occur within rewarding species and these are thought to be cheater flowers.”	(Thakar et al. 2003)
“caching systems based on reciprocal pilfering can be stable and are not necessarily susceptible to “cheaters”, animals that pilfer food but do not scatter hoard food themselves”	(Vander Wall and Jenkins 2003)
“When hoarders live in a group, an additional cost may arise from ‘cheaters’, who do not store food themselves but parasitize the caches made by other individuals.”	(Andersson and Krebs 1978)
““Aprovechados” are non-mutualistic species that take advantage of a mutualistic association. For example, some bees and birds utilize floral nectar without transferring pollen. “Cheaters” are non-mutualistic individuals within a mutualistic species. For example, individuals of some plants produce little or no nectar but are still visited by pollinators.”	(Tyre and Addicott 1993)
“In general, signals of quality require high and differential costs to remain honest (that is prevent low-quality cheaters from exploiting any fitness benefits associated with communicating high quality).”	(Tibbetts and Dale 2004)
“Cheating (sensu lato) occurs when individuals use mutualistic resources or services without providing mutualistic resources or services in return. Aprovechados (sensu Soberon and Martinez 1985) are individuals of nonmutualistic species, which exploit a mutualism, whereas cheaters are individuals that exploit a mutualism even though most other conspecifics act mutualistically. Both cheaters and aprovechados decrease the net benefit to the provider of the mutualistic services or resources.”	(Addicott and Tyre 1995)
“One should avoid ‘greedy’ individuals that may try to reap short-term benefit by not returning favours”	(Noe 2006)
“In a badge-of-status system, an obvious question is why individuals do not use their signal in an inappropriate manner or why cheating does not happen.”	(Nakagawa et al. 2008)
“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” practiced by the other members of the group”	(Koeslag and Terblanche 2003)
Intruding aphids cheat on the host clone by not helping in gall defence but instead invest in their development growth and reproduction.	(Abbot et al. 2001; Foster 2002)
“a cheater or a somatic parasite that does not participate in stalk formation but always forms spores can gain a relative fitness advantage.”	(Matapurkar and Watve 1997)
“‘Cheaters’ are individuals that hunt if they are the first to spot the prey, but stop if others join in and do not hunt if others are hunting.”	(Whitehouse and Lubin 1999)
“Cheating is defined as benefiting from an exaggerated advertisement that results from producing an inaccurately high level of the signal.”	(Briffa 2006)
“Anarchy is a counterstrategy against worker policing and an example of a ‘cheating’ strategy invading a cooperative system.”	(Barron et al. 2001)

Continued.

Table A1. Continued.

Cheat/cheating definitions	Reference
In gift-giving species, males that provide worthless nuptial gifts (cheats) could potentially invade a group that provide genuine gifts.	(LeBas and Hockham 2005)
“ ‘cheaters’ who signal a dominant status when they are actually subordinate (or true dominants who signal a subordinate status)”	(Molles and Vehrencamp 2001)
“Upon receiving a clutch of eggs to fertilize, a cheater should offer no eggs in return; in other words, it will try to play the male role instead of the female role.”	(Sella and Lorenzi 2000)
“Why not ‘cheat’, by displaying more intensely than normal, and increase the odds of driving off a rival?”	(Halperin et al. 1998)
“brood parasites—cheats that procure costly care for their dependent offspring by leaving them in another species’ nursery.”	(Kilner and Langmore 2011)
“a queen is prevented from ‘cheating’ (for example, by eating all the eggs of the other queen and replacing them with her own).”	(Reeve and Nonacs 1992)