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Behavioral Consequence of Exploitation

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Abstract

This chapter addresses the behavioral consequences of individuals (exploiters) that use the investments of others (investors) rather than investing time or effort in procuring a resource themselves. The optimal exploitation strategy has been traditionally studied in behavioral ecology using the producer–scrounger (PS) model, a simple evolutionary game theoretic model in which producers (investors) search for resources while scroungers (exploiters) use the resources found by producers. For simplicity, a key assumption of the PS model is that the producer remains passive toward scroungers. As the presence of scroungers is costly, both empirical and theoretical evidence is reviewed that one major consequence of having exploiters is the adoption by producers of strategies that reduce the benefits of scroungers, giving rise to countermeasures by scroungers. In addition, scroungers have effects on population structure, notably by generating consistent differences among individuals and affecting spatial preferences within groups. Finally, although the PS game reviewed here is set in an explicit social foraging context, it is argued that it can be generalized to a large number of situations of social exploitation. Reviewing the impact of scrounging on populations should help generate parallels to explore the consequences of such exploitative behavior in economics and public health.

Introduction

Just about any fitness-enhancing behavior that requires time and effort is open to exploitation—usurpation of the benefit by an individual who has not invested the time and effort to attain that benefit. Having offspring, for instance, requires considerable effort, especially in species that invest in parental care. Building a nest as well as feeding and protecting the young are costly activities. In egg-laying species, such as birds and insects, some individuals avoid these costs altogether by depositing their eggs directly in the nests of a

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conspecific. Female starlings, for instance, are known to engage in this form of brood parasitism (Andersson 1985). Grasshoppers and crickets are known for their choruses in which males stridulate species-specific songs to attract mating females. The same is true in many species of frogs. Calling, in both cases, is energetically costly and exposes the caller to predators. Not surprisingly, there are reports for both insects and frogs in which noncalling silent individuals position themselves close to a calling male and intercept females on the way to the caller. These so-called "satellite males," which "orbit" around the territorial boundary of a calling male, obtain mating opportunities by exploiting the calling efforts of another male. When a couple of lionesses successfully hunt down a wildebeest on the Serengeti Plains, they are soon joined by a few other females that partake of the quarry without having participated in the effort required to capture the prey. They, too, are taking advantage of the hunting effort of their conspecifics.

All of these cases are examples of exploitation, and there are many more in both animals and humans. It may seem surprising that an animal as dangerous as a lioness would do nothing to repel an exploiter that has come to eat her catch. Shouldn't she simply fight and attack the intruder to protect the precious resource that she just acquired? Similarly, should a female victim of a brood parasite do something to protect herself against this damaging exploitation of her parental effort? In this chapter we address the behavioral consequences of exploitation in terms of the individual that is exploited (i.e., the investor), the host, and the exploiter. We frame our discussion within evolutionary game theory using the producer–scrounger (PS) model. The game is set in an explicit social foraging context but we hope that it might be generalizable to all other systems of exploitation.

Origin of the Producer–Scrounger Game

When animals forage in a group in search of food that is distributed in discrete patches, one can assume that all individuals search for a patch and that, once one is discovered, all other group members will approach and obtain a share. This way of viewing group foraging is known as "information sharing," because the information about a location of a discovered patch is shared with all other group members. Information sharing constitutes a form of mutual or reciprocal exploitation: no member can gain anything by refraining from joining another individual's discovery, since every other individual will join when it discovers. Thus, under this scenario, all individuals engage in exploitation, and if the group size is G, the frequency of joining the population is $(G-1)/G$.

While observing the social foraging behavior of house sparrows, Barnard and Sibly (1981) quickly discovered that not all individuals in a flock invest equally in searching (investing) and joining (exploiting) behavior. So, instead

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of information sharing, Barnard and Sibly (1981) proposed that the searching and joining problem within a flock be analyzed as a two-option *n*-player evolutionary game in which the strategy “producer” corresponds to searching for food, and the strategy “scrounger” joins once a producer has been detected to find food. The game assumes that the payoffs to the scrounger are negatively frequency dependent: when scroungers are rare, they receive more than producers, but when scroungers are common, they receive less than the producers. This assumption means that the payoff curves of producer and scrounger will intersect at some frequency, when payoffs to both producer and scrounger are the same (see Figure 3.1 in Burton-Chellew, this volume).

The Evolutionarily Stable Strategy

One of the main differences between evolutionary game theory (i.e., the application of game theory to biology) and the traditional economic approach to game theory centers on the notion of evolutionary stability. Traditional game theory is based on the interactions of rational decision makers (i.e., humans). In evolutionary game theory, the payoff is a surrogate for Darwinian fitness, and strategies evolve over many repeated iterations of the game to reach the evolutionarily stable strategy (ESS), defined as a strategy that cannot be displaced by the occurrence of an initially rare mutant strategy. This can be illustrated intuitively with the classic hawk–dove evolutionary game: the hawk is an escalating strategy that quits only when injured, whereas the dove is a non-escalating ritualized fighter that concedes victory without injury as soon as the opponent initiates a fight. Although everyone in a population would fare much better if the population were composed solely of doves, this is not an acceptable solution in an evolutionary game because a mutant hawk would certainly win every fight against each dove it encountered. The hawk would clearly have higher fitness and thus spread throughout the population, eventually replacing the dove strategy entirely. Being a dove alone, therefore, is not an ESS and hence not an expected solution to the game.

In the case of the PS game, the scrounger strategy, by itself, is not an ESS. In a population comprised solely of scroungers, it is easy to imagine that if no one searches for food, then all will die of starvation. Likewise, a population made up solely of producers does not provide an ESS solution either because the game assumes that when a rare scrounger mutant arises in the population, its payoffs will be greater than those to producers; hence scroungers increase in frequency within the population. Because the game assumes that the payoff curves to producer and scrounger intersect, the number of scroungers increases until it reaches that equilibrium frequency where payoffs to both are equal. At that point, natural selection is stuck at a stable point, and the equilibrium combination of producers and scroungers is now a mixed ESS.

The Behavioral Stable Strategy

The argument for the PS game and its ESS solution are based on genetic change operating between generations. However, many of the behaviors of interest in this volume are not genetic, and the alternatives to "host" and "parasite" (investor and exploiter, respectively) are not necessarily genetically coded. In addition, most systems of interest reach solutions within the lifetime of the individuals. Thus selection is not required to act between generations. In the past, behavioral ecologists have not focused on these types of issues and have applied evolutionary game theory and its ESS solutions to all systems indiscriminately. This is due to an assumption that natural selection has equipped the brains of animals with learning rules which are the quickest at allowing individuals to reach outcomes that are equivalent to evolutionary solutions or the ESS (Harley 1981; Maynard-Smith 1982). We have referred to this credo as the *behavioral gambit* (Giraldeau and Dubois 2008), an assumption that learned outcomes of games will be those that match the outcome of evolution by natural selection. Until disproven, we suggest that it would be wise and more precise to distinguish evolved solutions from those achieved by behavioral decision by calling the former an ESS and the latter a behaviorally stable solution (BSS).

Up to now, the PS game (and its solutions) assumed that the producer remains passive in the face of the scrounger. Moreover, it failed to indicate whether scroungers should attempt to usurp the whole resource or simply part of it. In the real world, however, producers and scroungers are rarely passive, friendly companions. In some birds, like juncos, the scrounger aggressively displaces the producer from the discovered food source and takes it all. In many species of gulls, the scrounger aggressively pursues the resource holder until it drops the prey, generating impressive aerobatic flights. Lionesses tolerate each other at a kill but a lion does not. Hence there is a great deal of behavioral richness in real-life "social parasitism" (i.e., exploitation) that is not captured by a simple PS game. Below we explore how the scrounger strategy has given rise to a series of countermeasures. Our hope is that parallels can be generated to explore the consequences of such exploitative behavior in economics and public health.

Adaptations to Reduce Theft

Hoarding

The risk that a resource discovered by an investor is usurped by an exploiter is particularly high when there is a delay between the moment of discovery and use of the resource. This situation occurs in several bird and mammal species that store food for later use, hence leaving it unattended for several weeks or even months. In food-storing species, animals have developed different

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strategies to diminish the probability that their food is discovered and to mitigate the negative consequences that a pilferer may have on their fitness. More precisely, many food-storing animals scatter hoarded food items throughout their habitat, instead of accumulating them in a central place (e.g., a cavity in the ground or a burrow), as chipmunks and many other rodents do (Elliot 1978). Although scatter hoarding requires spatial memory abilities to allow individuals to retrieve food from a large number of locations (Shettleworth 1990; Pravosudov and Roth 2013), this strategy reduces both the risk of major loss (Vander Wall 1990; Jenkins et al. 1995) and the probability of pilferage, because dispersed food caches provide lower concentrations of food and hence are less attractive to other animals compared to central places. To avoid others learning the location of their food caches, individuals frequently modify their caching behavior when in the presence of observers, notably by choosing caching sites that are away from the observers and out of sight (Henrich and Pepper 1998; Lahti et al. 1998; Clayton et al. 2001; Bugnyar and Kotrschal 2002; Dally et al. 2005; Leaver et al. 2007; Shaw and Clayton 2013).

Aggression

Conversely, when food is consumed immediately or within a very short period of time after discovery, the owner of the food patch (the investor) may behave aggressively toward "joiners" (exploiters) by chasing them away from the patch, thus securing exclusive access to the food. Empirical evidence indicates that individuals seem to switch from peaceful sharing of food to aggressive encounters depending on ecological factors, such as the value of exploited patches or their level of spatial or temporal predictability (Goldberg et al. 2001). From a theoretical point of view, the question of which competitive tactic should be used has been frequently addressed by game theoretical models, most notably the hawk–dove game (Maynard-Smith and Price 1973); for an alternative approach based on economic conflict theory, see King et al. (this volume). The hawk–dove game considers a pair of opponents that compete for a resource using either an aggressive (hawk) or a nonaggressive (dove) behavior. It predicts that hawk is an ESS when the value of winning over a food patch (v) exceeds the cost of losing an aggressive encounter (c). Otherwise, the solution is a mixed ESS. The dove strategy, therefore, can never exist as a pure ESS, although nonaggressive resource sharing has been reported for a large number of animal species.

Since its original formulation, several variants of the hawk–dove game have been developed to generate more realistic predictions that apply to the process of foraging in groups, as will be reviewed here. One important deviation from the usual hawk–dove game is that in a foraging group, the two contestants do not arrive simultaneously at a food patch. The first to arrive (i.e., the finder) can thus exploit a patch before a joiner arrives, thus gaining a finder's share. This role asymmetry makes aggressive appropriation less profitable as the finder's

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share increases: the remaining food becomes insufficient to cover the cost of fighting, and the joiner retreats in the face of conflict escalation (Dubois et al. 2003). The finder should always compete aggressively when opponents are equal in their fighting ability, regardless of the size of the finder's share (Dubois and Giraldeau 2003, 2005; Dubois et al. 2003). Even if they could do better by sharing the remaining food, the first to decide on a strategy (i.e., the finder) should never play dove, because the joiner would then systematically play hawk and get all the remaining resource at no cost. Sharing could arise, however, if a finder that is prone to sharing, and hence to playing dove, changes its decision when its opponent decides to play hawk. In this case, food sharing should occur notably when food patches are of intermediate value, or when there is uncertainty about the value of the remaining resource (Dubois and Giraldeau 2007). Food sharing should also be more common when resource distribution is heterogeneous (e.g., nonrandom distribution of food patches, food patches of variable quality), as heterogeneity likely increases joiner uncertainty about the availability and quality of food patches. Accordingly, higher levels of aggression in nutmeg mannikins (*Lonchura punctulata*) have been reported when birds had no information about the value and location of the food patches (Dubois and Giraldeau 2004).

Another reason why the pure dove strategy is never an ESS is because hawk–dove games typically consider only a single contest. Most group foraging situations, however, involve opponents that interact repeatedly over discovered food patches. To counter this, Dubois and Giraldeau (2003) developed an iterated hawk–dove game which predicts that animals should share the resources without aggression when they face situations analogous to a prisoner's dilemma. Specifically, when the cost of escalation is relatively small, mutual dove provides a higher payoff than mutual hawk. Here, however, a dilemma emerges: playing hawk against a dove results in maximum payoff while playing dove against a hawk results in maximum losses. Under such conditions, playing hawk is the best strategy for both contestants if they interact only once. If they interact repeatedly, however, a conditional strategy such as tit-for-tat (i.e., playing dove on the first round and then doing what the opponent did on the previous round) can guard against the invasion of hawk players. The probability that food patches are peacefully shared between the two contestants depends on, among other parameters, the finder's share (i.e., the fraction of the patch that can be exploited exclusively by the finder before a joiner arrives). More precisely, the rate of aggression is expected to increase as the finder's share decreases, and then should increase with patch quality. Given that increasing competitor numbers likely reduce mean distances among individuals, the amount of food that can be gained by the finder before a joiner arrives should decline. Hence the benefits of defending increase with the number of competitors. As such, aggression should be more frequent in large group sizes (Dubois and Giraldeau 2003).

Another unrealistic assumption of the original hawk–dove game is that food patches are always contested by two opponents. In many instances, however, a large number of individuals converge at the patch, thereby forcing the finder to defend its resource against a large number of intruders. In this case, greater competitor numbers increase not only the benefits but also the costs of defense, resulting in a dome-shaped relationship between the frequency of aggression and the density of competitors (Dubois and Giraldeau 2003). Experimental evidence indicates that the aggression rate peaks at intermediate group sizes (Jones 1983; Goldberg et al. 2001). Dubois and Giraldeau (2003) assume that all intruders should always attempt appropriation of an owner's resources and hence analyze only whether appropriation should be aggressive or not. The question of whether a resource is worth defending, however, is relevant only when the resource obtained by a competitor is worth appropriating. To address this issue, Dubois and Giraldeau (2005) developed a game theoretical model that incorporates both the producer–scrounger and hawk–dove games, to explore how the interaction between appropriation and defense generates patterns of aggression in resource patches. Like other variants of the hawk–dove game (Sirot 2000; Dubois and Giraldeau 2003; Dubois et al. 2003), their model predicts that the frequency of aggressive interactions should decrease as the encounter rate with food patches increases. However, the predicted decrease in aggression with increasing patch density does not result from a decrease in individuals' level of aggressiveness but from a decrease in the proportion of scroungers whose aggression levels remains somewhat constant. Similarly, Dubois and Giraldeau's model (2005) predicts a dome-shaped relationship between group size and aggression frequency, as does Dubois et al. (2003), but the number of competitors has almost no effect on aggressiveness.

Finally, because of the finder's share, finders can gain more from a resource than joiners. Therefore, hawk–dove games which apply to foraging groups typically predict that the finder should always compete aggressively unless its fighting ability is well below that of its opponent(s). When engaged in defense, however, the finder would be incapable of preventing "distraction sneakers" (i.e., individuals that employ distraction so as to sneak into an area) to gain access to a resource left temporarily unguarded, leading to a reduction in the benefits of defending. The presence of sneakers should affect the expected level of aggression within groups. Supporting this idea, Dubois et al. (2004) demonstrated that introducing a distraction-sneaking tactic into the hawk–dove game decreases the expected proportion of aggressive animals playing hawk, particularly when sneakers search for both unchallenged resources and opportunities to appropriate food patches.

Ganging Up

When the resources are not defendable by a single individual, the finder may attract other individuals in an effort to form coalitions, thus increasing its

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chance of keeping the resources and minimizing the risks of aggression and injury. This type of strategy is mostly used by young or low-ranking individuals who benefit from "ganging up" to evict competitors with higher fighting ability (Heinrich and Marzluff 1991). Coalitions may also prevent interspecific kleptoparasitism. In particular, in social carnivores, one major argument for the sociality of lions has been to be able to defend their prey against theft by hyenas. Similarly, hyenas form large raiding groups to dislodge lions from their captures (Kruuk 1972).

Thus, whenever it is in the interest of finders to recruit others at resource patches, recruitment signals can be expected to evolve. For instance, when juvenile ravens find a carcass in winter, they call to attract others to form a group. This group of recruits is able to keep territorial owners at bay and consume the food (Heinrich and Marzluff 1991). Thus the decision to produce recruitment calls depends on the possibility of obtaining a sizable share of the resources. In a seminal paper, Elgar (1986) showed that house sparrows mostly produced recruitment calls when resources are divisible among the users. The use of recruitment calls to attract recruits at the resource patch has been proposed to play a role in the establishment of certain animal associations (Richner and Heeb 1996).

Consequences for Spatial Structure of Groups

When foraging in social groups, the spatial position of individuals within these groups is not neutral. The costs and benefits of individuals in groups may depend on their spatial position. Individuals using a producer or scrounger strategy might benefit from adopting specific locations. Barta et al. (1997) examined whether the strategies of producer and scrounger played by an individual should affect its spatial position within a group and the geometry of the foraging group. They found that the existence of the scrounger strategy leads to a decrease in the surface area occupied by foraging groups, and the average distance from the center of the groups or the average distance to the nearest neighbor was smaller. Scroungers tended to occupy positions in the middle of the group, close to other subjects, whereas producers tended to occupy the periphery. The authors concluded that groups containing producers and scroungers should be more compact compared to an equivalent group made up solely of producers. They argue that scrounging may be an alternative (or additional) factor in the promotion of the dominants' known preference for central positions (Barta et al. 1997).

However, the distinct positional advantages of each strategy suggest that an individual alternating between optimal producer and scrounger alternatives would likely incur a cost associated with a shift in spatial position within the group. Depending on their value, these costs would lead to the stabilization of specific strategies in given locations. The spatial location of an individual

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within a foraging group likely affects the payoffs anticipated from using the producer or scrounger tactics. A producer, for example, profits most by being furthest from any others, reducing competition by fellow producers while increasing the time required by scroungers to reach its discovery. A scrounger, on the other hand, benefits most by being as close as possible to all potential food finders, minimizing the time elapsed between the food discovery and its arrival at the patch.

Later studies examined the role of PS strategies in explicit spatial scenarios. Flynn and Giraldeau (2001) examined whether the exploitation of companions' food discoveries had spatial consequences for the foraging individual. Specifically, they examined the association between tactic use and the spatial characteristics of foraging flocks of nutmeg mannikins (*L. punctulata*) as a model organism. They predisposed some individuals toward the producer tactic by pretraining them to find food hidden under lids. They also predicted that in dominance-structured PS games, subordinates should prefer to play producer (because their position in the hierarchy prevents them from getting food by scrounging) and place themselves on the periphery of the groups. Being at the center of groups provides the possibility of accessing more information, and scroungers are expected to be more numerous. Centrally located individuals must scan to detect scrounging opportunities. The study of vigilance behaviors in foraging groups has received quite a lot of interest from biologists. The association between scrounging and vigilance suggests that scanning frequencies reported within central portions of foraging groups may have to do with the use of scrounger strategies, and probably less with predation hazard (Coolen et al. 2001). It follows that antipredatory vigilance behavior may be more directly measured in peripheral individuals whose scanning is unlikely to be related to the use of scrounger tactics.

In confirmation with earlier studies, Flynn and Giraldeau (2001) concluded that individuals who frequently use the producer tactic forage preferentially away from the center of the flock, whereas those that favor scrounger tactics prefer more centrally located positions. If this result holds in other scenarios, this implies that symmetric PS games will not apply in natural conditions, and that other models would need to be developed to take position asymmetries into account.

Exploiting Information from Others

In contrast to solitary animals, which generally must acquire information directly from the successes and failures of their own decisions, social animals are able to obtain information by sampling the environment themselves as well as by observing the decisions of their companions. These sources of social information add value to different alternatives (Danchin et al. 2004).

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The degree to which animals will rely preferentially on social information appears to depend on the ease with which social and personal information can be simultaneously collected and the difficulty of gathering accurate personal information from the sampling of their environment (Templeton and Giraldeau 1995). When animals gather information in this way, the information provided by a sequence of social tutors can induce herd-like phenomena or “informational cascades”: decisions are made regardless of the personal information at hand. In this scenario, individuals “blindly” copy the decision they witnessed (Bikhchandani et al. 1998). Although copying predecessors’ actions often leads to the adoption of the correct decision, it is also prone to the adoption of incorrect decisions, imposing fitness-related costs (Bikhchandani et al. 1998; Giraldeau et al. 2002). Such costly cascades are expected to occur when the observation of companions is limited to their decisions rather than the cues on which these decisions were based (Bikhchandani et al. 1998; Giraldeau et al. 2002). Results obtained by Rieucau and Giraldeau (2009) provide experimental evidence that nutmeg mannikins (*L. punctulata*) tend to disregard personal information when social information is sufficiently convincing. These birds relied on social information more when the cue used failed to predict the location of the fast feeder. Their study provides the first experimental evidence in nonhuman animals that is consistent with the propagation of informational cascades observed in human crowds (Bikhchandani et al. 1998). Their results raise the issue that the use of personal information, independent of its quality, does not insulate individuals from the use of social information (Valone and Giraldeau 1993).

In nature, competitive situations can exist where it pays for the finder to hide or conceal public information. For example, the behavior or performance of one species can be used as a source of information about mutually exploited resources by putative competitors (Danchin et al. 2004; Goodale et al. 2010). Increased overlap in resource use may result in costs for the information source in terms of enhanced interference and exploitation competition, resulting in an “evolutionary arms race” that favors acquiring and hiding information (Seppänen et al. 2007). As an example, studies have shown that pied flycatchers (*Ficedula hypoleuca*) use great tits (*Parus major*) as a source of information in habitat and nest-site selection decisions (Loukola et al. 2014). The flycatchers can gain fitness benefits (by laying larger clutches) from the information they obtain concerning nesting sites, by observing the clutch size laid by the tits when nesting in proximity to great tits. In contrast, tits suffer from the association and resulting competition (they lay smaller clutches). In response to this form of “social parasitism,” tits attempt to hide the information provided by their clutches by covering their eggs with different materials (e.g., hair, moss, moss sporangia, grass). After performing an experiment where the risk of having flycatchers as parasites were increased, Loukola et al. (2014) found that tits put more hair on the eggs and covered them more carefully. These results illustrate the fact that when exploitation is costly, it pays for the “producer” (investor) to reduce the amount of information available to the “scroungers” (exploiter).

When animals forage socially, individuals can obtain prey by using the behavior of others when they inadvertently provide information that food has been located. This inadvertent social information can be of two types (Danchin et al. 2004): it may provide social information simply by indicating the location of the resource, or it may provide public information to indicate the quality of the resource based on the performance of the individual already engaged in exploiting it (Valone 2007). For the individual using the information provided, public information is considered to be better than social information because it is used preferentially when it is equally costly to obtain as other types of inadvertent social information (Coolen et al. 2005). It would be interesting, however, to explore situations where public information provides no additional benefit to inadvertent social information (e.g., when resource quality has no variance or similar situations). Because scrounging, and hence the use of inadvertent social information, is mutually incompatible with producing (Coolen et al. 2001), any increase in the stable equilibrium frequency of scrounging results in a decreased number of producers that are concurrently searching for prey, and thus in lower predator search efficiency. Therefore, prey may be expected to evolve characteristics that can induce high rates of scrounging in their predators to reduce predator search efficiency (e.g., prey crypticity; Barrette and Giraldeau 2006). Another such trait may be prey clumpiness: larger prey clump sizes are predicted to increase the stable equilibrium frequency of scrounging (Caraco and Giraldeau 1991) and have been demonstrated to reduce predator efficiency at finding patches (Coolen 2002). Predators increased their use of the scrounger tactic in response to increased average prey clump size.

In a simulation study, Hamblin et al. (2010) further tested some of the evolutionary outcomes of these predictions. As predicted, they found that as prey grouped together, the frequency of scroungers among predators increased and stabilized after prey reached a certain clump size. Surprisingly and contrary to expectations, their simulations showed that prey evolved toward the highest clumping against predators without social information. Prey evolved toward smaller clump sizes when facing predators with social and public information predators. Their study was the first to demonstrate how information use by predators evolves in response to prey–predator dynamics. The prey survived better when the predators used either social or public information, which shows that scrounging, and hence the use of inadvertent social information in any form, actually reduced predator efficiency. Consistent with this suggestion, predators reduced their investment in scrounging much more rapidly when they had access to public information compared with when they had access only to social information. This suggests that there would be an advantage to prey to evolve traits that reduce the ability of predators to provide public information while they are being exploited. It would be interesting

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to explore which traits are selected to reduce the availability of inadvertent social information.

The fact that behavioral strategies of predators, in particular scrounging, can affect the behaviors of their prey can lead to population regulation through their effects on individuals' reproductive rate and mortality. Coolen et al. (2007) explored the effects of scrounging on prey–predator population dynamics and showed that the presence of scrounging predators allows an increased predator population size and contributes to the regulation of both predator and prey populations. This result may have general value. For instance, if the prey in one context is a valuable resource (say a forest or a stock of fish), then one could envisage implementing measures to increase scrounging among the individuals engaged in exploiting it as a means of increasing the sustainable use of the resource (see Valone et al., this volume).

Spying on others as they go about their lives can have significant consequences. On one hand, those being spied upon become vulnerable to having their efforts exploited. However, in some contexts, the presence of spies can provide opportunities to control social interactions more effectively. This could select for those being spied upon to act in ways to minimize exploitation by information parasites, or even to manipulate spies through the information being observed. Either way, the availability of inadvertently provided information often changes the behavioral strategies we expect to evolve (McNamara 2013).

Guarding against Information Parasitism

It seems obvious that it is rarely in an individual's interest to have his behavior monitored, since this would put the individual at risk of having the fruits of his labors exploited. Clearly the adjustments discussed above in scatter hoarding (i.e., changes in caching behavior in the presence of conspecific observers to minimize the risk of pilferage) might be thought of as strategies to mitigate the risk of information parasitism. Nevertheless, putative pilferers can also adopt sophisticated counterstrategies once they know that their behavior is being monitored. For instance, common ravens will regularly cache excess food, and it is well known that such hoarders adjust their behavior in the presence of potential pilferers to mitigate the risk that their hoards are pilfered (Bugnyar and Heinrich 2005, 2006). This involves attacking known witnesses to their caching attempts or quickly retrieving caches in the presence of such individuals, depending on the relative social status of the individuals involved (Bugnyar and Heinrich 2005). Such strategic defenses have counterstrategies that involve the strategic use of social misinformation by the wannabe pilferers. For instance, putative pilferers of dominant hoarders will delay approaching known cache locations by cursorily searching the general areas around the caches (and thereby acting deceptively ignorant) only when the hoarder is

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present (Bugnyar and Heinrich 2006). This provides opportunities to pilfer the caches before the dominant bird has a chance to drive them off.

Such strategic deception in the presence of potential information scroungers has also been documented in nonfood-hoarding contexts. It seems to be a particularly effective ploy when the putative information parasites are dominant to the potential victims. For instance, in captive food retrieval experiments in chimpanzees, dominant individuals typically monopolize any food for which they know the location. In response, when subordinates have exclusive knowledge of some food locations but can only access them in the presence of dominants, they will engage in strategic maneuvering by waiting or hiding to obtain pieces of food or even proactively distracting the dominants by deceptively socializing with them to keep them away from the food (Hare et al. 2000). Thus, in at least some cognitively complex species, individuals can assess what conspecifics can or cannot see or know, and deploy some sophisticated strategies to counter the threat of being exploited by information parasites.

Being Watched Enhances Social Information

During social (including sexual) encounters, an individual's behavior is often influenced by the interactions of other conspecifics and the predictable responses that they make (Dall et al. 2004; McNamara et al. 2009; Bergmüller and Taborsky 2010; Schuett et al. 2010; Wolf et al. 2011). Thus, when animals interact socially, they can pay attention to each other's behavior to make better decisions. Once individuals use such basic social information, it changes selection and the day-to-day reinforcement of behavioral patterns over time in the presence of audiences. In some contexts (e.g., when competing aggressively for resources or interacting cooperatively), this can favor (both evolutionarily and behaviorally) individual behavioral differentiation (Dall et al. 2004; McNamara et al. 2009; Wolf et al. 2011). However, it can also make negative frequency-dependent payoffs to be adaptively flexible (Wolf et al. 2008; Dubois et al. 2010).

To see why, consider the hawk–dove game. In the basic game of competition over resources of value v, given that getting into an escalated fight costs $c > v$, the ESS (or BSS) is for a proportion v/c of individuals to assume the hawk strategy (always escalate if challenged) while $1 - v/c$ play the dove role (always capitulate without fighting) at any given moment. There are, however, two ways in which the ESS mixture of tactics in a population can be maintained by frequency-dependent payoffs alone:

1. Each individual can perform actions randomly with fixed probabilities, and thus generate the predicted mix of strategies in large populations.
2. Fixed proportions of individuals can play each strategy consistently.

The conditions favoring the evolution and maintenance of one or another of these forms of evolutionarily (or behaviorally) stable mixtures of behavior

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have yet to be elucidated in general, although investigating the adaptive dynamics of biological games may generate insights (Bergstrom and Godfrey-Smith 1998). Indeed, for the basic hawk–dove game in finite populations, such analysis suggests that populations of ESS (BSS) mixtures of individuals specializing in each strategy will always evolve toward monomorphic populations of individuals playing hawk OR dove randomly with ESS (BSS) probabilities (Bergstrom and Godfrey-Smith 1998). This is because stochastic variation in the frequency of hawkishness (e.g., due to demographic noise) within populations will penalize individuals that commit themselves to playing either strategy consistently (Bergstrom and Godfrey-Smith 1998).

However, adding the possibility that individuals might "eavesdrop" on one another (e.g., base their tactics on the outcomes of their opponents' last fights; Johnstone 2001) to the hawk–dove game with adaptive (e.g., replicator) dynamics favors the alternative outcome: strategies that generate consistent individual differences in aggression will be at an advantage in monomorphic populations in which all individuals play hawk and dove randomly at ESS (BSS) probabilities. This is because, with eavesdropping in the population, more consistent aggressiveness (high or low) is favored since, by being more predictable, individuals can avoid getting into extended (costly) fights. Moreover, with increased interindividual variation in aggressiveness, increased levels of eavesdropping will be favored to minimize the chance of fighting with the more aggressive individuals (who are more likely to have won their last fight), and so on. This dynamic feedback will eventually result in polymorphic populations that are composed of extreme types at ESS (BSS) frequencies, in which individuals are always either hawks, doves, or eavesdroppers (Dall et al. 2004). Thus, adding the possibility of being spied upon while fighting results in a qualitatively distinct evolutionary or behavioral outcome, since consistency can be favored when being predictable gets competitors to respond, in the future, to improve focal individuals' payoffs. Perhaps the fact that fights over resources rarely occur in social isolation can explain why consistent individual differences in aggressiveness, manifest in dominance hierarchies, are common in a wide range of species.

In general, it is possible that when individual behavior is being monitored, variation itself can promote further variation by favoring social information use. This is because the existence of stable interindividual variation means that there is something to learn from monitoring others, which in turn can favor individual differentiation among those being monitored (McNamara 2013). Indeed such intuition also holds in a model of trust and cooperation (McNamara et al. 2009), where allowing individuals to monitor each other's cooperative tendencies, at a cost, can favor polymorphisms in trustworthiness. This variation, in turn, favors costly "social awareness" in some individuals (McNamara et al. 2009). Indeed, feedback of this sort might explain the individual differences in trust and trustworthiness so often documented by economists in experimental public goods games across a range of cultures (e.g., Fischbacher et al. 2001).

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Conclusion

The optimal frequency of exploiters and investors within populations has been traditionally analyzed using the PS game. Although several predictions of the PS model have been supported by experimental evidence, it is based on highly simplified assumptions. In particular, though producers are generally considered as passive competitors that do nothing to prevent scroungers from exploiting their efforts, they frequently adopt behavioral strategies aimed at reducing the benefits of scrounging. For instance, when competing for food, producers can use aggressive behavior to chase away the scroungers and get exclusive access to the resource instead of sharing. Similarly, individuals that cache food or sample their environment to select a suitable habitat to settle may modify their behavior when in the presence of others to reduce the risk of pilferage or information parasitism, thereby reducing the proportion of exploiters. Alternatively, although PS models consider all group members as equally effective in searching and joining, individuals may modify the costs and benefits associated with both strategies simply by adjusting their spatial location within the group to their strategy. Since scroungers have effects on the structure and dynamics of populations, notably by generating consistent differences among individuals or by contributing to the regulation of both predator and prey populations, it is important to develop more realistic models that include these behavioral adaptations. Such models might be useful to evaluate measures aimed at sustaining resources of economic value, for instance by manipulating predation pressure (i.e., the proportion of producers) on prey populations.

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