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Distraction Sneakers Decrease the Expected Level of Aggression within Groups: A Game-Theoretic Model

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ABSTRACT: Hawk-dove games have been extensively used to predict the conditions under which group-living animals should defend their resources against potential usurpers. Typically, game-theoretic models on aggression consider that resource defense may entail energetic and injury costs. However, intruders may also take advantage of owners who are busy fighting to sneak access to unguarded resources, imposing thereby an additional cost on the use of the escalated hawk strategy. In this article we modify the two-strategy hawk-dove game into a three-strategy hawk-dove-sneaker game that incorporates a distraction-sneaking tactic, allowing us to explore its consequences on the expected level of aggression within groups. Our model predicts a lower proportion of hawks and hence lower frequencies of aggressive interactions within groups than do previous two-strategy hawk-dove games. The extent to which distraction sneakers decrease the frequency of aggression within groups, however, depends on whether they search only for opportunities to join resources uncovered by other group members or for both unchallenged resources and opportunities to usurp.

Keywords: resource exploitation, aggression, distraction sneakers, game-theoretic model.

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When animals live in groups, they must frequently decide whether to defend resources against potential usurpers. Defense may be energetically costly (Puckett and Dill 1985) and entail risk of injury or death from aggressive interactions (Enquist et al. 1990) or predators (Martel and Dill 1995). Another potential cost of defense is that owners may be taken advantage of while engaged in defense (sometimes called "aggressive neglect"; Wilson 1975). Intruders may take advantage of owners who are busy fighting or chasing neighbors or intruders to sneak into the unguarded food patch (Chapman and Kramer 1996; Hamilton and Dill 2003*a*) or to court an unguarded female (Grant et al. 1995). Such intruders may synchronize their approach with other intruders (surgeonfish: Barlow 1974; Foster 1985) or even recruit other intruders (juvenile ravens: Marzluff and Heinrich 1991) to overwhelm the defense of resource owners. We call these sneakers "distraction sneakers" because they take advantage of the resource owner's involvement in an alternative activity in order to gain access to the resource that is temporarily left unguarded. Distraction sneakers can have important effects on the level of aggression within groups because they impose a cost of lost resources on aggressive resource defense or appropriation over and above the usual energetic and injury costs that are typically considered by optimality models (Brown 1964; Emlen and Oring 1977; Myers et al. 1981; Grant 1993).

Distraction sneaking is one of a suite of tactics, collectively referred to in the literature as "sneaking," that involve the use of stealth, speed, mimicry, or distraction to avoid receiving aggression from defending resource owners. Such sneaking appears to be ubiquitous and exhibits considerable variability. In some cases, sneaking and territoriality are employed by different individuals. For example, in the bluegill sunfish (*Lepomis macrochirus*) large males build nests and defend territories whereas smaller males hide nearby and use a sneaker strategy to approach nests and spawn with females (Gross 1984). Similarly, adult ravens (*Corvus corax*) defend carcasses, whereas immature ravens sneak in large groups to acquire food (Marzluff and Heinrich 1991). In other systems, many individuals use a

combination of sneaking and resource defense (Östlund-Nilsson 2002; for an example in a foraging system with distraction sneakers, see Hamilton and Dill 2003b). Theoretical models have considered the ecological factors that affect the frequency of sneakers (but not sneakers that take advantage of aggressive interactions) within populations (Gross 1984, 1996; Repka and Gross 1995) and on the tactics that may be employed by sneakers (i.e., whether to invade alongside or following other sneakers or to assist territory holders in defense; Hamilton and Dill 2002, 2003a). However, little attention has been directed to the issue of how the presence of sneakers affects the expected levels of aggression within groups. In this study we investigate the consequence of including distraction sneakers in analyses of the economics of resource defense.

The hawk-dove game is perhaps the most general approach to modeling aggressive interactions over resources (Maynard Smith and Price 1973). This game can take symmetric or asymmetric forms, depending on whether individuals play distinct roles (e.g., defender and intruder or finder and joiner; Dubois et al. 2003). Thus it can be tailored both to territorial systems with relatively permanent resource locations, in which there is a distinction between territory owners and intruders, and nonterritorial systems with ephemeral resource locations where such asymmetries may or may not be present (Giraldeau and Caraco 2000). The hawk-dove game is often analyzed as a two-player game where individuals meet in pairs (e.g., Sirot 2000; Dubois et al. 2003). When groups of animals compete for local clumps of resources, however, interactions often take the form of n-person scrambles. Hence in this article, we modify the two-player hawk-dove game into an n-player scramble hawk-dove-sneaker game that incorporates a distraction-sneaking tactic to investigate the ecological conditions that favor this tactic and explore its consequences on the expected level of aggression within groups. The success of distraction sneakers as a resource exploitation strategy depends on the frequency of aggression initiated by other group members. We expect the sneaker strategy, therefore, to have negative frequency-dependent success; distraction sneakers will have high fitness when they are rare and aggression is common in the population, and they will have low fitness when they are frequent and aggression is rare.

The Model

For this model we will consider a foraging scenario, but the general conclusions should hold for any resource that can be exploited simultaneously by more than one individual. We hypothesize a group of $(G + 1)$ foragers. When an animal finds a clump of food containing F items, all remaining G group members become intruders and con-

gregate to appropriate the finder's resource. The resource finder always gets a secure fraction of a resource (a) which, following Vickery et. al. (1991), we call the "finder's advantage." Once the joiners arrive at the patch, the finder's advantage has been consumed, and what is left ($F - a$) will be termed the "joiner's share" (Vickery et al. 1991). Animals can use one of the three appropriation strategies: hawk, dove, or sneaker. The parameters p, q, and r denote the frequency of each strategy within the whole group, with $p + q + r = 1$. Although we will relax this assumption later, for now we assume that hawks and doves search for food but that sneakers never search and that they rely on resources uncovered by other group members. Therefore, only individuals playing hawk or dove can obtain the finder's advantage, and their probability of discovering resources does not depend on the strategy they use. Whereas hawks use force to chase the other competitors and gain exclusive access to the remaining resource, both dove and sneaker players use a nonaggressive strategy and share the resource with any other group member that tolerates them. If at least one of the individuals at the patch plays hawk, whether owner or intruder, doves retreat and leave the joiner's share behind. A sneaker, however, gains some fraction of the joiner's share by feeding while the hawks are busy fighting. We assume that animals do not differ in their fighting abilities such that all animals that use the hawk strategy have the same probability of winning the joiner's share.

Unlike earlier hawk-dove games, hawks in our game are not injured. Instead the escalated fights involve both time and energetic costs that vary according to the number of competitors playing hawk at the patch (Dubois et al. 2003). In particular, we consider that the time and energetic cost of fighting are t and c, respectively, when an animal has to chase only one opponent from the patch. Conversely, when the patch is contested by pG other competitors playing hawk, the time spent fighting is $T = pGt$, and the energetic cost C is proportional to the duration of the fights such that $C = Tc$. When they are not engaged in any other activities, animals obtain x units of resource per time unit. So, during a time T, each animal playing sneaker can potentially obtain xT units of resource. For simplicity's sake, we assume that x is smaller than $4(F - a)/tG^2$. Thus, whatever the proportion of animals playing sneaker or hawk, the patch is never completely depleted because the aggressive contestants cease fighting, and the quantity of remaining resource obtained by the winner of the fights is then Q, with

$$Q = (F - a) - xTrG, \tag{1}$$

where $T = pGt$ is the total duration of the fights and r the proportion of animals playing sneaker.

The sneakers have a probability β of being still present on the patch as the winner of the fights returns to the patch to feed. In this case, they are attacked by the victorious contestant and suffer an energetic cost c.

To simplify the analysis, we ignore simultaneous patch discoveries and assume that patch discovery is rare and occurs sequentially. We assume that the time required for an individual foraging alone to detect a food patch is t_s. In a group of G foragers, however, the time before a food patch is discovered equals $\tau = t_s/G^i$, where i ($0 \leq i \leq 1$) determines how the searching contribution of an individual changes as a function of foraging group size. According to this equation, the time required for an individual to detect a food patch is not affected by being in the group when $i = 0$ but decreases with increasing group size when $i > 0$. Moreover, we consider that patch exploitation time is negligible when there is only one forager on the patch but that the addition of competitors increases the time required to deplete a patch through interference competition. Thus, when the finder and the joiners all play either dove or sneaker, the exploitation time of the patch is $T_E = \alpha(G - 1)$, where α corresponds to the level of interference that depends among other parameters on patch size. We express the mean payoff of each strategy as the mean number of food items gained by an individual in a patch divided by the time it spent searching and exploiting the patch, including the time spent in fights. Hence the average rate of energy intake of an animal playing hawk is

$$W_H = \left[\frac{a}{1 + (p + q)G} + \frac{Q}{1 + pG} - Tc\right]\bigg/(\tau + T). \quad (2)$$

Given that an animal playing dove leaves the patch when at least one competitor plays hawk, its average rate of energy intake is

$$W_D = \left[\frac{a}{1 + (p + q)G} + \frac{F - a}{1 + G}\right]\bigg/(\tau + T_E) \quad \text{if } p = 0,$$
$$(3a)$$

or

$$W_D = \left[\frac{a}{1 + (p + q)G}\right]\bigg/\tau \quad \text{if } p > 0. \quad (3b)$$

Similarly, an animal playing sneaker shares the contested resource with the other competitors if none of them behaves aggressively; otherwise, it races to gain access to as much of the resource as possible while the animals playing

hawk are engaged in fights. Thus the expected gain of an animal playing sneaker is

$$W_S = \left(\frac{F - a}{1 + G}\right)\bigg/(\tau + T_E) \quad \text{if } p = 0, \quad (4a)$$

or

$$W_D = \frac{xT - \beta c}{\tau + T} \quad \text{if } p > 0. \quad (4b)$$

Analysis

Playing hawk is the evolutionarily stable strategy (ESS) if the expected gain of an animal playing hawk is greater than the gain expected by an animal playing any alternative strategy when the other G group members play hawk (i.e., $p = 1$). Solving $W_H > W_D$ and $W_H > W_S$ requires $c < c_1^*$ and $c < c_2^*$, with

$$c_1^* = \left(\frac{1}{1 + G}\right) \times \left(\frac{F - a}{Gt} - \frac{a}{\tau}\right), \quad (5)$$

$$c_2^* = \left(\frac{1}{tG - \beta}\right) \times \left(\frac{F}{1 + G} - xtG\right). \quad (6)$$

When the cost of fighting is smaller than the threshold values c_1^* and c_2^*, neither dove nor sneaker can invade a group in which all individuals play hawk, and hence hawk is the ESS. Conversely, when the G intruders all play dove (i.e., $q = 1$), the quantity of resource expected to be gained by an animal is always greater if it plays hawk because the doves leave the patch as soon as one competitor plays hawk, thereby allowing the aggressive animal to get the whole joiner's share at no cost. As a consequence, playing dove is never the ESS. Neither can playing sneaker be the ESS because this strategy never searches for food.

When hawk cannot resist against the invasion of at least one alternative strategy (i.e., when $c > c_1^*$ and/or $c > c_2^*$), the solution of the game is a mixed strategy $\{p^*, q^*, r^*\}$. However, three different situations can occur, depending on whether hawk can coexist with only one alternative strategy ($q^* = 0$ or $r^* = 0$) or with both dove and sneaker. We consider each in turn.

Hawk and Dove but No Sneaker

The mixed ESS is $\{p^*, 1 - p^*, 0\}$ and hence the expected proportion of animals playing sneaker at equilibrium r^* is equal to 0 if $W_S < W_D$ when $r = 0$ and the proportion

of animals playing hawk is such that the expected gain of an animal playing hawk equals that of an animal playing dove. When the proportion of animals playing sneaker is equal to 0, the condition $W_H = W_D$ is satisfied if

$$\left. \left(\frac{a}{1+G} + \frac{F-a}{1+pG} - Tc \right) \middle/ (\tau + T) \right. = \left. \left(\frac{a}{1+G} \right) \middle/ \tau. \right. \quad (7)$$

Solving equation (7) requires that the proportion of animals playing hawk is p^*, with

$$p^* = \frac{-t\psi + \sqrt{t\psi \times [t\psi + 4\tau(F-a)(1+G)]}}{2Gt\psi}, \quad (8)$$

with $\psi = a + \tau c(1+G)$. When the proportion of animals playing hawk and dove are p^* and $1 - p^*$, respectively, the expected gain of an animal playing sneaker is smaller than that of an animal playing dove if the cost of fighting is greater than the critical value c_3^*, with

$$c_3^* = \frac{1}{\beta} \times \left[p^* Gtx - \frac{a(\tau - p^* Gt)}{\tau(1+G)} \right]. \quad (9)$$

Hawk and Sneaker but No Dove

The mixed ESS is $\{p^*, 0, 1 - p^*\}$, and hence the expected proportion of animals playing dove at equilibrium q^* is equal to 0 if $W_D < W_S$ when $q = 0$, and the proportion of animals playing hawk is such that the expected gain of an animal playing hawk equals that of an animal playing sneaker. When the proportion of animals playing dove is equal to 0, the condition $W_H = W_S$ is satisfied if

$$\left. \left(\frac{a}{1+pG} + \frac{Q}{1+pG} - Tc \right) \middle/ (\tau + T) \right. = \frac{xT - \beta c}{\tau + T}. \quad (10)$$

Solving equation (10) requires that the proportion of animals playing hawk is p^*, with

$$p^* = \frac{c(\beta - t) - tx(1+G) + \sqrt{N}}{2Gtc}, \quad (11)$$

where $N = 4tc(F + c\beta) + [c(t - \beta) + tx(1+G)]^2$. When the proportions of animals playing hawk and sneaker are $1 - r^*$ and r^*, respectively, the expected gain of an animal playing dove is smaller than that of an animal playing sneaker provided that the cost of fighting is smaller than the critical value c_4^*, with

$$c_4^* = \frac{1}{\beta} \times \left[p^* Gtx - \frac{a(\tau + p^* Gt)}{\tau(1+p^*G)} \right]. \quad (12)$$

Hawk, Dove, and Sneaker

When the cost of fighting is smaller than c_3^* but greater than c_4^*, the three strategies coexist within the population, and the expected proportions of each strategy at equilibrium $\{p^*, q^*, r^*\}$ satisfy the following condition: $W_H = W_D = W_S$.

From these results, we can define the solution of the game according to the loss of energy associated with fighting c:

When $c < c_1^*$ and $c < c_2^*$, neither dove nor sneaker can invade a group in which all individuals play hawk and the ESS is $\{1, 0, 0\}$.

When $c > c_1^*$ and/or $c > c_2^*$, $c > c_3^*$, and $c > c_4^*$, hawk and dove coexist within the population and the ESS is $\{p^*, 1 - p^*, 0\}$, with the expression of p^* given by equation (8).

When $c > c_1^*$ and/or $c > c_2^*$, $c < c_3^*$, and $c < c_4^*$, hawk and sneaker coexist within the population and the ESS is $\{1 - r^*, 0, r^*\}$, with the expression of r^* given by equation (11).

When $c > c_1^*$ and/or $c > c_2^*$, $c < c_3^*$, and $c > c_4^*$, hawk, dove, and sneaker coexist within the population, and the frequencies of each strategy at equilibrium $\{p^*, q^*, r^*\}$ satisfy $W_H = W_D = W_S$.

Predictions

The model predicts that hawk is the only appropriation strategy that can never reach 0 frequency at equilibrium. Thus, there is no condition in which group members should all use nonaggressive appropriation strategies. The likelihood that all-hawk is the ESS appropriation strategy increases as the number of intruders competing for the patch decreases (fig. 1A). When the number of intruders is low, the time spent fighting and the cumulative energetic cost associated with fighting are both very low. Thus, a sneaker mutant could exploit the patch only during a very short time, and the quantity of resource it would obtain would be insufficient to allow it to invade a group of hawks. Similarly, when the number of intruders in the group is low, each intruder has a high probability of success in chasing the other intruders and hence of obtaining the joiner's share at a relatively low cost. The benefits of defending are then greater than the costs of fighting, which prevents dove from invading a hawk population. In contrast, when the number of intruders is large, the time and
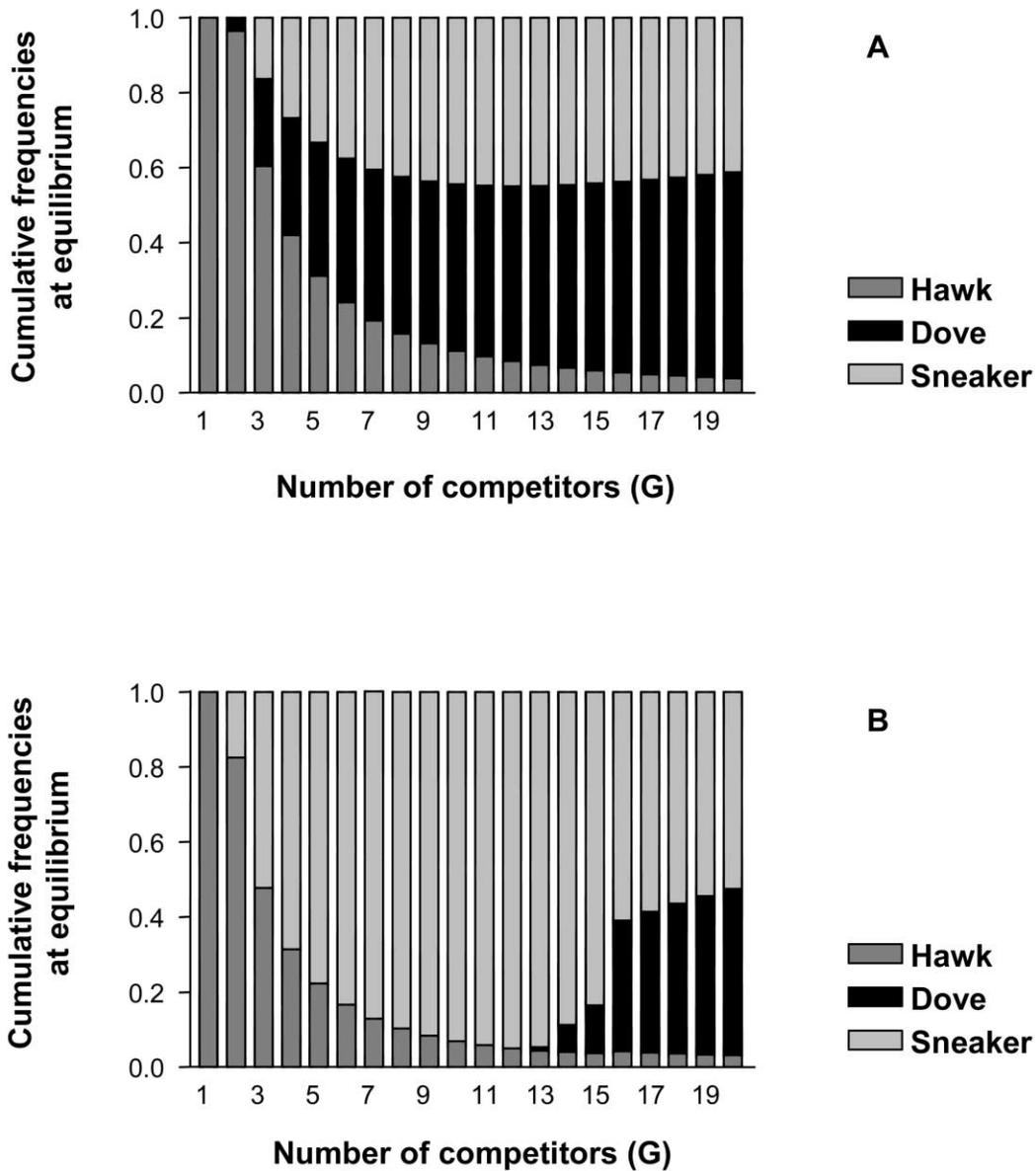
Figure 1: Expected frequencies of hawk, dove, and sneaker in relation to the number of competitors when sneakers search only for opportunities to join resources uncovered by other group members (*A*) or for both unchallenged resources and opportunities to usurp (*B*). In this figure, $F = 10$, $a = 2$, $c = 1$, $t = 1$, $\beta = 0.5$, $x = 1$, $t_S = 2$, $i = 0.2$.

energy required to chase the intruders out of the patch increase. So the model predicts that increasing the number of intruders will decrease the proportion of aggressive animals (p^*) but increase the frequency of both dove (q^*) and sneaker (r^*).

When the energetic costs of fighting are very low, the model predicts that the proportion of animals playing dove should be very low because then the joiner's share is very large relative to the energetic cost of fighting, and the sneaker should dominate the population. When the energetic value of the resource exceeds the energetic cost of aggression (low c), intruders have an incentive to fight for the resource. However, when all intruders play hawk, the time spent in fights increases such that sneakers can obtain a larger fraction of the joiner's share, leaving insufficient resources for the returning victorious hawk to cover the costs it expended while fighting. Increasing the energetic cost c leads to an increase in the proportion of animals
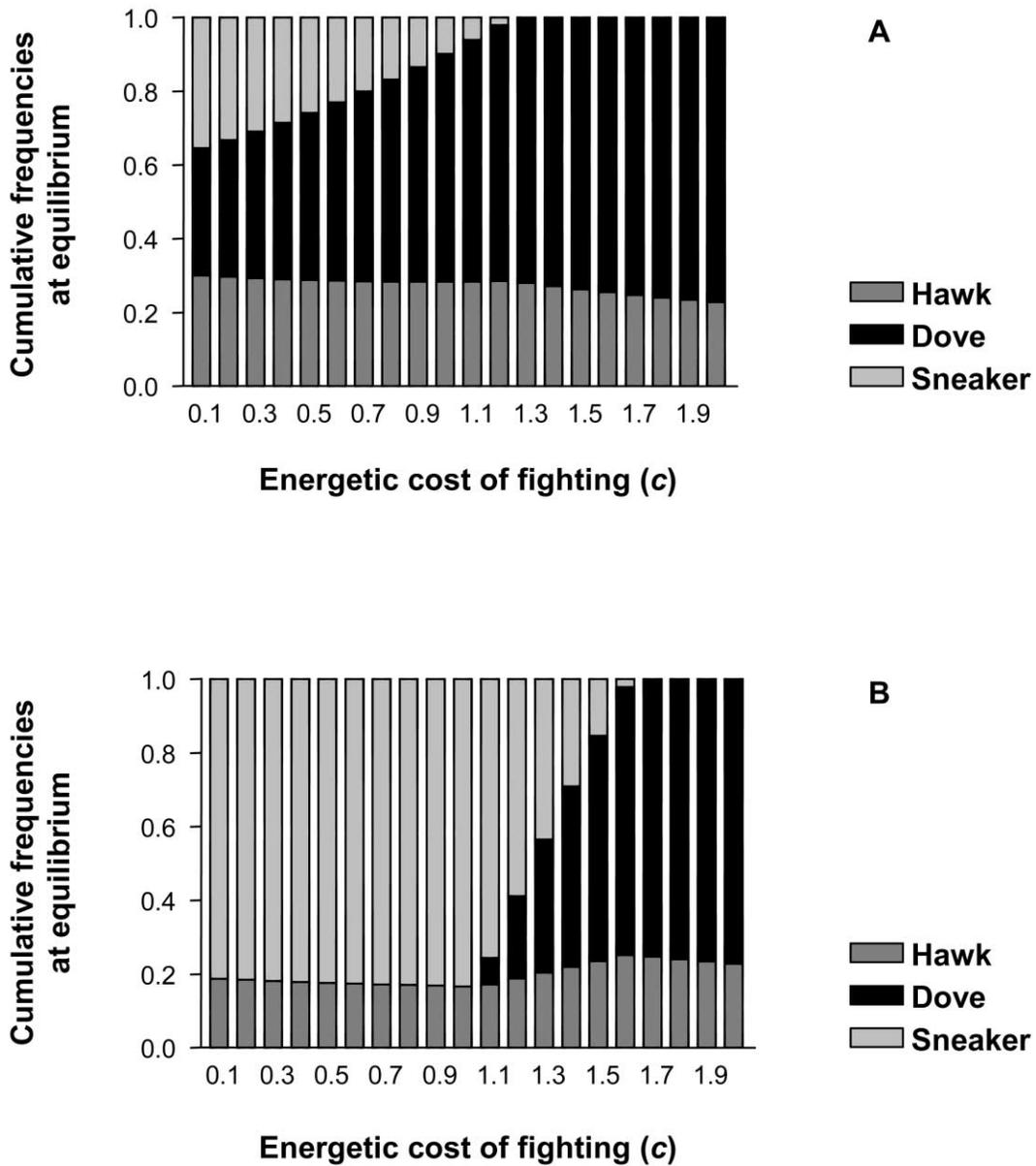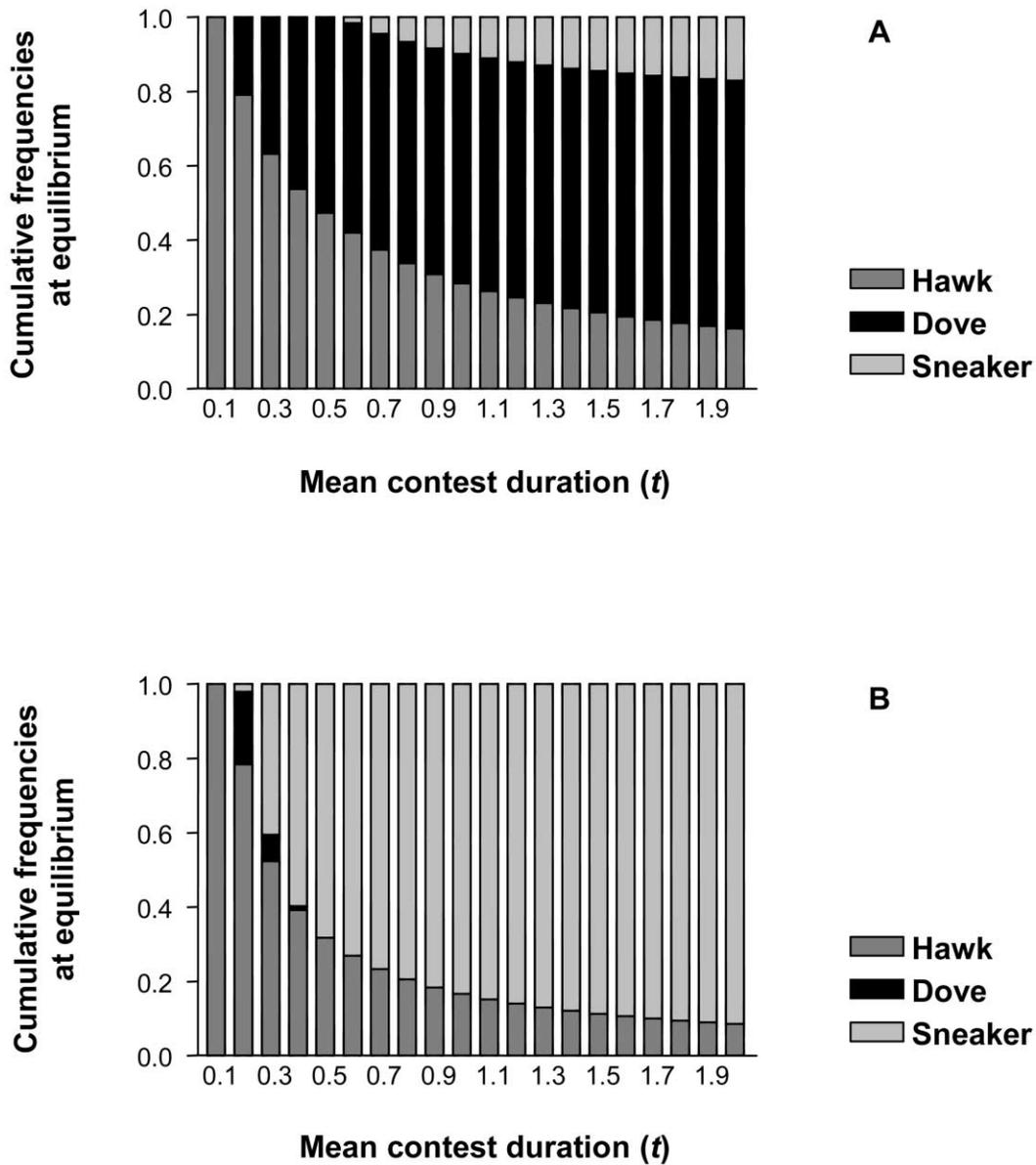
Figure 2: Expected frequencies of hawk, dove, and sneaker in relation to the energetic cots of fighting when sneakers search only for opportunities to join resources uncovered by other group members (*A*) or for both unchallenged resources and opportunities to usurp (*B*). In this figure, $G = 6$, $F = 10$, $a = 2$, $t = 1$, $\beta = 0.5$, $x = 1$, $t_S = 0.9$, $i = 0.2$.

playing dove but, surprisingly, has little effect on the frequency of hawk. As the proportion of animals playing hawk decreases, the cumulative costs of fighting all other hawks decreases, while the expected cost of fighting for sneakers does not depend on the average strategy adopted by the other group members. Therefore, as the energetic cost c increases, we predict that animals should reduce their use of the sneaker strategy, leading to an increase in the quantity of resource that can be gained by the winner

of the fights. Thus, not only the costs but also the benefits of aggressive appropriation increase as the energetic expenditure caused by each contest increases. This is the reason why variations in the energetic cost of contests have no marked influence on the expected frequency of hawk (fig. 2*A*).

When the mean duration of contests is short, most individuals should play hawk (fig. 3*A*). When this is so, the quantity of resource that can be gained by an animal play-

Figure 3: Expected frequencies of hawk, dove, and sneaker in relation to the mean duration of contest when sneakers search only for opportunities to join resources uncovered by other group members (*A*) or for both unchallenged resources and opportunities to usurp (*B*). In this figure, $G = 6$, $F = 10$, $a = 2$, $c = 1$, $\beta = 0.5$, $x = 1$, $t_s = 0.9$, $i = 0.2$.

ing sneaker is relatively small, particularly if patches deplete slowly (low x). Moreover, when the mean contest duration is short, the time required to detect food patches is very large in relation to the time spent fighting, particularly if food density is small (large τ), and a large proportion of animals are then expected to compete aggressively. Increasing the mean duration of contests leads to an increase in the amount of resource that can be gained by an animal playing sneaker, but it also leads to a decrease

in the value of the remaining resource that can be gained by an animal playing hawk. However, when the mean contest duration becomes very long, the time required to chase the intruders out of the patch is likely to exceed the time required to uncover an equivalent replacement food patch. Consequently, increasing the mean duration of contests is predicted to increase the proportion of animals playing both dove and sneaker but decrease the proportion of animals playing hawk (fig. 3*A*).
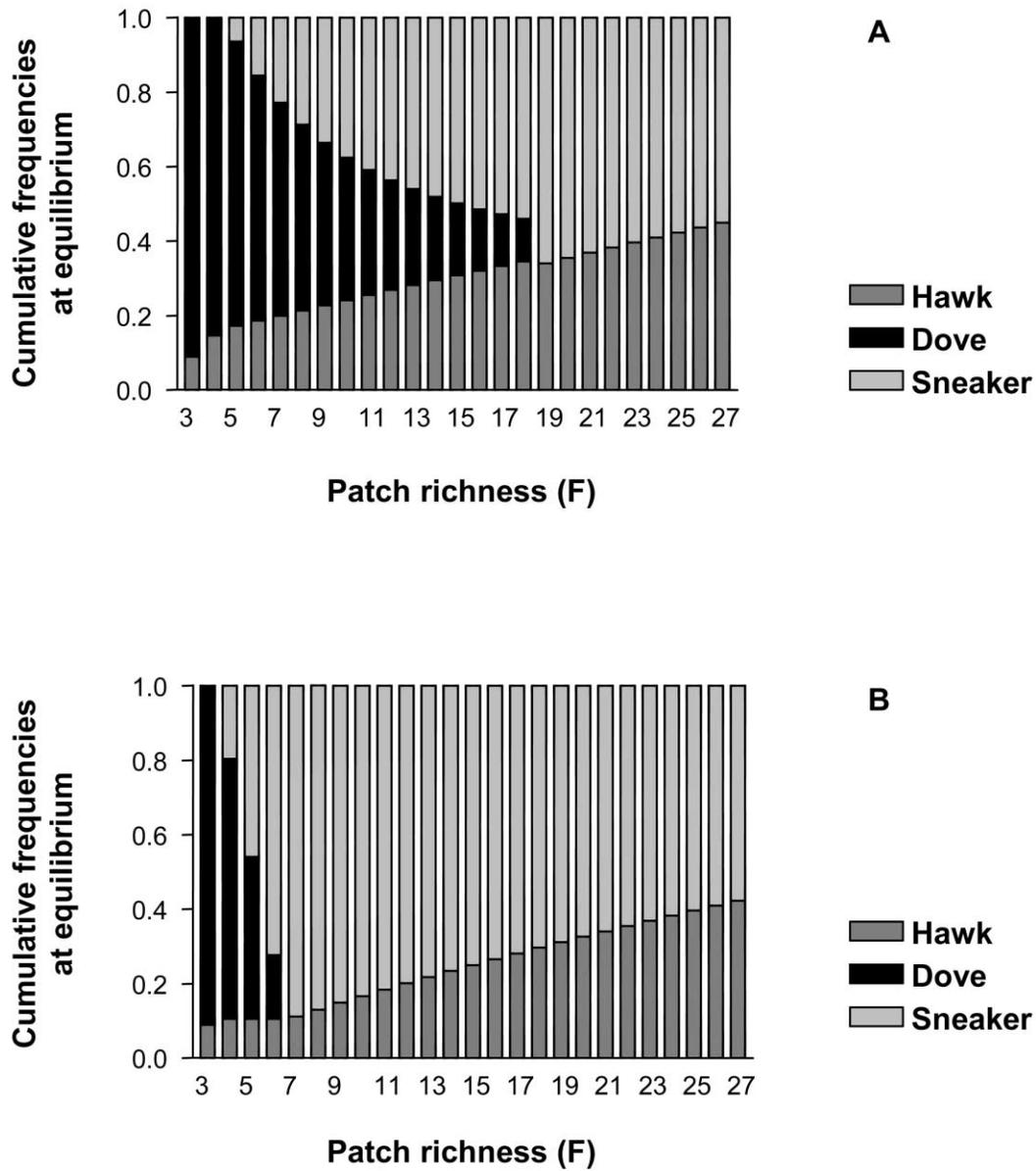
Figure 4: Expected frequencies of hawk, dove, and sneaker in relation to patch richness when sneakers search only for opportunities to join resources uncovered by other group members (*A*) or for both unchallenged resources and opportunities to usurp (*B*). In this figure, $G = 6$, $a = 2$, $c = 1$, $t = 1$, $\beta = 0.5$, $x = 1$, $t_S = 2$, $i = 0.2$.

The use of the nonaggressive dove strategy is predicted to decline as *F*, patch richness, increases (fig. 4*A*). When patches are poor (low *F*), the joiner's share is unlikely to be sufficient to cover the costs of fighting. For this reason, only a small proportion of animals should play hawk. Moreover, given that the proportion of aggressive encounters and the time spent in fights are very low when the frequency of hawk at equilibrium is small, the potential gain as a sneaker is low. When patches are rich, on the other hand, the benefits of defending are increased. Increasing patch richness, therefore, should lead to an increase in the proportion of intruders playing either hawk or sneaker but also to a decrease in the proportion of animals playing dove. Similarly, the frequency of dove should be maximal when the finder's advantage (*a*) is large and hence the joiner's share is insufficient to cover the cost of fighting. Decreasing the finder's advantage, conversely, should increase the frequency of both hawk and

sneaker but also decrease the proportion of animals playing dove.

Allowing Sneakers to Search for Unchallenged Resources

In the previous game, only hawks and doves could find resources. We now relax this assumption and allow sneakers to also find resources. All other elements of the game remain unchanged. Under these conditions, the expected gain of an animal playing hawk after τ time units becomes

$$W_H = \left(\frac{a}{1+G} + \frac{Q}{1+pG} - Tc\right)\bigg/(\tau + T), \quad (13)$$

where Q is the quantity of the remaining resource obtained by the winner of the fights and whose expression is given by equation (1).

However, the gain expected by an animal playing dove after τ time units is

$$W_D = \left(\frac{F}{1+G}\right)\bigg/(\tau + T_E) \quad \text{if } p = 0, \quad (14a)$$

or

$$W_D = \left(\frac{a}{1+G}\right)\bigg/\tau \quad \text{if } p > 0, \quad (14b)$$

whereas the expected gain of an animal playing sneaker becomes

$$W_S = \left(\frac{F}{1+G}\right)\bigg/\tau \quad \text{if } p = 0, \quad (15a)$$

$$W_S = \left(\frac{a}{1+G} + xT - \beta c\right)\bigg/(\tau + T) \quad \text{if } p > 0. \quad (15b)$$

Analysis

Playing hawk is the only ESS intruder strategy when the expected gain of an animal playing hawk is greater than the gain expected by an animal playing any alternative strategy if the other G group members play hawk (i.e., $p = 1$). Solving $W_H > W_D$ and $W_H > W_S$ requires $c < c_5^*$ and $c < c_6^*$, with

$$c_5^* = \left(\frac{1}{1+G}\right) \times \left(\frac{F-a}{Gt} + \frac{a}{\tau}\right), \quad (16)$$

$$c_6^* = \left(\frac{1}{Gt-\beta}\right) \times \left(\frac{F-a}{1+G} - xGt\right). \quad (17)$$

When the cost of fighting is smaller than the threshold values c_5^* and c_6^*, neither dove nor sneaker can invade a group in which all individuals play hawk, and hence hawk is the only ESS, and all intruders should use escalated aggressive appropriation. Conversely, when the G intruders all play either dove or sneaker (i.e., $q = 1$ or $r = 1$), the amount of resource expected to be gained by an animal is always greater if it plays hawk rather than dove or sneaker. As a consequence, neither all dove nor all sneaker can be ESS solutions to the game.

When hawk cannot resist against the invasion of at least one alternative strategy (i.e., when $c > c_5^*$ and/or $c > c_6^*$), the solution of the game is a mixed strategy $\{p^*, q^*, r^*\}$, but three different situations can occur, depending on whether hawk can coexist with only one alternative strategy ($q^* = 0$ or $r^* = 0$) or with both dove and sneaker.

Hawk and Dove but No Sneaker

The mixed ESS is $\{p^*, 1 - p^*, 0\}$, and hence the expected proportion of animals playing sneaker at equilibrium r^* is equal to 0 if $W_S < W_D$ when $r = 0$ and the proportion of animals playing hawk is such that the expected gain of an animal playing hawk equals that of an animal playing dove. When the proportion of animals playing sneaker is equal to 0, the condition $W_H = W_D$ is satisfied if

$$\left(\frac{a}{1+G} + \frac{F-a}{1+pG} - cT\right)\bigg/(\tau + T) = \left(\frac{a}{1+G}\right)\bigg/\tau. \quad (18)$$

Solving equation (18) requires that the proportion of animals playing hawk is p^*, with

$$p^* = \frac{-t\psi + \sqrt{t\psi \times [t\psi + 4\tau(F-a)(1+G)]}}{2Gt\psi}, \quad (19)$$

where $\psi = a + \tau c(1+G)$. When the proportion of animals playing hawk and dove are p^* and $1 - p^*$, respectively, the expected gain of an animal playing sneaker is smaller than that of an animal playing dove if the cost of fighting is greater than the critical value c_7^*, with

$$c_7^* = \left(\frac{p^* Gt}{\beta}\right) \times \left[x - \frac{a}{\tau(1+G)}\right]. \quad (20)$$

Hawk and Sneaker but No Dove

The mixed ESS is $\{p^*, 0, 1 - p^*\}$, and hence the expected proportion of animals playing dove at equilibrium q^* is equal to 0 if $W_D < W_S$ when $q = 0$ and the proportion of animals playing hawk is such that the expected gain of an animal playing hawk equals that of an animal playing sneaker. When the proportion of animals playing dove is equal to 0, the condition $W_H = W_S$ is satisfied if

$$\left(\frac{a}{1 + G} + \frac{Q}{1 + pG} - Tc\right)\bigg/(\tau + T) =$$

$$\left(\frac{a}{1 + G} + xT - \beta c\right)\bigg/(\tau + T). \qquad (21)$$

Solving equation (21) requires that the proportion of animals playing hawk is p^* with

$$p^* = \frac{c(\beta - t) - tx(1 + G) + \sqrt{N}}{2Gtc}, \qquad (22)$$

where $N = 4ct(F - a + c\beta) + [c(t - \beta) + tx(1 + G)]^2$. When the proportion of animals playing hawk and sneaker are p^* and $1 - p^*$, respectively, the expected gain of an animal playing dove is smaller than that of an animal playing sneaker, provided that the cost of fighting is smaller than the critical value c_8^*, with

$$c_8^* = \left(\frac{p^*Gt}{\beta}\right) \times \left[x - \frac{a}{\tau(1 + G)}\right]. \qquad (23)$$

Hawk, Dove, and Sneaker

When the cost of fighting is $< c_7^*$ but $> c_8^*$, the three strategies coexist within the population, and the expected proportions of each strategy at equilibrium $\{p^*, q^*, r^*\}$ satisfy this condition: $W_H = W_D = W_S$.

From these results, we can define the solution of the game according to the loss of energy associated with fighting c:

When $c < c_5^*$ and $c < c_6^*$, neither dove nor sneaker can invade a group in which all individuals play hawk and the ESS is $\{1, 0, 0\}$.

When $c > c_5^*$ and/or $c > c_6^*$, $c > c_7^*$, and $c > c_8^*$, hawk and dove coexist within the population and the ESS is $\{p^*, 1 - p^*, 0\}$, with the expression of p^* given by equation (19).

When $c > c_5^*$ and/or $c > c_6^*$, $c < c_7^*$, and $c < c_8^*$, hawk and sneaker coexist within the population and the ESS is $\{1 - r^*, 0, r^*\}$, with the expression of $p^* = 1 - r^*$ given by equation (22).

When $c > c_5^*$ and/or $c > c_6^*$, $c < c_7^*$, and $c > c_8^*$, hawk, dove, and sneaker coexist within the population, and the frequencies of each strategy at equilibrium $\{p^*, q^*, r^*\}$ satisfy $W_H = W_D = W_S$.

Predictions

As above, the expected proportion of intruders playing hawk can never decline to 0 and, of the three appropriation strategies, only playing hawk can exist as a pure ESS. Thus, once again, there is no condition in which group members should share the resources without any sign of overt aggression. However, by allowing sneakers to find their own food, we now predict lower frequencies of hawk and hence lower frequencies of aggressive interactions than in the previous model. Another consequence of allowing sneakers to find food is a narrower range of conditions under which to expect the coexistence of all three appropriation strategies (fig. 1*B*).

The likelihood of hawk being an ESS is again greatest when groups are small (fig. 1*B*) because the time and energetic costs of fighting are low. This prevents sneaker or dove from invading a population of hawks. When the number of competitors is large, in contrast, the time required to chase other competitors is increased, allowing sneakers to obtain a larger fraction of the joiner's share. Increasing intruder number should therefore decrease the frequency of hawk and increase the frequency of sneaker (fig. 1*B*). As the frequency of playing hawk declines, however, so does the quantity of resource that can be gained by playing sneaker. This means that, eventually, dove is able to invade in large groups, particularly if clump density is high (low τ) and the frequency of sneakers decreases with group size (fig. 1*B*).

Playing dove is most effective when hawk and sneaker suffer large energetic costs of fighting, such that they are unlikely to obtain sufficient resources to cover these costs. Therefore, increasing c is predicted to increase the frequency of dove (fig. 2*B*). As in the previous model, there is little effect of the energetic cost of fighting on the frequency of hawk.

Increasing the mean contest duration raises the quantity of resource that can be gained by an animal playing sneaker but decreases the resource available to victorious hawks returning to the patch. We then predict, as in the above version of the model (where sneakers could not find their own resources), that increasing the mean contest duration reduces the individuals' level of aggressiveness but in-

creases the frequency of sneaker (fig. 3*B*). In contrast to the previous model, however, we now predict that the frequency of dove should first increase and then decrease rapidly as the mean contest duration increases (fig. 3*B*). As in the previous model, the frequency of hawk and sneaker should increase with increasing size of the joiner's share, whereas the frequency of dove is predicted to increase as the finder's advantage increases and to decrease with increasing patch richness (fig. 4*B*). When food patches are very rich or when the finder's advantage is very small, the benefits of aggressive appropriation are very large in relation to the cost of fighting. Moreover, given that the number of aggressive intruders is large under these conditions, the time spent fighting is long, allowing sneakers to obtain a large fraction of the joiner's share. As the patch richness decreases, in contrast, the benefits of aggressive appropriation decrease, which in turn reduces the success of the sneaker strategy. So decreasing the joiner's share should decrease the frequency of both hawk and sneaker but increase the frequency of dove.

Discussion

The presence of the distraction sneaker strategy introduces a number of important differences to games of resource defense, compared with the usual two-strategy hawk-dove games. Our three-strategy hawk-dove-sneaker game predicts lower proportions of hawk and hence lower frequencies of aggressive interactions within groups compared with previous two-strategy hawk-dove games (Sirot 2000; Dubois et al. 2003). Previous game-theoretic analyses of aggression predict a large increase in the frequency of aggressive individuals when the value of resources for which animals compete is large because the energetic costs of fighting become comparatively small (Sirot 2000; Dubois et al. 2003). Our analysis shows that if aggression becomes common (hawks are numerous), the increasing quantity of time spent chasing aggressive competitors offers an opportunity for distraction sneakers to gain a large portion of the finder's share. As a consequence, the quantity of energy that can be gained by the victorious aggressive hawk becomes insufficient to cover its fighting costs, leading to a reduced level of aggressiveness compared to situations without the sneaker strategy. Sneakers therefore reduce the incidence of aggressive encounters by imposing an additional cost on the use of the escalated hawk strategy. Allowing sneakers to search for undiscovered resources and to appropriate resources uncovered by conspecifics further reduces the expected frequency of aggression within groups. Thus our model predicts that the extent to which sneakers decrease the frequency of ag-

gression within groups will depend on their likelihood of suffering an attack from a returning hawk and whether searching for unchallenged resources and sneaking are compatible activities. Given that escalated fighting has been reported to be relatively uncommon in most species (Enquist et al. 1990), our three-strategy model may provide a more realistic depiction of the economics of resource defense than those of previous game-theoretic models (Sirot 2000; Dubois et al. 2003). If we are correct, then we predict that the existence and abundance of opportunities for distraction sneaking would predict the frequency of aggression. For example, a resource that can be carried by the owner will provide fewer sneaking opportunities and promote higher levels of aggression than patches that are left unguarded during defense. Fulmars (*Fulmarus glacialis*) may provide just such an example. Large fish carcasses provide ample sneaking opportunities, attract many birds, and promote scramble competition, whereas smaller carcasses are carried and monopolized by owners who engage in intense fights with intruders (Enquist et al. 1985).

Our models predict that the proportion of animals that avoid conflicts by leaving the resource (playing dove) should be very low under most conditions. Given that the expected proportion of hawk can never reach 0, playing dove is ineffective in most circumstances because a dove that faces an aggressive competitor always leaves all of the remaining resource to the hawk without a fight and hence, at best, can obtain only the finder's advantage. An animal that plays sneaker, in contrast, is not constrained to the finder's share but, rather, can take advantage of all remaining food while its owner is busy chasing away intruders. Sneakers, therefore, can do better than the dove strategy, especially when the probability of being attacked by a hawk is relatively low or when the energetic cost resulting from an attack is relatively small. The ESS for the game in these conditions is a combination of hawk and sneaker players. However, given that animals playing sneaker do not leave before the patch is totally depleted, contrary to those playing dove, the likelihood that the three strategies will coexist within the population is maximal when food density is high because the time spent in fights is then likely longer than the time required to uncover an equivalent replacement food patch.

In an earlier two-strategy hawk-dove game adapted to a group foraging scenario, Dubois et al. (2003) predicted that an increase in the finder's advantage should decrease the expected proportion of hawks within groups because the value of the remaining resource for which animals compete becomes insufficient to cover the costs of fighting. The three-strategy hawk-dove-sneaker game, in contrast, predicts that the finder's advantage should not have any marked influence on the proportion of encounters re-

sulting in aggression. This arises because increases in the finder's advantage give way to two opposing effects. Increasing the finder's share reduces the benefits of fighting because the remaining fraction of the patch is less likely to be worth the fight. Increasing the finder's advantage also reduces the amount of food available to sneakers and so leads to a reduction in the frequency of this tactic, which increases the payoffs to aggression. These two opposing forces mitigate the effect that the finder's share can have on the frequency of aggression when sneakers are present. We expect therefore that factors that influence the finder's advantage will strongly affect the expected level of aggression within groups only when distraction sneakers are absent.

Simple two-strategy hawk-dove games (Sirot 2000; Dubois et al. 2003) predict that the frequency of aggression should decrease as the energetic expenditure of contests increases. Our three-strategy hawk-dove-sneaker game, however, predicts little or no effect of the energetic costs of fights on the expected frequency of aggression because we assume that the cost of being attacked is the same as the cost of fighting. Increasing the costs of aggression increases the costs of fights but also increases benefits because less food is lost to sneakers as the cost of aggression increases and sneakers switch to another tactic. The net result is little to no effect of aggressive cost on the frequency of fighting when sneakers are present.

Our model predicts that the proportion of aggressive competitors and hence the proportion of encounters resulting in aggression should decrease with increasing competitor number. Observations of giant danio fish (*Danio aequipinnatus*) defending a food patch (Chapman and Kramer 1996) and male dung flies (*Scatophaga stercoraria*) defending a cowpat (Borgia 1980) provide strong support for this prediction. Two-strategy hawk-dove games predict either that aggression should increase with competitor number (Sirot 2000) or that it should reach a peak at intermediate competitor densities in a group foraging context (Dubois et al. 2003). Our game predicts a decline because it assumes that all nonsneakers will converge on every food discovery and aggressively challenge its owner. The owner therefore faces an increase in the costs of fights with an increase in group size such that the remaining food becomes increasingly unlikely to be worth the fight. We expect that if we had relaxed this assumption of all nonsneakers systematically challenging the food discoverer, a dome-shaped relationship like the one predicted in Dubois et al. (2003) would have been expected (see Grant et al. 2000). It would therefore be useful for future games to permit frequencies of challengers to vary according to the payoffs expected from using this strategy. Because the benefits of performing sneaking behavior depend on the number of intruders and hence on the proportion of in-

dividuals playing scrounger, further extensions to this model should take into account both aspects.

To simplify the analysis, we have assumed in this study that animals do not differ in their fighting abilities and are equally capable of detecting unchallenged resources. Recent findings, however, suggest that almost all alternative phenotypes are due to alternative tactics within a conditional strategy. In salmon mating systems, for instance, small males usually employ a behavioral tactic that involves sneaking, while larger males employ a behavioral tactic that employs fighting. So adult salmon males choose their behavioral tactics, fighting or sneaking, based on their competitive fighting ability. Nevertheless, the same individual may adopt both tactics at different times of life. Research in several systems has demonstrated that the points at which animals switch between alternative tactics are sensitive to how ecological and demographic events influence tactic fitness (Gross 1996). This indicates that populations most often experience frequency-dependent selection and condition-dependent selection simultaneously. As a consequence, assuming that individuals may differ in their fighting ability would have probably changed the expected level of aggression but not the qualitative results of this study. For instance, we suspect that the relative size of sneakers compared to hawks will be an important variable influencing sneaker strategy. In salmon mating systems, the ability of sneakers to court and mate with females in the absence of a hawk (i.e., discover a patch) probably increases with the relative body size of the sneaker (Hutchings and Myers 1988). Similarly, the costs of attack increase when sneakers are small compared to hawks. In Atlantic salmon (*Salmo salar*), sneakers at only 2% of the weight of adult males are often killed during mating competition (Hutchings and Myers 1987). Because sneakers are relatively larger in Pacific than in Atlantic salmon, we would expect higher levels of aggression among males in the former than in the latter. In both cases, however, we predict that sneaking behavior should become more profitable than fighting behavior as densities increase and male-male competition intensifies, selecting for a shift of the critical body size to a larger one.

In conclusion, our game suggests that the presence of distraction sneaking within groups will profoundly affect the extent to which factors such as competitor density, food abundance, and the costs of fights will affect the levels of aggression within groups. Studies of resource defense have been interested in characteristics that make a resource defendable or not. Our study points to the potential for sneaking as a major contributor to resource defense. It may be profitable, therefore, to explore the characteristics of resources that promote sneaking because this may be a convenient way of predicting the extent of aggression within groups.

Acknowledgments

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