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Food unpredictability drives both generalism and social foraging: a game theoretical model

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Resource predictability can influence foraging behavior in many ways. Depending on the predictability of food sources, animals may specialize on a few food types or generalize on many; they may aggressively defend feeding territories or nonaggressively share food with others. However, food defense and diet breadth have generally been studied separately. In this paper, we propose that variation in resource predictability could drive both of them together. We construct a game theoretic model to test whether situations in which resources are unpredictable might favor both generalism (the ability to use multiple food types) and nonaggressive social foraging. Our model predicts that the proportion of social generalists is highest when resources are unpredictable, whereas a predictable resource distribution favors territorial specialists. We discuss our result within the context of animal cognition research, where diet breadth and social foraging are associated with the 2 dominant views of the evolution of cognition: the "ecological" and the "social brain" hypotheses. Our results suggest that social and dietary demands on cognition might be less independent than is often assumed. *Key words:* ecological intelligence, game theory, generalism, hawk–dove, resource predictability, social brain hypothesis, social foraging. *[Behav Ecol 19:836–841 (2008)]*

Animals differ in the variety of foods they consume as well as in the size and structure of the groups in which they feed. The degree to which animals specialize on narrow diets or generalize on broader ones, as well as the degree to which they feed alone or in groups, have been the subject of large, but separate, bodies of theoretical and empirical research (diet: Levins and MacArthur 1969; Futuyma and Moreno 1988; Kassen 2002. Social foraging: reviewed in Giraldeau and Caraco 2000).

Social organization varies on a continuum that goes from year-round territorial exclusion (leading to solitary foraging or tolerance of a mate and offspring) to participation in large, nonaggressive groups. One theory that has proven useful in accounting for this variation is resource defense theory, first proposed by Brown (1964). This theory states that when food occurs in moderately dense patches that are stable in space and time, animals may profit more from excluding others than from sharing. At the other extreme, if food occurs in large clumps that are difficult to predict in space and time, it may be more profitable to forage in mobile groups than to attempt to defend the resources against others. There is growing empirical evidence that this theory can successfully predict the conditions in which animals should adopt aggressive modes of solitary foraging or nonaggressive modes of social foraging. For example, Zenaida Doves (*Zenaida aurita*) and Convict Cichlids (*Cichlasoma nigrofasciatum*) switch from nonaggressive group foraging to food defense when resources become clumped and predictable (Grant and Guha 1993; Goldberg et al. 2001). Social foraging may also be beneficial in unpredictable environments if individuals provide others with information about food, an idea that is supported both by a recent model (Hancock and Milner-Gulland 2006) and by experiments with European Starlings (*Sturnus vulgaris*; Rafacz and Templeton 2003).

The same factors that drive variation in social foraging might also drive variation in diet breadth. An unpredictable and/or variable resource distribution is thought to favor generalism (MacArthur and Levins 1967; MacArthur 1975; reviewed in Futuyma and Moreno 1988). Although conservative specialists may thrive only when their preferred food type is abundant and predictable in space and time, ephemeral foods that are difficult to find might instead favor opportunistic generalism. Empirical evidence of this comes primarily from field research on invertebrates (Moldenke 1975; Krasnov et al. 2006; Šimková et al. 2006). Experiments with deer mice (*Peromyscus leucopus*) have also shown that when resource availability and resource type are unpredictable, individuals adopt more generalist foraging behavior (Gray 1981).

Diet breadth and social foraging each correspond to one of the dominant theories for the evolution of animal cognition. It has been proposed that generalism—eating a wide variety of foods—requires greater cognitive abilities than specialization because it requires the ability to process more information about multiple food types (Reader and MacDonald 2003), maintain a larger repertoire of foraging patterns (Changizi 2003), and show a greater degree of behavioral flexibility (Reader and Laland 2002; Ratcliffe et al. 2006). Alternatively, social foraging is thought to impose greater demands on the brain than does foraging alone because it requires a larger "neural computer" to store and manipulate information about social relationships (Humphrey 1976; Dunbar 1998). The 2 views, most often referred to as the ecological (Parker and Gibson 1977; Eisenberg and Wilson 1978; Byrne 1997) and social brain (Jolly 1966; Byrne and Whiten 1988; Flinn 1997) theories of cognition, are usually presented as alternatives (e.g., Seyfarth and Cheney 2002).

Although resource unpredictability has been examined in the literature on diet breadth and, separately, that on social foraging, its potential role in driving the 2 together has not been considered. In this study, we test whether the proportion

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of generalists and nonaggressive foragers increases when resources are unpredictable in the environment. We model social foraging and generalism using a game theoretical model. Game theory has been used as a tool for understanding the dynamics of aggressive interactions between individuals (Maynard Smith and Price 1973). More recently, hawk–dove games have begun to explore the conditions under which animals may forage in nonaggressive social groups (Sirot 2000). These games have expanded to include factors such as the asymmetry of players, multiple interactions between players (Dubois et al. 2003), and additional strategies such as "sneakers" (Dubois et al. 2004).

In this paper, we construct a game theoretic model that includes variation in the ability of individuals to use multiple resources (specialist vs. generalist) as well as variation in the use of aggression to exclude others from food (territorial hawk vs. social dove). We find that unpredictability of resources in the environment can drive a population toward both feeding generalism and nonaggressive food sharing.

THE MODEL

All parameters of the model are listed in Table 1. We consider a group of G foragers that exploit 2 different resources. Each resource is characterized by its profitability F_1 and F_2 as well as by its abundance and by its predictability. Both resource abundance and predictability affect the rate at which food items are encountered. We denote the probability that a forager discovers a resource of type 1 at a given time by λ_1 and the probability that a forager discovers a resource of type 2 by λ_2. We create the simplest distinction between generalist and specialist feeding techniques: Consumers can be either specialists of one or the other resource (i.e., they search and consume only 1 of 2 resource types) or generalists. The degree of predictability of resources (α) varies between 0 and 1. When resources are unpredictable (i.e., $\alpha = 0$), both generalists and specialists have the same probability of discovering food items. When the degree of predictability of the food increases, so does the rate at which specialists encounter their preferred food items. Hence, the probability that a specialist discovers a resource of type 1 is $\lambda_1^{(1-\alpha)}$. We assume that generalists are less efficient in their food extraction than are specialists: Specialists get either F_1 or F_2 food items, whereas generalists only get a fraction x ($0 \leq x \leq 1$) of each type of resource they encounter.

Table 1
Parameters used in the model

Symbol	Meaning
λ_i	Probability that a generalist discovers a resource of type i (with $i = 1$ or 2) at a given time
α	Degree of predictability of resources
$\lambda_i^{(1-\alpha)}$	Probability that a specialist of type i (with $i = 1$ or 2) discovers a resource at a given time
F_i	Quantity of energy that can be gained from a resource of type i (with $i = 1$ or 2)
x	Fraction of energy that a generalist can extract from each resource
C	Energetic cost of fighting
G	Number of foragers within the group, including both generalists and specialists
p	Proportion of group foragers that are specialists of resource type 1
q	Proportion of group foragers that are specialists of resource type 2
r	Proportion of group foragers that are generalists of both types of resources
p'	Proportion of specialists of type 1 that play Hawk
q'	Proportion of specialists of type 2 that play Hawk
r'	Proportion of generalists that play Hawk
β	Probability that a resource discovered by a forager is not discovered simultaneously by any of the other (G−1) foragers

Resources cannot be exploited by more than 2 competitors, and when the same resource is discovered simultaneously and, therefore, contested by 2 competitors, each of them can adopt 1 of 2 strategies: (territorial) hawk or (social) dove. We assume that contestants do not differ in their fighting abilities. Thus, if both contestants play hawk, they each have a probability of 50% of obtaining the whole contested resource while both suffer an energetic cost of fighting C. On the other hand, if both contestants play dove, the food is shared equally between the 2 competitors at no cost. If only one contestant plays hawk, the dove retreats and the aggressive competitor gets the whole resource.

Given that we have 3 exploitation strategies (i.e., specialists of type 1, specialists of type 2, and generalists) and 2 appropriation strategies (i.e., hawk and dove), we have 6 different strategies: $\mathrm{S_1H}$, $\mathrm{S_1D}$, $\mathrm{S_2H}$, $\mathrm{S_2D}$, GH, and GD. $W(\mathrm{S_1H})$ thus represents the payoff of a specialist that exploits only resources of type 1 and is aggressive against other foragers, $W(\mathrm{GH})$ is the payoff of a generalist that is aggressive, $W(\mathrm{S_2D})$ is the payoff of a specialist that exploits only resource 2 and is nonaggressive, and so on. The parameters p, q, and r represent the proportion of specialists of type 1, specialists of type 2, and generalists, respectively, with $p + q + r = 1$, whereas p', q', and r' denote the respective proportion of individuals playing hawk among them. Resource exploitation time is assumed to be negligible, and all group members (G) search for resources of type 1 or 2, at any given time. It is important to note that generalists search for both types of resources simultaneously while specialists search for only one type of resource. At any given time, therefore, the number of foragers searching for resources of type 1 is equal to the number of specialists of type 1 plus the number of generalists (i.e., $p\mathrm{G} + r\mathrm{G}$), whereas the number of foragers searching for resources of type 2 is equal to the number of specialists of type 2 plus the number of generalists (i.e., $q\mathrm{G} + r\mathrm{G}$). In addition, as specialists and generalists do not have the same efficiency at discovering food items, the probability that one resource is discovered simultaneously by at least 2 foragers does not depend only on the total number of foragers searching for prey of type 1 or 2 but also on the relative proportion of generalists and specialists searching for either prey type. Hence, the gain expected by each individual is affected by both the strategy it uses and the values of p, q, and r. For instance, the average gain expected for a specialist of type 1 that plays hawk is $W(\mathrm{S_1H})$:

$$W\left(\mathrm{S_1H}\right) = \lambda_1^{(1-\alpha)} \times \left\{\beta \mathrm{F}_1 + \left(1-\beta\right)\left[u\left(\frac{F_1}{2} - C\right) + vF_1\right]\right\}. \tag{1}$$

The first term of this equation, $\lambda_1^{(1-\alpha)}$, corresponds to the probability that the animal discovers a resource of type 1 at a given time, whereas the parameters β and $(1-\beta)$ represent the probability that the animal can exploit the resource alone or must compete with another group forager to get the F_1 units of energy, respectively. The probability β depends on both the number of foragers that are searching for resources of type 1 simultaneously and their respective finding efficiency with:

$$\beta = (1-\lambda_1)^{rG} \times \left[1-\lambda_1^{(1-\alpha)}\right]^{pG-1}. \qquad (2)$$

The first term of equation (2) represents the probability that the resource is not discovered simultaneously by any of the rG generalists that have each a probability λ_1 of finding resources, whereas the second term represents the probability that the resource is not discovered simultaneously by any of the other ($pG-1$) specialists of type 1 that have each a probability $\lambda_1^{(1-\alpha)}$ of finding resources.

As indicated by equation (1), the food finder gets F_1 units of energy when the resource is not contested by another group forager. Otherwise, its expected gain depends on the strategy used by its opponent: If the opponent plays hawk with a probability u, they engage in an escalated fight and both competitors have the same probability of chasing away the other contestant. Conversely, if the opponent plays dove with a probability $v = 1-u$, the individual obtains the entire resource at no cost because the nonaggressive competitor retreats, leaving behind all of the remaining resource for the hawk.

As the parameters p' and r' represent the proportion of specialists of type 1 and generalists that play hawk, the probability that the opponent plays hawk is u with

$$u = \frac{p' + r'}{p + r}.$$

Using this procedure, we can estimate the average gain expected for each category of individuals and then calculate the proportion of each type of foragers for the next generation. To do that, we consider that group size is constant from one generation to the next and that the proportion of each category of individuals during each generation is proportional to the relative success of each strategy during the previous generation. Thus, once we have calculated the average expected gains, we can deduce the frequency at which each strategy will be used for the next generation and repeat this procedure over consecutive generations until the frequency of each strategy reaches a stable point.

RESULTS

In our model, as food becomes more predictable, both the level of aggressiveness and the proportion of specialists increase. Accordingly, the model predicts that the proportion of nonaggressive (social) generalists is greatest when food is unpredictable (Figure 1). This occurs because food predictability affects the rate at which specialists can detect new resources, whereas it has no effect on the food finding efficiency of generalists. Thus, as food becomes more predictable, individuals benefit from specializing. Further, as specialists are more efficient not only in their finding efficiency but also in their food extraction abilities, the quantity of food they can obtain from a resource is more likely to exceed the cost of fighting, thereby allowing specialists to become more aggressive.

The model also suggests that the number of foragers should have a greater effect on aggressiveness than on generalism. Increasing the number of foragers is predicted to increase the proportion of individuals playing hawk among both specialists and generalists (Figure 2), whereas the proportion of specialists should remain relatively constant when the number of competitors within the group increases. Similarly, the energetic cost of fighting has almost no effect on the expected proportion of generalists and specialists but profoundly affects the level of aggressiveness that tends to decrease as the cost of fighting increases (Figure 3).

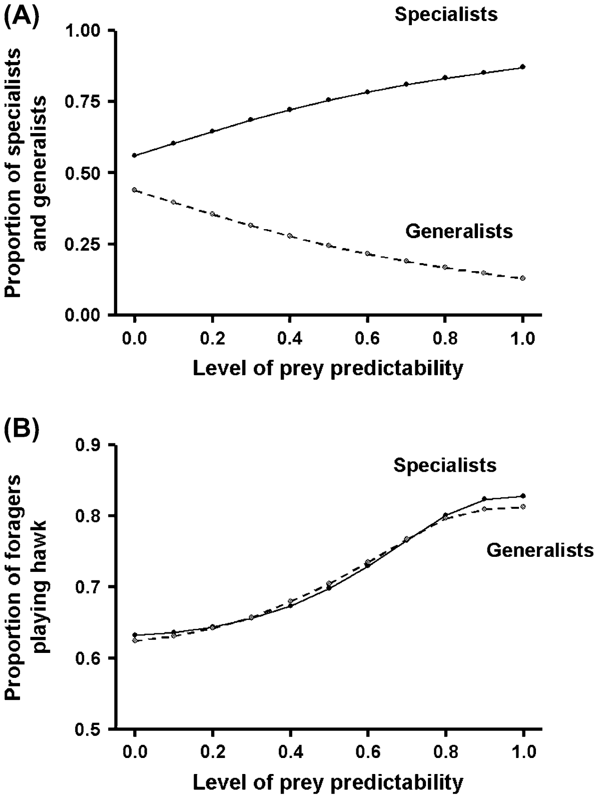

Figure 1
The expected proportion of specialists and generalists (A) and the expected frequency of individuals playing hawk (B) in relation to the degree of predictability of prey (α). In this figure, $F_1 = F_2 = 5$, $\lambda_1 = \lambda_2 = 0.2$, $C = 1$, $G = 10$, and $x = 0.8$.

Finally, the model predicts that the proportion of generalists should be very low when the fraction of food they can extract from a prey is small compared with the quantity of energy that can be gained by specialists (Figure 4A), and consequently the level of aggressiveness is lower for generalists than for specialists when generalists' efficiency is low (Figure 4B).

DISCUSSION

In this study, we expand current game theoretic models of foraging behavior to test how resource predictability simultaneously influences diet breadth and social foraging. Our model demonstrates that an unpredictable resource distribution can drive a population toward both feeding generalism and nonaggressive food sharing.

Diet breadth and social foraging have generally been treated separately in the literature, and bringing these together may have implications for theories in ecology and in animal cognition. Experimental tests in which food predictability has been manipulated have focused on the effects of either diet breadth (Gray 1981) or social foraging strategy (Grant and Guha 1993; Goldberg et al. 2001). Our results suggest that measuring both of these variables within a single system where resource predictability is manipulated could provide a new perspective on how variation in foraging behavior evolves. Such a test could be applied to a variety of systems where one or the other of these variables has already been measured, including insects (Krasnov et al. 2006, Šimková et al. 2006), fish (Grant and Guha 1993), birds (Goldberg et al. 2001), and mammals (Gray 1981). Researchers of animal cognition have proposed that there are 2 distinct pressures on the evolution of brains

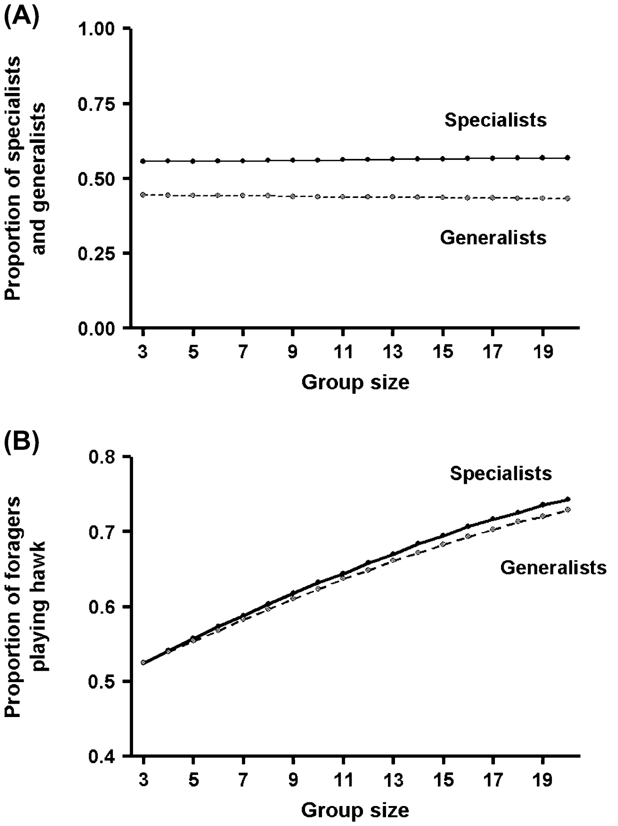

Figure 2
The expected proportion of specialists and generalists (A) and the expected frequency of individuals playing hawk (B) in relation to the group size (G). See Figure 1 for values of parameters F_1, F_2, λ_1, λ_2, C, and x. In this figure, $\alpha = 0$.

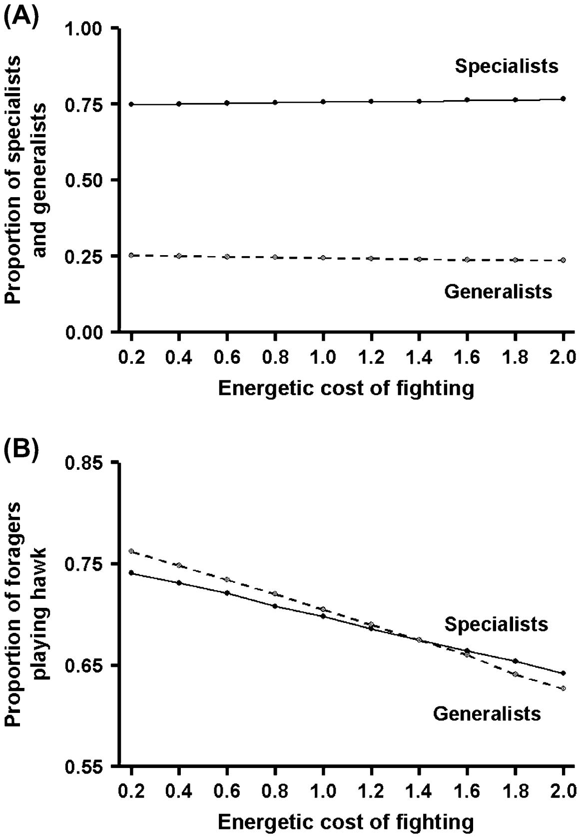

Figure 3
The expected proportion of specialists and generalists (A) and the expected frequency of individuals playing hawk (B) in relation to the energetic cost of fighting (C). See Figure 1 for values of parameters F_1, F_2, λ_1, λ_2, and x. In this figure, $\alpha = 0.5$.

and intelligence: social and ecological. Although social and ecological pressures have traditionally been treated separately, some workers have pointed out that sociality is not independent of ecology (e.g., Dunbar and Shultz 2007), and a recent study showed that brain size was associated with both habitat complexity and social organization in Cichlid fishes (Pollen et al. 2007). Our results further support the idea that ecological and social variables should both be included in empirical studies of behavior and/or cognition.

In our model, we use simple variables to describe variation in foraging behavior. However, our measures parallel those used in empirical studies of behavior and cognition. For example, diet breadth is positively correlated with brain size in a variety of taxa, including primates (Harvey et al. 1980; Reader and MacDonald 2003), small mammals, (Gittleman 1986), and beetles (Farris and Roberts 2005). Some authors have emphasized the importance of flexibility within the ecological intelligence hypothesis (Lefebvre et al. 1997, Reader and Laland 2002), and recent evidence suggests that generalism and flexibility may be related to each other; habitat generalism is positively correlated with innovativeness in foraging behavior in North American birds (Overington SE, Griffin AS, Sol D, Lefebvre L, unpublished data).

Based on Brown's (1964) resource defense theory, we consider 2 extremes of social foraging behavior: territoriality and peaceful food sharing. We use nonaggressive behavior as a measure of the degree to which an individual will forage socially, based on evidence from empirical studies demonstrating that aggressiveness is lowered when animals switch from solitary to social foraging (Barash 1974; Wiggins 1991). Empirical work should be done to expand on our finding and to incorporate other measures of social behavior, such as group size (Sawaguchi and Kudo 1990, Dunbar and Bever 1998), social complexity (Burish et al. 2004), and social network size (Kudo and Dunbar 2001). Our findings may be relevant both within and across species. There is emerging evidence to suggest that generalist feeding habits play a role in a species' ability to cope with changes in the environment. Comparative studies of birds show that large-brained generalist species have experienced the least amount of population decline within the last 40 years in Britain (Shultz et al. 2005) and that innovative birds are more successful than their less innovative counterparts when introduced to new habitats (Sol et al. 2005). Similarly, a study of Bornean butterflies found that generalist species were more resistant to El Nino caused disturbances (Charrette et al. 2006). In primates and small mammals, the fact that frugivores have relatively larger brains than do folivores has been attributed to differences in the predictability and distribution of food sources (Harvey et al. 1980), and the same rationale was used to explain brain size differences between frugivorous and insectivorous bats (Eisenberg and Wilson 1978). Incorporating social measures into these large-scales studies could provide a broader view of the way rapidly changing environments influence, or select for, foraging behavior.

Our prediction that aggressiveness should increase with group size and decrease as fighting becomes costly are both consistent with previous work on social foragers (Sirot

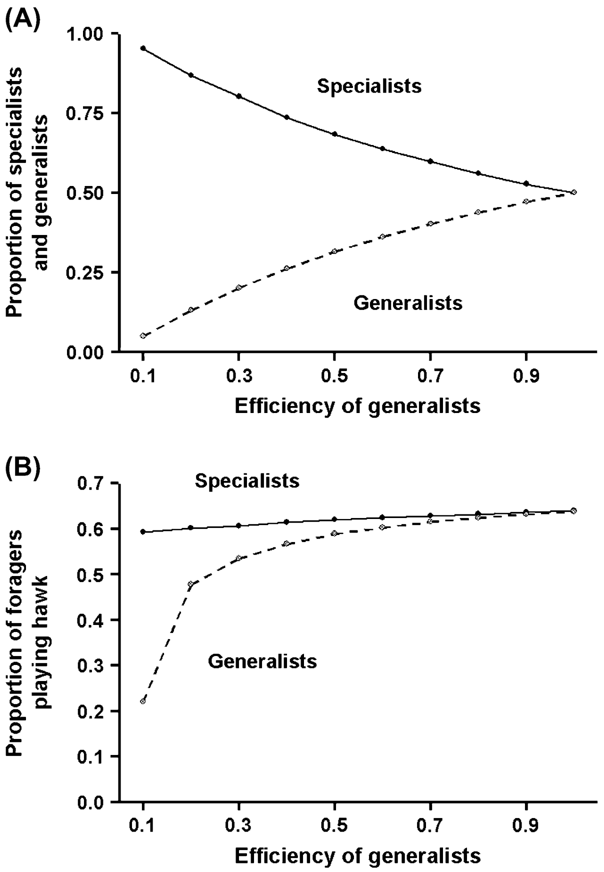

Figure 4
The expected proportion of specialists and generalists (A) and the expected frequency of individuals playing hawk (B) in relation to the proportion of food obtained (i.e., efficiency) by generalists from each resource (x). See Figure 1 for values of parameters F_1, F_2, λ_1, λ_2, and C. In this figure, $\alpha = 0$.

2000). However, increasing the number of competitors or the cost of fighting has no effect on feeding specialization. Indeed, the relationship between specialization and aggression may not be a perfect one as these variables are influenced by other parameters in different ways. For example, the shapes of the curves differ for the proportion of specialists and the proportion of territorial hawks with increasing unpredictability of resources (Figure 1). This is likely due to the fact that resource predictability has a strong effect on the rate at which specialists detect food, and therefore on the quantity of food they can obtain per unit of time, but does not affect generalists. Therefore, as resources become more predictable, individuals can increase their food intake rate by specializing on one particular food type. On the other hand, the level of aggressiveness of specialists and generalists does not increase monotonically with resource predictability in our model. This is because the probability of simultaneous food discoveries depends both on the rate at which individuals detect food items and the number of foragers searching for each type of prey, and both of these parameters vary with the level of resource predictability. Thus, when resources are unpredictable, specialists do not find food items more frequently than generalists. However, as resources become more predictable, the proportion of specialists increases, as does their food finding efficiency. Simultaneous food discoveries therefore become more frequent and increase the likelihood of an aggressive encounter.

Other findings from our model are consistent with ecological theory. For example, Levins (1962) asserted that if a strong trade-off exists between foraging efficiency and foraging generalism, then specialization is favored. Our model shows that the proportion of generalists should remain low when specialization confers a significant advantage in terms of the energy that can be extracted from prey (Figure 4A).

In this paper, we describe a model that may help us understand the conditions favoring both generalism and nonaggressive social foraging. We hope that our model will stimulate further empirical work that combines meaningful measures of both sociality (e.g., social complexity and social bond formation) and foraging strategy (e.g., generalism, flexibility, and innovativeness). The aim should be to create a cohesive framework enabling us to further our understanding of the ecological conditions that drive the evolution of brains and intelligence across taxa.

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