

Social Information on Fear and Food Drives Animal Grouping and Fitness

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ABSTRACT: Empirical studies in select systems suggest that social information—the incidental or deliberate information produced by animals and available to other animals—can fundamentally shape animal grouping behavior. However, to understand the role of social information in animal behavior and fitness, we must establish general theory that quantifies effects of social information across ecological contexts and generates expectations that can be applied across systems. Here we used dynamic state variable modeling to isolate effects of social information about food and predators on grouping behavior and fitness. We characterized optimal behavior from a set of strategies that included grouping with different numbers of conspecifics or heterospecifics and the option to forage or be vigilant over the course of a day. We show that the use of social information alone increases grouping behavior but constrains group size to limit competition, ultimately increasing individual fitness substantially across various ecological contexts. We also found that across various contexts, foraging in mixed-species groups is generally better than foraging in conspecific groups, supporting recent theory on competition-information quality trade-offs. Our findings suggest that multiple forms of social information shape animal grouping and fitness, which are sensitive to resource availability and predation pressure that determine information usefulness.

Keywords: social groups, public information, fitness trade-off, risk dilution, predator avoidance, local enhancement.

Introduction

Animals obtain sensory information through direct interactions with their environment (i.e., personal information) or by observing the positions or behaviors of other animals (i.e., social information; sensu Danchin et al. 2004; Dall et al. 2005; Schmidt et al. 2010). A rapidly growing body of empirical work suggests that the use of social in-

formation can fundamentally influence animal behavior and sociality, with broad implications for ecology and evolution (Danchin et al. 2004; Seppänen et al. 2007). A spate of recent theoretical publications suggests that individual decisions, mediated by social information, can drive complex vertebrate social behaviors, such as grouping (Hildenbrandt et al. 2010; Sumpter 2010) and group vigilance (Beauchamp et al. 2012). However, there remains a gap in general theory regarding the importance of social information as a driver of social grouping and the fitness benefits thereof (Cortes-Avizanda et al. 2014).

Animals can produce social information intentionally through signals (e.g., alarm calling) or unintentionally through cues (e.g., through evasive or foraging movements), and this information can spread rapidly over wide spaces and even across distantly related taxa. For example, social information via mechanical cues can travel rapidly over tens of kilometers to connect the movements of shoaling herring (Makris et al. 2009), and by eavesdropping on alarm calls of birds, other bird taxa—as well as mammals and reptiles—can better avoid predators (Zuberbühler 2001; Templeton and Greene 2007; Vitousek et al. 2007). Though social information can be used in diverse contexts—such as to establish dominance hierarchies, determine mating opportunities, and select breeding habitat (Schmidt et al. 2015)—it is most commonly exchanged regarding resources and predators (Danchin et al. 2004). Because social information can improve foraging and predator avoidance behavior, it has been proposed as a fundamental driver of the formation of both temporary and permanent single-species and mixed-species animal groups.

Grouping is ubiquitous across taxa and systems—including birds (Sridhar et al. 2009), mammals (Stensland et al. 2003), and fish (Ward et al. 2002)—and can take place between conspecifics and heterospecifics (e.g., Kotagama and Goodale 2004). These associations vary along a continuum of social and temporal cohesiveness: for instance, mixed-species groups of birds range from temporary foraging aggregations to highly complex systems that exhibit year-

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round group territoriality (Greenberg 2000). However, the ultimate mechanisms underlying group formation and maintenance remain a frontier in research at the interface of ecology, evolution, and behavior. When animals that share predators form a group, each group member can benefit directly through dilution of predation risk, even if group members do not communicate (i.e., do not share social information). This is because the risk of being killed during an attack is hedged across the number of individuals that are aggregated in space, as long as the predator cannot catch all of the individuals in one attack (Foster and Treherne 1981). Dilution of risk can also occur through an inherent confusion effect, in which larger numbers of fleeing individuals confuse predators and thus reduce their lethality (Neill and Cullen 1974).

The benefits of animal grouping behavior, however, extend beyond risk dilution, if we consider the presence of social information. Because information degrades over time and space, it is obtainable (and of use) only when in proximity to other individuals (Stephens 1989; Fernandez-Juricic and Kacelnik 2004; Fernandez-Juricic and Kowalski 2011). For instance, the benefits of social information flow in bird groups are restricted to small neighbor distances, which may explain why species aggregate at certain spatial scales (Fernandez-Juricic and Kacelnik 2004; Fernandez-Juricic and Kowalski 2011). Social information allows animals to observe one another's flight responses to an approaching predator, allowing for collective vigilance to enhance predator avoidance (i.e., the many-eyes effect; Pulliam 1973; Powell 1974). Vertebrates also commonly obtain social information about predators by eavesdropping on the alarm calls of other species both within (Langham et al. 2006; Magrath et al. 2009, 2015; Fallow and Magrath 2010; Carrasco and Blumstein 2012) and across (Rainey et al. 2004; Lea et al. 2008; Ito and Mori 2010) taxa. Similarly, the act of successfully foraging in a habitat patch by one animal can alert others nearby to valuable foraging opportunities (Waite and Grubb 1988; Templeton and Giraldeau 1995, 1996; Smith et al. 1999), and this has been shown across species that overlap in their foraging niche, for example, mixed groups of heron (Caldwell 1981) and carp and tilapia (Karpus et al. 2007). However, benefits to grouping do not come without costs; chief among them is increased competition, which could be exacerbated by social information (i.e., foraging animals and the information they produce can attract competitors). Furthermore, more closely related individuals (i.e., those with greater niche overlap) can provide more relevant social information to one another, but they can also compete more intensely for resources.

Researchers have recently proposed that an information quality-competition trade-off could select for the sharing of social information more strongly among heterospecifics than among conspecifics (Monkkonen et al. 1999;

Seppänen et al. 2007). Yet in some mixed-species groups of birds, species of similar size and in similar foraging guilds were more likely to associate than less similar species (Sridhar et al. 2012). Thus, the benefits of social information from closely related or ecologically similar species may help defray the competitive costs of associating with them. On the other hand, many mixed-species groupings of birds are led by specific information-producing species that produce a disproportionate amount of information about predation risk and may be considered keystone informant species (Schmidt et al. 2010; Contreras and Sieving 2011; Magrath et al. 2015). Such species more reliably and frequently signal the presence of a predator (Morse 1973; Gaddis 1980; Goodale and Kotagama 2005) and disseminate this information across heterospecifics (Suzuki 2012). The information from these keystone species can reach a near community-wide interspecific audience (Goodale and Kotagama 2005; Langham et al. 2006) and has been shown empirically to influence fitness (Dolby and Grubb 1998; Forsman et al. 2002).

Because benefits of social information are difficult to separate from benefits of risk dilution, and because competition can counteract these benefits, the specific effects of social information on animal grouping behavior and fitness are challenging to measure empirically and remain unexplored in many systems. Furthermore, despite a recent surge in interest in social information via both empirical and theoretical approaches (Danchin et al. 2004; Seppänen et al. 2007; Goodale et al. 2010; Beauchamp et al. 2012), general theory that models the importance of social information in driving social behavior remains underdeveloped (Cortes-Avizanda et al. 2014). Such theory is vital both to focus empirical work on the mechanisms that underlie social grouping and to reveal the often muddled relationship between social information and animal fitness.

Here, we use dynamic state variable modeling to directly quantify, for the first time, the effects of social information—accounting for inherent properties of animal grouping (i.e., risk dilution, competition)—on grouping behavior and fitness in foraging animals. Thus, we develop a generalized framework to predict under what ecological contexts we would expect animals to respond to social information. The advantage of dynamic state variable modeling is that it allows us to consider simultaneously the fitness effects of changes in resource availability and changes in predation risk. Further, we can identify strategies that maximize fitness among various choices, making possible direct comparisons of behavior and fitness across models with and without different forms of social information. We examine the robustness of our qualitative findings across a wide, ecologically relevant parameter space while highlighting natural systems to which our model assumptions and parameterizations apply.

Methods

General Approach

To identify the effects of social information on grouping behavior and fitness, we applied dynamic state variable modeling, a flexible approach that uses an intuitive mathematical framework to produce predictions for optimal animal behavior, on the basis of the fitness consequences of behavioral alternatives (Clark and Mangel 2000). More specifically, this approach models the sequence of decisions of a focal individual and identifies those state-dependent behaviors that maximize fitness—in our case, survival. Thus, the results of our models generate predictions of the expected behavior of an animal under a range of reasonable assumptions that can apply generally to various natural systems. By looking across a wide range of parameterizations, we also examined the generality of our findings.

Our core interest was in understanding effects of different forms of social information on animal grouping behavior and fitness; thus, we allowed a focal animal to decide whether to forage alone or within groups of different size (number of members) and species composition. Furthermore, we captured the food versus safety trade-off inherent to most animal systems (Brown and Kotler 2004) by including a second decision type, which allowed the focal individual to also choose whether to forage or be vigilant (i.e., actively scan for predators) within any of the available social contexts. In our models, we considered two crossed state variables: energy of the focal animal and time of day (i.e., within the diel foraging period). Following Clark and Mangel (2000), we established an end condition that translates end of day energy into fitness and then used backward iteration to calculate an optimal state-dependent decision matrix, including projected future fitness levels for every time \times energy combination. We then evaluated and compared structurally identical models with and without different forms of social information—about resources (SIR), about predators (SIP), and the effects of a keystone informant about predators (KIP)—to quantify effects on the behavior and fitness of the focal animal. We present a base model parameterized with a reasonable set of starting estimates for natural systems, but we also systematically varied many of our assumptions to explore the sensitivity of our model results to specific parameter assignments. Thus, for parameter values detailed below, we also note additional parameter values considered (in brackets).

Model Structure

All of our models took the same form and consisted of decision-making over a single diel period of foraging activity, which we arbitrarily assumed to be 20 time steps

in length, $T = 20$ [10, 40]. In each time step, an individual had any one of 30 energy levels, $X(t)$. Thus, we constrained the number of energy units an individual could store to 30 (X_{\max}) and assumed death by starvation if $X(t)$ fell below 1. Further, because of general physiological constraints, we limited an individual's consumption to 3 units of food (translating to a maximum energy gain of 3, or 10% of the maximum energy level) per time step, and in each time step, the forager expended 1 unit of energy. Finally, we assumed a decelerating positive relationship between an individual's energy state at the end of the day (i.e., at $t = 20$) and future fitness, Φ (table 1; sensu Clark and Mangel 2000), because for a given increase in energy state, we would expect improvements in survival to be greater for animals at lower energy states (i.e., those in worse condition): $\Phi = 60X(T)/(X(T) + 0.25X_{\max})$. Though we do not define Φ by specific units, this approach allows us to consider, in general, how survivorship probabilities change with alternative decisions. Given its energy state, at each time step, the focal animal made a decision to forage or to be vigilant in solitary or in social groups of 2, 5, 10, or 20 [3, 9, 12, 30] total individuals in a habitat patch. Foraging groups were either conspecific (comprised of the focal individual's species) or heterospecific (comprised of multiple species) to yield 18 total choices. The composition of these heterospecific groups was not further defined, except in the case of the keystone informant model (described below). We modeled the average expectation of the focal individual in these groups, as discussed in more detail below; thus, the consequences of specific variation in group composition is beyond the scope of this study. We identified the optimal strategy as that which maximized the product of the probability that an individual escaped predation (the first term in eq. [1], which consists of the sum of the probabilities that, given a predator arrived, the focal individual detected the predator and escaped predation, the predator was not detected yet the focal individual still escaped, or that no predator arrived) and the expected future of that individual (the second term in eq. [1]), given the probabilities that it consumed 0, 1, 2 or 3 units of food in each time step, which is dependent on whether it is able to forage (see full parameter definition list in table 1):

$$F(x, t, T) = \max_{b,g} \{ p[d(b,g) \times \gamma_d(g) + (1 - d(b,g)) \times \gamma_n(g)] + (1 - p) \} \times \{ \lambda(b,g)[c_0(g,r)F(x-1, t+1, T) + c_1(g,r)F(x, t+1, T) + c_2(g,r)F(x+1, t+1, T) + c_3(g,r)F(x+2, t+1, T)] + (1 - \lambda(b,g))F(x-1, t+1, T) \}. \quad (1)$$

Information Use

In our models, the focal animal could use two types of information: personal information (I_i), which depended on

Table 1: Model parameter definitions

Parameter	Definition
$\Phi(x)$	Fitness associated with final, end of day energy values
$X(t)$	Current energy state of the animal
X_{\max}	Maximum energy level (state) of the animal
t	Time during the day
T	Maximum time units (t) in a day
F	Expected fitness based on the energy value (x) as well as time (t)
b	Behavioral decision: forage (f) or vigilance (v)
g	Number of other individuals in the group
p	Probability that a predator visits a patch in a time step
r	Amount of resource available in a foraging patch in a time step
$\lambda(b, g)$	Probability that the focal animal will find food, dependent (via eq. [2]) on (1) personal information about resources (I_i) acquired through foraging behavior (vs. vigilance) and/or (2) social information about resources (S_i ; eq. [3]), when available
$d(b, g)$	Probability that the focal animal will detect a predatory threat, dependent (via eq. [2]) on (1) personal information about predators (I_p) acquired through vigilance behavior (vs. foraging) and/or (2) social information about predators (S_p ; eq. [3]), when available
$O_{i,j}$	Degree of niche overlap (shared resources or predators) between the focal animal and a member of its foraging group; this affects the relevance of i th types of social information (resources [r] or predators [p]) to the focal animal; this relevance also depends on membership to j th group types (conspecific [c] or heterospecific [h]), with members of heterospecific groups producing social information that can be less relevant than that of members of conspecific groups
$\gamma_n(g)$	Probability of escape from a predator, given the predator was not detected; this value depends on the number of group members that dilute an individual's risk of predation
$\gamma_d(g)$	Probability of escape from a predator, given detection; this value depends, in part, on the number of group members that dilute an individual's risk of predation
δ	Probability that each nonfocal group member will find food, dependent on the animal's personal (s_i) and social (S_i) information about resources
N_g	Number of other members of a foraging group, up to g , that potentially found food when the focal individual did
$c_{0-3}(r, g, o_{i,j})$	Probability that the focal animal will consume 0–3 units of food in a time step, dependent on its ability to find food ($\lambda(b, g)$) and the level of resource competition (eq. [4])

the animal's behavior (b ; forage vs. vigilance), and social information (S_i), defined below. Each type of information came in i th forms (information about resources [r] or predators [p]). Information about resources or predators affected the probabilities that the focal animal would find food, $\lambda(b, g)$, or detect an attacking predator, $d(b, g)$, respectively, in a given time step:

$$\lambda(b, g) \text{ or } d(b, g) = \frac{I_i + S_i}{I_i + S_i + 1}. \quad (2)$$

We assumed that these probabilities were positive, decelerating functions of both personal and social information (e.g., predator detection increases with group size if social information about predators is present, *sensu* the many-eyes effect; Pulliam 1973) because of expected thresholds in information value across information volume (i.e., we

expect diminishing returns in fitness for the focal individual as the volume of social information increases; e.g., Kenward 1978).

Social information available to the focal animal (S_i) increased linearly with the number of nonfocal group members (g), which each obtained personal information (s_i) that they shared through their behavior. However, niche overlap ($o_{i,j}$) affected information relevance (to the focal animal) on the basis of the i th information form and j th group type (conspecific [c] or heterospecific [h]):

$$S_i = g s_i o_{i,j}. \quad (3)$$

We assumed complete feeding niche and predator overlap (i.e., shared predators), $o_{r,c} = o_{p,c} = 1$, between the focal animal and group members of a conspecific group and partial feeding niche overlap, $o_{r,h} = 0.75$ [0.5, 0.9], and full to

partial predator overlap, $o_{p,h} = 1$ [0.5, 0.75, 0.9], between the focal animal and group members of a heterospecific group, for which we would generally expect average overlap to decline with group diversity. Our assumption that mixed-species group members differ in specific feeding niche but can share the same predators is supported by work in avian, ungulate, and fish systems (e.g., Morse 1970; Strand 1988; Templeton and Greene 2007; Creel et al. 2014). Finally, to model a heterospecific group member as a keystone informant species that produces a greater amount of information on predatory threats (e.g., birds of the family Paridae in Holarctic forests; Gaddis 1980; Langham et al. 2006; Schmidt et al. 2010; Contreras and Sieving 2011), we simply isolated one group member and multiplied its shared information term (s_i ; eq. [3]) by a factor >1 , in our case 10 [3, 5]: $S_i = (g - 1)s_i o_{i,h} + 10 \times s_i o_{i,h}$.

In the absence of social information, $S_i = 0$, the focal animal could find food only when foraging (not being vigilant) and could detect a predator only when being vigilant (not foraging): thus, when foraging, $I_r = 1$ and $\lambda(b, g) = 0.5$, while $I_p = 0$ and $d(b, g) = 0$, and when being vigilant, $I_r = 0$ and $\lambda(b, g) = 0$, while $I_p = 4$ [0.6, 1.5] and $d(b, g) = 0.8$ [0.4, 0.6] (eqq. [2], [3]). We modeled high effectiveness of vigilance (80% predator detection rate) that can be achieved in natural systems (e.g., Rasa 1989), but because this depends on the sensory acuity, light environment (e.g., due to activity period, location), and complexity of the habitat (i.e., degree of sensory obstruction) of the vigilant animal (Iribarren and Kotler 2012), we also examine effects of lower levels of effectiveness of vigilance [40% and 60% detection rate]. When present, social information about resources ($S_r > 0$) or predators ($S_p > 0$) allowed the focal animal to find food while being vigilant or to detect predators while foraging, respectively (eq. [2]; Fernández-Juricic et al. 2004).

Risk Dilution

Regardless of the presence or absence of social information, the probability of death by predation depended not only on predator detection but also on the dilution of risk afforded by foraging in a group (Neill and Cullen 1974; Foster and Treherne 1981). Thus, if a predator was not detected before an attack, the probability of escaping the attack was $\gamma_n(g) = 1 - 1/(g + 1)$. However, when an attacking predator was detected, the focal animal experienced an increase in escape probability (i.e., a predator detection bonus), functionally equivalent to an increase in the number of other risk-diluting group members, in this case 5 [2, 10], such that $\gamma_d(g) = 1 - 1/(g + 1 + 5)$. We further isolated the effect sizes of both risk dilution and social information, allowing us to directly compare their relative influ-

ence on animal fitness (see app. C; apps. A–C are available online).¹

Nonfocal Group Members

We modeled the probability that each nonfocal group member would find food (δ) as a function of the animal's personal (s_r) and (if present) social (S_r) information about resources, the same way that we modeled the focal animal, adjusted for niche overlap (i.e., information relevance):

$$\delta = \frac{s_r \times o_{r,j} + S_r}{s_r \times o_{r,j} + S_r + 1}. \quad (4)$$

Thus, if social information about resources was absent ($S_r = 0$), each forager found food independently. However, if social information about resources was present ($S_r > 0$), group members shared information about resources, improving each member's chance of finding food.

Excluding the focal animal, we modeled the behavior of each group member as the average across all group members, because it is this average effect that would drive optimal behavior in the focal animal (Clark and Mangel 2000). Thus, in a given time step, on average, a proportion of 0.1 [0.3, 0.5] of nonfocal group member activity was dedicated to vigilance, while the rest—a proportion of 0.9 [0.7, 0.5, respectively]—was instead dedicated to foraging (i.e., effectively, on average, 1 [or 3, 5] in 10 group members was vigilant while the others foraged during a time step). For conspecific groups ($o_{i,c} = 1$), we adjusted s_i ($s_i = 0.82$ [0.54, 0.32]; eq. [4]; $s_p = 0.09$ [0.33, 0.67]; eqq. [2], [3]) to mirror the base probabilities (i.e., personal information only) of finding food (0.5) and detecting predators (0.8) of the focal animal (eq. [2]), multiplied by the aforementioned proportions (0.9 [0.7, 0.5] and 0.1 [0.3, 0.5]) to yield probabilities of 0.45 [0.35, 0.25] and 0.08 [0.25, 0.40] that each nonfocal group member would find food and detect predators, respectively, in a time step. We simply multiplied s_i by $o_{i,h}$ to calculate the probability that a nonfocal member of a heterospecific group would (1) find food using its personal information (0.38 [at $o_{r,h} = 0.5$ and 0.9: 0.29 and 0.42, respectively; at a group foraging proportion of 0.7 and 0.5: 0.29 and 0.19, respectively]; eq. [4]) or (2) alert the focal animal of a predatory threat, if social information about predators was present (eqq. [2], [3]; 0.08 [at predator overlap of 0.5, 0.75, and 0.9: 0.04, 0.06, and 0.07, respectively; at a group vigilance proportion of 0.3 and 0.5: 0.25 and 0.40, respectively]). We also took the lower predator detection

1. Code that appears in the *American Naturalist* is provided as a convenience to the readers. It has not necessarily been tested as part of the peer review.

probabilities modeled for the focal animal (0.4 and 0.6; see “Information Use,” last paragraph) and simultaneously applied these to nonfocal members (adjusting for the base proportion of group vigilance behavior of 0.1) of conspecific and heterospecific groups [0.04 and 0.06, under the base predator overlap, $o_{p,c} = o_{p,h} = 1$].

Competition for Resources

If the focal animal found food in a given time step, it could consume 0, 1, 2, or 3 units of food. The probability of each of these four outcomes (c_m , where m reflects 0, 1, 2, or 3 units consumed) depended on resource availability (r) and, if present, the focal animal’s group. Thus, when the focal animal was solitary ($g = 0$), c_m simply reflected the Poisson probability that m units of food were found, given that the mean of the distribution is r , rescaled such that $\sum_{m=0}^3 c_m = 1$. When the focal animal was foraging in a group, $g > 0$, resource competition occurred; thus, the probability that the focal animal consumed m units of food also depended on the number and type (conspecific vs. heterospecific) of other group members that simultaneously found food.

When the focal animal was in a group, we estimated c_m as the sum—across all possible numbers of competitors within the group (n_g)—of the product of the Poisson probability that m units of food were consumed by the focal animal, given that the mean of the distribution was $r/(n_g \times o_{i,j})$ and the probability of the presence of each possible number of competitors n_g . This latter probability was estimated as the binomial probability that n_g individuals within a group of size g found food for which the focal forager competed, when the individual probability (for each other forager) of finding this food was δ (defined above). This yields

$$c_m(r, g, o_{i,j}) = \sum_{n_g=0}^g P\left(k = m, \frac{r}{n_g \times o_{i,j}}\right) B(n_g, \delta). \quad (5)$$

Again, these values were rescaled such that $\sum_{i=0}^3 c_i = 1$. Thus, in raising the probability that each nonfocal group member would find food (eq. [3]), social information about resources increased the level of competition faced by the focal animal.

Results

Within-Model Variation in Behavior

We observed consistent patterns across state space (energy by time; e.g., fig. 1) within the range of model parameterizations we examined. First, the focal animal was solitary (i.e., not in a group) only at very low energy states, that is, near the point of starvation, when lower resource competition carried a greater fitness benefit than dilution of risk

(fig. 1). Universally, grouping behavior and group size increased with energy state; at higher energy states, animals can better afford increased competition for resources in exchange for higher dilution of predation risk (fig. 1). Similarly, vigilance behavior, when exhibited, was generally restricted to intermediate to high energy states, when animals could energetically afford to not forage in exchange for heightened awareness of predators. Near the end of the day, individuals joined larger groups and were less vigilant. This strategy provides both protection from predation and foraging opportunities to balance the demands for both survival and a high final energy state (which translated to increased survivorship).

Effects of Social Information on Animal Behavior

Focal animals were frequently vigilant in models with social information about resources. In these models, the proportion of vigilance (vs. foraging) behavior increased demonstrably with both resource availability and predation risk (e.g., from <0.08 to >0.95 , with a change in resources of 3–15 and predator visitation probability of 0.005–0.5; figs. 2, 3, S1, S2; figs. S1–S19 are available online). Conversely, in models without social information, focal animals were rarely vigilant, except when resources were low and predation risk was high, in which case vigilance provided equivalent fitness to foraging for high energy states (figs. 2, S2). In models with social information about predators, focal animals refrained from vigilance behavior in nearly every instance, indicating that predator avoidance was sufficiently enhanced by social information to preclude the need for the focal animal to be vigilant (figs. 2, 3, S1, S2).

Animals engaged in grouping behavior with heterospecifics far more frequently than solitary behavior or grouping with conspecifics. For models without social information about resources, grouping behavior was least common when both resource and predation levels were lowest, and grouping increased asymptotically as either resource or predation levels increased. In contrast, in models with social information about resources, grouping was ubiquitous (i.e., for all state-combinations, it was never optimal for an animal to be solitary) across all resource and predation levels tested. Animals grouped with conspecifics only under a limited set of circumstances. First, at higher resource levels, animals increasingly grouped with conspecifics; at the highest resource levels, animals always grouped with conspecifics, while at the lowest resource levels, animals always grouped with heterospecifics. It is important to note that in the former case, the fitness associated with conspecific and heterospecific grouping are increasingly similar, suggesting that under surplus resources, single versus mixed species grouping have similar fitness consequences from the perspective of food

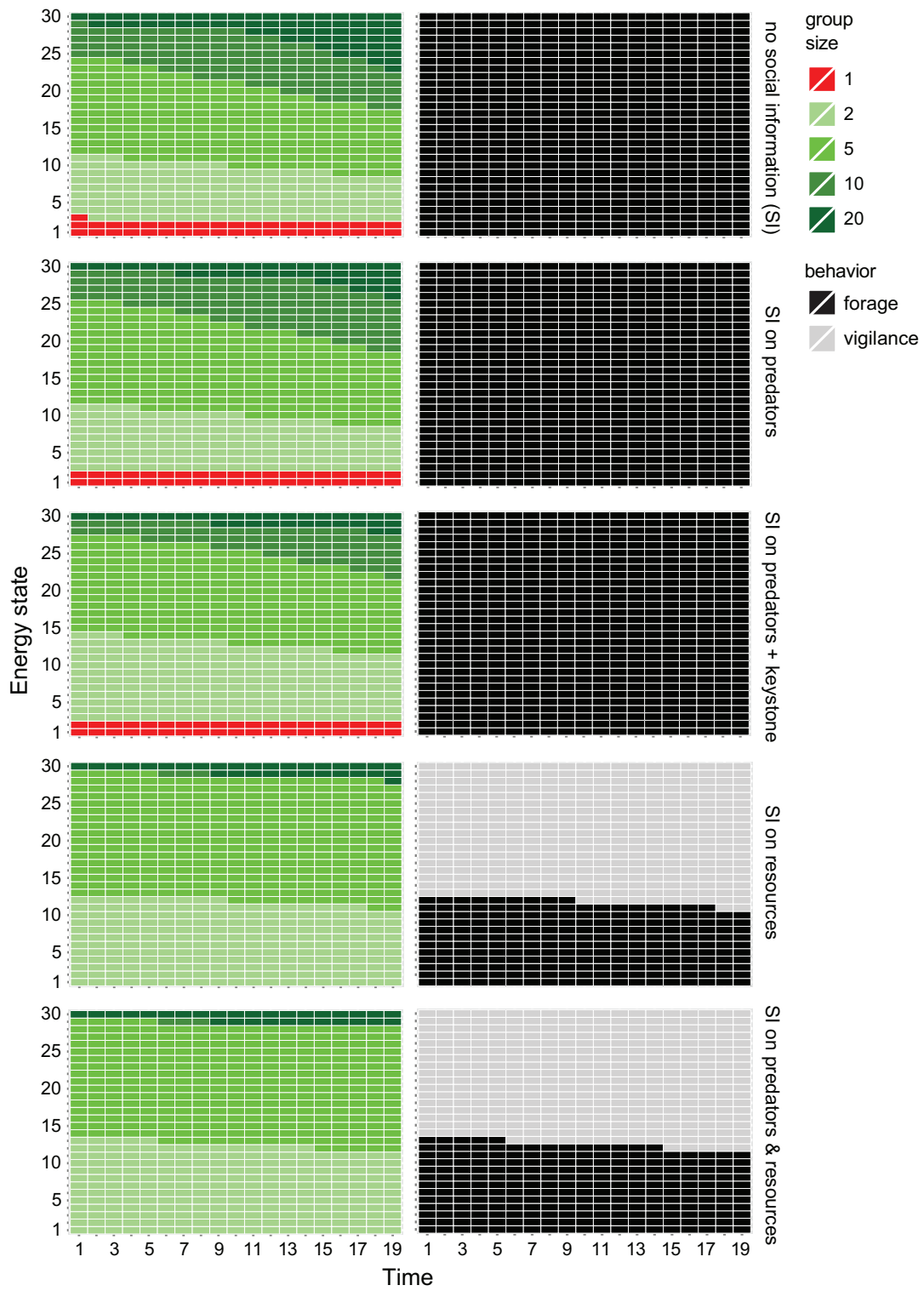


Figure 1: State-space plots of optimal grouping and behavioral decisions across energy state and time, when resource availability is at three energy units and the probability of a predator attack is 0.05. Group size indicates the total number of individuals in the group, including the focal animal; in this case, all grouping by the focal animal was within mixed-species groups, meaning that these groups were optimal.

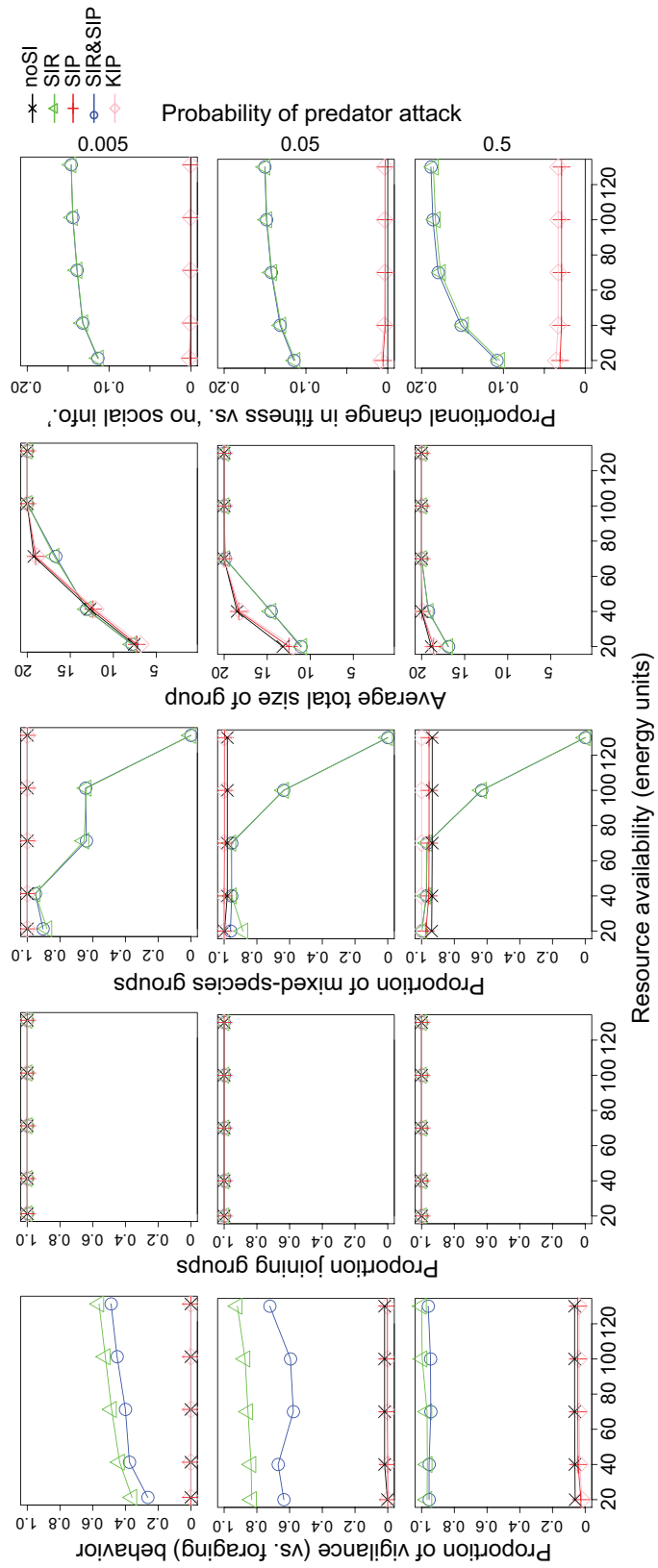


Figure 2: Effects of predation level (rows: 0.005, 0.05, 0.5) and resource level (X-axes: 3, 6, 9, 12, 15) on forager behavior and fitness across five models with different forms of social information (noSI, no social information; SIR, social information about resources; SIP, social information about predators; SIR&SIP, social information about resources and predators; KIP, social information about predators with a keystone informant species).

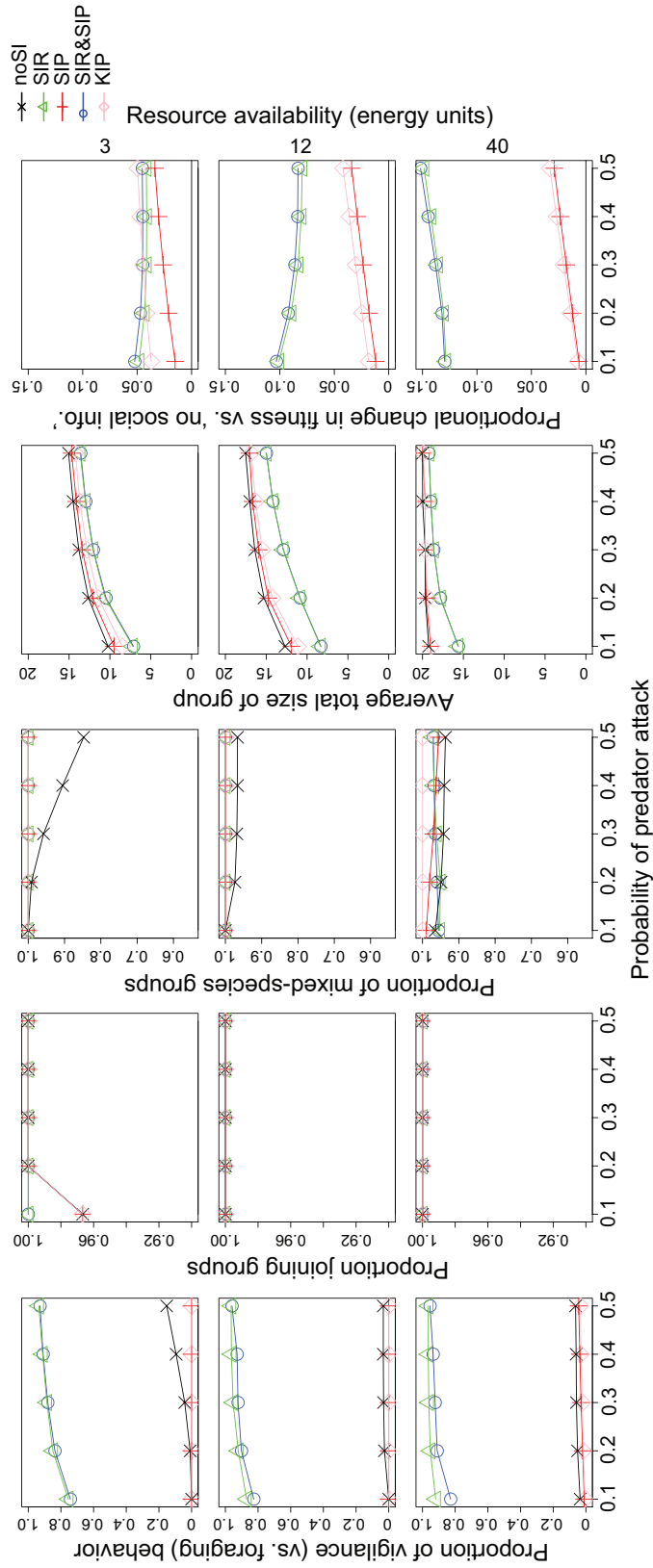


Figure 3: Effects of resource level (rows: 3, 12, 40) and predation level (X-axes: 0.005, 0.015, 0.025, 0.05, 0.075) on forager behavior and fitness across five models with different forms of social information (noSI, no social information; SIR, social information about resources; SIP, social information about predators; SIR&SIP, social information about resources and predators; KIP, social information about predators with a keystone informant species).

acquisition and safety. Furthermore, equivalent fitnesses were observed in our models but only in the special case in which there was no social information, very low resources, and very high predation risk. This caused a peak in the proportion of conspecific groupings (figs. 2, S1), because a tie-in fitness between a conspecific grouping choice and a heterospecific grouping choice in our model resulted in a conspecific grouping decision (by default).

Animals increasingly favored small groups (two or five total individuals) with greater availability of social information (i.e., animals selected small groups more frequently when social information about resources or predators was available and even more frequently when both forms of social information were available; fig. 1). Furthermore, with the exception of the lowest predation level tested, social information always reduced optimal group size. This effect was strongest for models with social information about resources, which led to reductions in average group size of approximately 35%, relative to the model with no social information. In addition, across models, increases in either resources or predation pressure led to increases in group size: more resources alleviate competition, and higher predation pressure raises the value of risk dilution. When resources were very high, animal groups reached their maximum size, and this peak occurred at lower resource levels as predation pressure increased.

Effects of Social Information on Animal Fitness

To understand the potential evolution of the use of social information, we compared the fitness associated with optimal decisions among the social information models and our model with no social information. Despite the stimulation of competition (when social information about resources was present), social information almost never reduced fitness (although for a detailed discussion of the results of further parameter exploration, see below and app. B), but the fitness benefits (relative to a system with no social information) varied considerably with information type and environmental context (i.e., resource availability and predation pressure). Generally, the model with social information about both resources and predators (SIR&SIP) provided the highest fitness advantage, which increased asymptotically with resource availability, reaching 19% greater fitness than the no SI model at high resource levels in our base parameterization (fig. S1). The SIR model followed a similar pattern of fitness gains to the SIR&SIP model. As resources increased, these models achieved fitnesses that were an order of magnitude larger than those of the SIP model and the KIP model. These latter two models followed a different pattern of fitness gains across all environmental contexts examined and reached peak fitness gains (relative to the no SI model) of only 3.7% and 5.0%, respectively, at low re-

source and high predation levels in our base parameterization (fig. S1). This suggests that social information about resources played a dominant role over social information about predators in shaping the dynamics of the SIR&SIP model. We further show that at very low probabilities of predation (i.e., 0.005), social information about resources contributes a greater fitness benefit than that of risk dilution from grouping, which contributes more to fitness in scenarios lacking social information about resources or under greater predator attack probabilities (fig. S19).

Fitness benefits of optimal decisions in models containing only social information about predators increased and scaled approximately linearly with the probability of predator visitation. In contrast, these same models were generally insensitive to changes in resources, with the exception that fitness benefits decreased slightly (particularly for the KIP model) across low resource levels. At low and intermediate resource levels, the fitness advantages of optimal decisions in the SIR and SIR&SIP models decreased slightly across very high predation levels (fig. S2). In contrast, at high resources levels, the fitness advantages of optimal behavior in models with social information about resources increased slightly across high predation levels (likely because of the rising value of social information about resources with higher levels of predation). Across predation levels, increasing resource availability increased the effect of social information about resources and slightly reduced the effect of social information about predators on fitness.

Changing Parameter Values

To a great extent, our qualitative findings were consistent across varying parameterization (app. B). Namely, social information increased fitness, heterospecific groups were generally preferred, and social information (combined with moderate to high predation) promoted smaller group size. Our model qualitatively deviated from our general conclusion only in a case of fairly extreme parameter values. Specifically, we found social information about resources (in SIR and SIR&SIP models) to reduce fitness relative to the case of no social information when predation was high, resources were low, and when the average foraging behavior of the group was low (i.e., collectively there was less food being found; app. B; figs. S17, S18). We describe these findings, including more minor patterns of deviation, in appendix B.

Discussion

Our study is the first to explicitly isolate effects of social information about resources and predators from effects of intrinsic properties of grouping (i.e., risk dilution, competition) and reveals that social information drives vigilance

behavior (supported by other theoretical and empirical work; Jackson and Ruxton 2006; King and Cowlshaw 2007; Pays et al. 2009; Beauchamp et al. 2012), grouping behavior, and individual fitness (figs. 2, 3). Despite heightened competition caused by social information about resources, in our models, social information was not detrimental to fitness (with a single exception under extreme environmental conditions; see app. B; figs. S17, S18); social information consistently led to fitness benefits that exceeded fitness costs (figs. 2, 3, S3–S16). In accordance with empirical findings (Dolby and Grubb 1998; Watson et al. 2007), small differences in foraging versus vigilance behavior and/or grouping behavior produced relatively large differences in fitness among models that included different forms of social information. In nearly all contexts tested, having social information about both resources and predators (as opposed to each form alone) yielded the highest fitness, frequently >10% higher than the model without social information (e.g., figs. 2, S1, S2; app. B). This suggests that animals should generally respond to (and thus pay attention to) social information regarding patchy resources and shared predators. Although empirical tests comparing social information acquisition from heterospecifics about both food and predation are lacking, there is strong evidence that the same species can supply both types of information. For example, temperate forest chickadees can supply social information about both food location (social facilitation and copying; Krebs 1973; Waite and Grubb 1988) and predator presence (alarm calls; Morse 1970; Gaddis 1980) to the heterospecifics with which they group in winter. Thus, we highlight empirical opportunities to test expectations set by our study that individuals produce and are influenced by multiple forms of social information.

Social information increased grouping behavior, but—except at the lowest predation level—it also reduced the average group size that maximized fitness (figs. 2, 3). This suggests that while social information promotes grouping, it also selects for group member quality over quantity: because group members experience diminishing returns from more information in larger groups (eqq. [2], [3]; e.g., Kenward 1978), smaller groups—which afford reduced competition—are more advantageous in the presence of social information. Our finding that heterospecific groups were optimal more frequently than conspecific groups also results from a reduction in competition; in all models, we assumed complete foraging niche overlap among conspecifics and lesser foraging niche overlap among heterospecifics (including 75% [figs. 1–3], 50% [fig. S13], and 90% [fig. S14]). Notably, this pattern of more frequent membership to heterospecific versus conspecific groups held when we looked beyond scenarios with complete predator overlap among heterospecific group members to instances where predators were only partially shared; that is, the relevance of social information about pred-

ators produced by members of heterospecific groups was 50% (fig. S10), 75% (fig. S11), or 90% (fig. S12) of that of members of conspecific groups. This result aligns with the theoretical competition-information quality trade-off inherent to grouping (Monkkonen et al. 1999; Seppänen et al. 2007) and agrees with empirical findings that for social information exchange, there is an optimal context-dependent degree of niche overlap (Jaakkonen et al. 2015). We consider our model conservative in that we always assumed foraging niche overlap—and thus interspecific competition—to be high. Because niche overlap among heterospecifics more closely resembles that of conspecifics, we would expect the choice to group with conspecifics versus heterospecifics to be less deterministic and more stochastic, because the costs of competition are increasingly similar. Furthermore it is important to note that conspecific grouping could be optimal because of other factors not included in our models, such as increased mating success, kin selection, or a lack of heterospecifics that share predators or resources (Danchin et al. 2004; Port and Cant 2013).

Though our model establishes qualitative and quantitative theoretical predictions about general effects of social information on animal behavior and fitness (figs. 1–3, S1, S2) that can be applied to various general systems (e.g., table 2), it lacks the complexity inherent to many natural systems. For example, our model did not consider that increased vigilance associated with mixed-species foraging groups can increase the foraging niches available to an animal by allowing them use of more risky microhabitats. A Neotropical forest bird, for instance, broadened its foraging sites to include more exposed (and therefore more dangerous) microhabitats while in mixed-species groups relative to solitary foraging (Darrah and Smith 2013), increasing foraging efficiency. Furthermore, our models do not consider a potential drawback to grouping regarding predator avoidance: predators can be attracted to larger groups of prey and may even use social information (from other predators) to modulate this attraction (Hamblin et al. 2010). In such cases, our findings of the importance of group member quality over quantity would likely be reinforced. Our model also predicts that social information about resources globally grants a greater fitness benefit than social information about predators (relative to scenarios with no social information) and can even exceed the fitness contribution of risk dilution from grouping, when predation pressure is low (fig. S19). However, the magnitude of these differences in relative fitness gain depend on parameter values over the ranges tested (app. B), including assumptions made about niche overlap between individuals as well as the spatial distribution and partitioning of resources.

Our models that included social information about resources (SIR) assumed that food resources were clumped and interspecific foraging niche overlap was high (50%, 75%, or 90%), meaning that we modeled the case in which

Table 2: Assumptions and example systems for the social information models

Model	Model assumptions				Example systems
	Resource distribution	Niche overlap	Information-producing species present	Shared predators	
Social information about resources	Clumped/unpredictable	High	No	No	Scavenger species of fishes, reptiles, birds and mammals (e.g., in forest, savannah, or benthic habitat)
Social information about predators	Homogeneous	Low	No	Yes	Mixed-species flocks of insectivorous birds, grazing ungulates, planktivorous pelagic fishes
Social information about resources and predators	Clumped/unpredictable	High	No	Yes	Conspecific groups of granivorous or frugivorous birds, mixed-species fish groups in nearshore benthic marine systems
Keystone information about predators	Homogeneous	Low	Yes	Yes	Systems with a keystone information-producing species; temperate and tropical mixed-species bird groups
No social information	Either	Either	No	Either	Systems with low animal densities (desert, tundra, deep-water pelagic); species limited to short-range communication modalities (e.g., touch, electrical stimuli)

SIR would be particularly valuable because of reduced competition and high relevance of SIR. However, if resources are evenly spaced or individuals do not have overlapping foraging niches, then SIR is of lesser value. Nonetheless, our model suggests that SIR may constitute an important driver of conspecific grouping when resources are spatially and/or temporally heterogeneous but abundant. This agrees with the previously held view that the costs of trial and error searching for resources are much reduced when other group members are supplying inadvertent SIR (Danchin et al. 2004), as long as resources are abundant enough for all group members to benefit from the discovery of a resource patch. Indeed, in an aviary setting, SIR use was shown to explain grouping in finch species that exploit unpredictable but abundant pine seed crops (Smith et al. 1999).

We also made assumptions about the availability and quality of social information, making it equally relevant and available to all members of a group, on average. However, the availability of social information is contingent on an overlap in sensory modalities and sensory ranges between species, which varies widely on the basis of the evolutionary history (preadaptations) and the media in which species are communicating (Bradbury and Vehrencamp 2011). We also did not assign quality to the social information provided in our model; it assumes both high reliability and relevance of information for all group members, given the short time periods over which information was shared (Stephens 1989). Reliability refers to the accuracy of the sig-

nal emitter, or the likelihood they will produce a false alarm regarding a predatory threat; false alarms are quite common in the small number of systems in which they have been quantified (Cresswell et al. 2000; Blumstein et al. 2004; Kahlert 2006; Beauchamp 2010). While responding to false alarms is energetically costly, the costs of ignoring an accurate alarm call are higher than those of responding unnecessarily to a false one (Searcy and Nowicki 2005), and reliability may be of lesser concern when modeling social information exchange, particularly regarding ephemeral threats or opportunities. In contrast, the relevance of social information to the receiver will greatly affect any fitness benefit obtained. Where species do not share food resources or predators, social information may be of little or no value, regardless of predation risk or food availability. Among Australian passerines, for example, species that shared few predators with an alarm caller did not respond to calls by individuals of that species (Magrath et al. 2009). Thus, information is not necessarily equally available or relevant to group members.

We chose to model a fundamental benefit of grouping behavior (risk dilution) in addition to social information exchange. However, traditional explanations for grouping behavior have focused on additional direct benefits. For example, socially dominant individuals can shield themselves from predation risk by remaining near the center of a social group and forcing subdominant individuals to occupy peripheral locations (the selfish herd, *sensu* Hamilton 1971).

Similarly, direct benefits to the foraging efficiency of group members have been observed to result from flushing of prey by other individuals (Satischandra et al. 2007) and even manipulation of social information to facilitate kleptoparasitism from other group members (Munn 1986). While risk dilution and social information undoubtedly represent two fundamental drivers of social behavior, other direct benefits can and should be modeled where applicable to a given system.

While we intended our model to be broadly applicable, our different model variants reflect a range in both the availability and relevance of social information as well as life-history characteristics of animals in natural systems (table 2). We encourage others to further parameterize and extend our model to better characterize the complex nature of specific systems and the role of social information therein. Our models reveal demonstrable individual fitness benefits to social information about resources and predators under a wide range of contexts. Consequently, social information about resources or predators could affect the demographics and persistence of populations (e.g., via Allee effects, sensu Schmidt et al. 2015) in the countless terrestrial and aquatic systems in which consumers share foraging grounds and/or predators.

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The formation of multispecies groups—such as those commonly found in coral reefs—may be fostered by information sharing. Pictured are the parrotfish *Scarus rivulatus* (foreground) and the rabbitfish *Siganus guttatus* (background), both roving herbivores. Photo credit: Heather Hillard.

Correction

After publication of “Social Information on Fear and Food Drives Animal Grouping and Fitness” by Gil et al. (*The American Naturalist* 189:227–241), the authors discovered that the files for figures 2 and 3 had been inadvertently replaced with figures from the online supplement, which show different parameter ranges of the same relationships. The correct figures 2 and 3 appear below. The authors regret the error.

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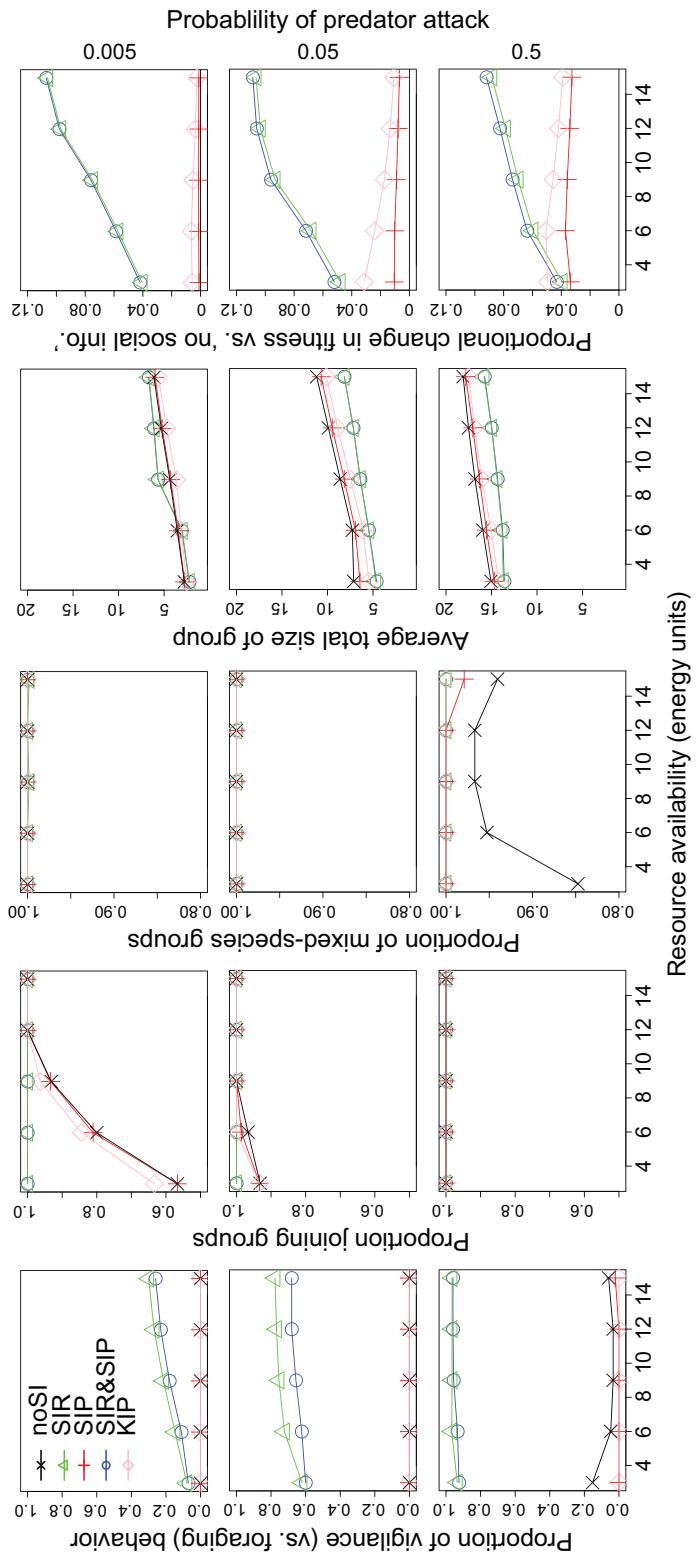


Figure 2: Effects of predation level (rows: 0.005, 0.05, 0.5) and resource level (X-axes: 3, 6, 9, 12, 15) on forager behavior and fitness across five models with different forms of social information (noSI, no social information; SIR, social information about resources; SIP, social information about predators; SIR&SIP, social information about resources and predators; KIP, social information about predators with a keystone informant species).

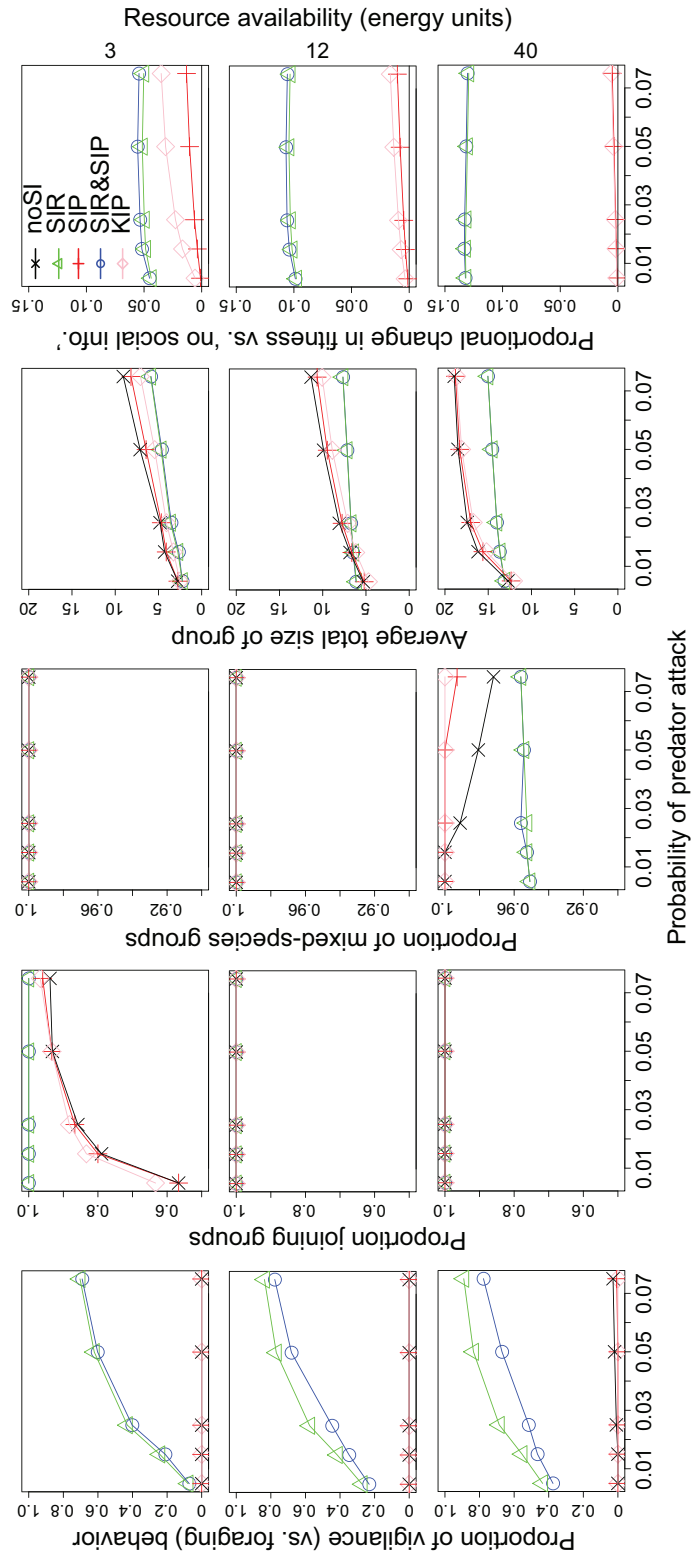


Figure 3: Effects of resource level (rows: 3, 12, 40) and predation level (X-axes: 0.005, 0.015, 0.025, 0.05, 0.075) on forager behavior and fitness across five models with different forms of social information (noSI, no social information; SIR, social information about resources; SIP, social information about predators; SIR&SIP, social information about resources and predators; KIP, social information about predators with a keystone informant species).