

# Opposing Responses to Scarcity Emerge from Functionally Unique Sociality Drivers

Albert B. Kao,<sup>1,2,\*†</sup> Amanda K. Hund,<sup>3,\*†</sup> Fernando P. Santos,<sup>4</sup> Jean-Gabriel Young,<sup>5</sup> Deepak Bhat,<sup>6</sup> Joshua Garland,<sup>7</sup> Rebekah A. Oomen,<sup>8</sup> and Helen F. McCreery<sup>2,9,\*†</sup>

1. Santa Fe Institute, Santa Fe, New Mexico 87501; 2. Biology Department, University of Massachusetts, Boston, Massachusetts 02125; 3. Department of Ecology, University of Minnesota, St. Paul, Minnesota 55108; and Department of Biology, Carleton College, Northfield, Minnesota 55057; 4. Informatics Institute, University of Amsterdam, Amsterdam 1098 XH, The Netherlands; and Department of Ecology and Evolutionary Biology, Princeton University, Princeton, New Jersey 08544; 5. Department of Mathematics and Statistics, University of Vermont, Burlington, Vermont 05405; and Vermont Complex Systems Center, University of Vermont, Burlington, Vermont 05405; 6. Department of Physics, School of Advanced Sciences, Vellore Institute of Technology, Vellore, Tamil Nadu, India; 7. Center on Narrative, Disinformation and Strategic Influence, Arizona State University, Tempe, Arizona 85281; 8. Centre for Ecological and Evolutionary Synthesis, University of Oslo, Oslo 0315, Norway; and Centre for Coastal Research, University of Agder, Kristiansand 4360, Norway; 9. School of Engineering and Applied Sciences, Harvard University, Cambridge, Massachusetts 02138

Submitted June 3, 2022; Accepted December 12, 2022; Electronically published July 27, 2023

Online enhancements: supplemental PDF.

**ABSTRACT:** From biofilms to whale pods, organisms across taxa live in groups, thereby accruing numerous diverse benefits of sociality. All social organisms, however, pay the inherent cost of increased resource competition. One expects that when resources become scarce, this cost will increase, causing group sizes to decrease. Indeed, this occurs in some species, but there are also species for which group sizes remain stable or even increase under scarcity. What accounts for these opposing responses? We present a conceptual framework, literature review, and theoretical model demonstrating that differing responses to sudden resource shifts can be explained by which sociality benefit exerts the strongest selection pressure on a particular species. We categorize resource-related benefits of sociality into six functionally distinct classes and model their effect on the survival of individuals foraging in groups under different resource conditions. We find that whether, and to what degree, the optimal group size (or correlates thereof) increases, decreases, or remains constant when resource abundance declines depends strongly on the dominant sociality mechanism. Existing data, although limited, support our model predictions. Overall, we show that across a wide diversity of taxa, differences in how

group size shifts in response to resource declines can be driven by differences in the primary benefits of sociality.

**Keywords:** social behavior, resource abundance, resource scarcity, optimal group size, cooperation.

## Introduction

Organisms across the tree of life—including bacteria, insects, and mammals—have evolved to live in groups, and understanding why sociality is so common has been a fundamental area of biological research for centuries. Sociality is particularly interesting because of its inherent cost: organisms living in groups necessarily face increased resource competition. For the countless diverse organisms that live in groups, this cost must be overcome by one or more evolutionary benefits. For example, sociality may decrease predation risk (Cresswell 1994), increase mating opportunities (Mayer and Pasinelli 2013), or increase the survival probability of offspring (Silk 2007). Regardless of the benefit a given social species enjoys, when resources become scarce—and the cost of resource competition increases—one may reasonably expect the cost-benefit calculation to tip away from sociality and for group sizes to decrease. Indeed, this expectation is borne out in many species (Smith et al. 2008), perhaps especially the charismatic mammals frequently presented as examples of social animals, such as lions (which form smaller groups when

\* Corresponding authors; email: albert.kao@gmail.com, amanda.k.hund@gmail.com, hmccreery@gmail.com.

† These authors contributed equally to this work.

**ORCID:** Kao, <https://orcid.org/0000-0001-8232-8365>; Hund, <https://orcid.org/0000-0001-7758-6757>; Santos, <https://orcid.org/0000-0002-2310-6444>; Young, <https://orcid.org/0000-0002-4464-2692>; Bhat, <https://orcid.org/0000-0001-9387-4951>; Garland, <https://orcid.org/0000-0002-6724-2755>; Oomen, <https://orcid.org/0000-0002-2094-5592>; McCreery, <https://orcid.org/0000-0003-3811-7960>.

prey is less abundant; Caraco and Wolf 1975) and bottlenose dolphins (which form smaller foraging groups when prey is at low densities; Campbell et al. 2002).

However, there are also many social species for which group sizes increase under scarcity. This occurs in taxonomically diverse groups, including some bacteria and yeast (which aggregate into flocs or form biofilms under low-nutrient concentrations; Koschwanetz et al. 2011; Fisher and Regenberg 2019) and Mormon crickets (*Anabrus simplex*, which transition from solitary to gregarious when resources are scarce; Simpson et al. 2006; Bazazi et al. 2011). Yet other groups maintain a stable group size despite changing resource availability, including mule deer (which have consistent group sizes regardless of the patch size; Bowyer et al. 2001). In addition to the direction of the group size change, the magnitude of these group size shifts can also vary greatly. For example, cavies exhibit relatively small increases in group size (Taraborelli and Moreno 2009), whereas for locusts, the transition from a solitary phase to a gregarious phase triggers the formation of massive swarms (Bazazi et al. 2011; Pruitt et al. 2018). In table S1, we provide a nonexhaustive list of known examples of organisms across taxa for which group sizes were measured across different resource abundances, with some decreasing, some increasing, and some showing no change in group size as resources become scarce. The fact that different species have opposing responses to scarcity is interesting and, on first inspection, surprising. What accounts for these differing responses, and specifically, why do some species form larger groups, ostensibly amplifying resource competition, when the resource pool shrinks?

One potential explanation for the observation that some species form larger groups when resources decrease is that the benefits of sociality for such species become stronger under scarcity, overcoming the increased resource competition. For example, one can imagine that in some species, large groups may be somewhat more successful at finding common resources than small groups but much more successful at finding rare resources. In principle, this added benefit of sociality under scarcity could more than offset the added competition cost. Different types of benefits may vary in the extent to which they are strengthened (or weakened) by scarcity. Perhaps locusts and lions have opposite responses to scarcity because the benefit of sociality for locusts gets stronger under scarcity, while a different benefit important for lions does not. In actuality, a given species will rarely derive only one benefit from sociality, but a subset of the potential benefits (and costs) will dominate, and the balance of their magnitudes will determine the typical group size within a given ecological context (Alexander 1974; Macdonald 1983). The response of a given group to a reduction in available resources should depend on how scarcity affects the spe-

cific key benefits exerting the strongest selection pressures and driving sociality in that group. In short, we hypothesize that different species may have opposing responses to scarcity because they gain fundamentally different key benefits from sociality.

It is currently difficult to apply this hypothesis to make predictions about whether a given species' group size will grow, shrink, or remain stable during periods of changing resource availability, for two main reasons. First, there are countless possible benefits that organisms may derive from living in groups, and it remains challenging to identify which proposed benefits are most important for particular species. Second, even if a given species' key benefits of sociality are known with relative certainty, the potential effects of changes in resource abundance on the strength of these benefits may be nonintuitive; for example, it is hard to guess whether and how resource availability will affect the social benefit of reduced predation risk. There is currently no framework for predicting such effects. However, if we can overcome these challenges, we may gain insight into why groups exhibit such variable responses to resource scarcity. If the key sociality benefits for an organism are known, this would allow us to predict how groups will respond to changing resource availability—which is of increasing importance in the context of a changing global climate. Furthermore, in principle, this may allow us to perform the reverse inference and use observed group size changes resulting from shifts in resources to make predictions about the biological and ecological factors underlying sociality for particular species. Because group size is typically relatively easy to measure, this may prove valuable for understanding the key drivers of group living across the tree of life, which is among the most important challenges in the study of social systems.

There is already a large body of literature on the costs and benefits of group living across taxa. Researchers typically focus on the effects of a single candidate benefit of sociality or a very small number of benefits whether using models (e.g., Ioannou et al. 2012) or empirical approaches (e.g., Bilde et al. 2007). Studying each benefit in isolation may allow a researcher to understand the selection pressure for that particular benefit, but it does not allow one to determine the relative contribution of different benefits toward maintaining sociality or to identify the most important benefits for a particular species. One might imagine that to identify the most important benefit of sociality, a researcher needs to perform experiments or analyze models investigating all of the myriad potential benefits simultaneously, a likely infeasible task (Packer and Ruttan 1988; Silk 2007). Certain types of social systems are particularly well studied (e.g., cooperative breeding), providing a broader understanding of how ecological and social dynamics affect group size in these systems. However, it is

difficult to generalize the insights gained across the behaviorally and taxonomically diverse social organisms, as the influence of different social and ecological costs and benefits on group size is remarkably variable both within species and across species (Barnard and Sibly 1981; Johnson et al. 2002; Fronhofer et al. 2018). A new approach—examining changes in group size as containing signals of sociality drivers—would be a valuable contribution to this literature.

Here, we present the first steps toward the larger goal of understanding how different key benefits of sociality may affect the direction and magnitude of group size shifts under resource scarcity and therefore explaining why some groups grow rather than shrink in response to increased resource competition. First, we looked across the literature, collating resource-related benefits of sociality and identifying six functionally distinct categories. We focused primarily on resource-related benefits because they are most likely to affect the response to scarcity (further described in “Scope”). Second, we developed a flexible modeling framework that incorporates these categories of benefits to investigate how they may cause shifts in group size when resource availability shifts. Third, we compared the results of our model with existing empirical data, although such data are currently scant. In “Discussion,” we highlight limitations of the present work and describe future work that would extend our results and move further toward a unified understanding of sociality across biology.

### Scope

Our study is motivated by the observation that sudden decreases in resource abundance seem to cause varying—even opposing—responses in different species. We therefore focus on changes in the abundance of resources (i.e., food) that occur over relatively short ecological timescales (within generations). While we consider how differential evolutionary drivers of sociality may account for the variance in groups’ responses, the responses themselves are behavioral (plastic) rather than evolutionary. Our model therefore operates on short timescales, and we do not model reproduction. To include in our framework the broad diversity of social organisms across the tree of life, we made several additional assumptions and definitions. We define sociality as living in groups, and we use group size as a proxy for the degree of sociality. This proxy is incomplete, and we acknowledge that it is possible for a group to become more or less social in terms of individuals’ behaviors while the group size remains stable; for example, individuals could remain in a group but become less cooperative. We maintain that group size is a valuable proxy in the context of our broad framework however, be-

cause it applies to, and can generally be measured or estimated in, virtually all species across the tree of life. Furthermore, group size is relatively unambiguous, although we acknowledge that there are groups for which assigning a size can be subjective, such as in superorganisms like eusocial insects. In this case, we treat the members of a eusocial colony as separate individuals because each must consume resources.

While it would be ideal to look across all of the benefits of sociality in a single conceptual and modeling framework, for the present work we focus specifically on resource-related benefits because we expect such benefits to have potentially large effects on groups’ responses to resource scarcity. Additionally, a model incorporating all possible benefits of sociality is likely to be infeasible, and modeling every benefit of sociality at once (potentially many dozens) would make it difficult to gain an intuitive understanding of the results of the model or to then apply those results to future research. Furthermore, resource-related benefits have been shown to be a central and important type of social benefit for a wide variety of species (Sumpter 2010). Indeed, variability in social groups, within and across populations and species, is often attributed to underlying variation in ecological resources (Emlen and Oring 1977; Lott 1991), and many models have been developed to explain the influence of ecological conditions on social organization or group size (Orians 1969; Carr and Macdonald 1986; Johnson et al. 2002; Korb and Heinze 2016). Even limiting our focus to resource-related benefits, however, leaves a wide diversity of benefits, especially when looking across taxa. A unifying classification of such benefits that allows for comparative work is currently lacking. Such a taxonomy will allow for a much clearer picture of the variety and types of resource-related benefits that sociality can provide.

For these reasons, the benefits we explicitly include in our model are those that relate directly to the acquisition and expenditure of caloric resources. Our goal was to include all of the benefits that allow groups to get more energy from their environment or to spend less energy in doing so. However, rather than completely ignoring other costs and benefits of sociality, we gather these other factors into a single category (see “Non-Resource-Related Benefits and Costs of Sociality”). We acknowledge that this category includes a great diversity of costs and benefits of sociality, such as cooperative breeding and reduced predation risk, which are important for many species. Some of these other factors have been well studied; for example, there is a robust literature on the reproduction-related effects of sociality, including their effects on group size (e.g., Shen et al. 2017). Our goal is to complement, rather than replace, this literature and the wealth of

research focusing on costs and benefits of sociality that do not directly relate to acquiring and expending caloric resources.

### Identifying Fundamental Resource-Related Benefits and Costs of Sociality

#### *Literature Survey*

To accomplish our first goal of classifying resource-related benefits of sociality into functionally distinct categories, we searched the literature for evidence of benefits and costs of sociality to resource acquisition. Typically, this evidence consisted of observations or experiments measuring the success of groups of different sizes. Rather than being exhaustive, our broad literature review was meant to provide examples of different resource-related benefits of sociality. Because we were looking so broadly across taxa, we were not able to use consistent search terms, as the literatures associated with different taxonomic groups often use markedly different terminology. Instead, we updated search terms as we found those most relevant for a particular taxon. We also relied on forward and backward citation searches, finding additional studies by searching both articles that cited and articles cited by those already identified. We began our search broadly and subsequently conducted more targeted searches for particular taxa (e.g., birds, fish, insects).

#### *Fundamental Benefit/Cost Categories*

Although the myriad resource-related benefits described in the literature appear to be very different, we found that many benefits perform a fundamentally similar function. Indeed, we were able to collapse these benefits into just six functionally distinct classes to create a unified comparative framework (fig. 1). Importantly, organisms can and do gain benefits from multiple classes simultaneously. Figure 1 is not meant to be exhaustive: listed species may access other benefits, and many unlisted species also access these benefits. In addition, we do not claim that the listed proximate form is the most important social benefit for that species. See table S2 for a brief explanation of why each example species is listed in its respective benefit class.

#### *Fundamental Resource-Related Benefits of Sociality*

*Collective territoriality: larger groups are able to potentially access more resources.* This describes organisms that can occupy larger territories in groups or those that can travel farther as a group to explore a larger area. For ex-

ample, larger groups of capybaras have larger and higher-quality home ranges (Herrera and Macdonald 1989), while larger *Volvox* colonies move farther in the water column to exploit larger productive areas (Solari et al. 2008).

*Collective detection/capture: larger groups detect and capture resources with higher probability.* This includes organisms that use shared information or other mechanisms to individually capture more resources when in a group—for example, larger flocks of birds are more likely to find rich food patches (Carrascal and Tellería 1990)—as well as organisms that actively cooperate to capture resources, such as *Myxococcus* bacteria, which more efficiently predate on cyanobacteria at higher densities (Fraleigh and Burnham 1988).

*Collective niche expansion: larger groups can capture larger or higher-quality resources.* This benefit expands a species' dietary niche by allowing members of larger groups to consume novel resources inaccessible to smaller groups. This includes social spiders that use collective web structures to capture larger prey (Majer et al. 2018) and some pathogenic bacteria that suppress their virulence until a quorum is reached to overcome a host's immune responses (Crespi 2001).

*Collective consumption: individuals in larger groups can consume more of a captured resource before it is lost.* Larger groups may be able to better defend resources from others, as with coyotes (Bowen 1981). Alternatively, collective consumption can permit the capture of a larger fraction of a resource, such as biofilms that encapsulate a resource and slow the diffusion of nutrients (Rosenberg et al. 1977; Koschwanez et al. 2011) or humpback whales that use bubble nets to feed on a school of fish (Jurasz and Jurasz 1979).

*Collective energetics: individuals in larger groups expend less energy, on average, per unit time.* This may be due to aerodynamic or hydrodynamic benefits, such as with great white pelicans, which fly in a V formation (Weimerskirch et al. 2001). Other social animals, such as emperor penguins (Ancel et al. 2015), are better able to thermoregulate in a large group, lowering the energetic costs of maintaining homeostasis.

*Collective dispersal: larger groups can more easily disperse from a poor habitat to a new habitat.* This benefit may arise because groups move more efficiently while searching for a new environment, such as slime molds that self-assemble into a spore-laden fruiting body (Gadagkar and Bonner 1994). Alternatively, larger groups may disperse more successfully by accessing other group benefits when traveling, such as storks collectively sensing air thermals (Flack et al. 2018), or when they arrive at their new habitat, such as some ants that exhibit increased survival when multiple queens found nests together (Johnson 2004).



Resource-related benefit of sociality	Benefit description	Example proximate forms	Examples across taxa
Collective territoriality	Increase number of resources available to group	Accessing larger/higher quality territories	capybara (Herrera and MacDonald 1989), white-throated magpie-jays (Langen and Vehrencamp 1998), coyote packs (Lamprecht 1981), acacia ants (Palmer 2004), chimpanzees (Lowen and Dunbar 1994), <i>Volvox</i> colonies (Solari et al. 2008), ring-tailed lemurs (Pride et al. 2006)
Collective detection/capture	Increase probability of capturing a resource	Spending less time looking for predators (and more time foraging)	mule deer (Bowyer et al. 2001), greater rheas (Fernández et al. 2003), degus (Ebensperger et al. 2006), brown-headed cowbirds (Fernández-Juricic et al. 2007), rabbitfishes (Brandl and Bellwood 2015), tamarins (Hardie and Buchanan-Smith 1997)
		Detecting resources with higher probability	goldfish (Pitcher et al. 1982), forest tent caterpillars (Despland and Le Huu 2007), mixed bird flocks (Carrascal and Telleria 1990), Brewer's blackbirds (Horn 1968), guppies (Snijders et al. 2018)
		Capturing resources with higher probability	zebra lionfish (Lönnstedt et al. 2014), aplomado falcons (Hector 1986), lions (Stander and Albon 1993), groupers and giant moray eels (Bshary et al. 2006), chimpanzees (Boesch and Boesch 1989), <i>Myxococcus</i> bacteria (Fraleigh and Burnham 1988), spinner dolphins (Benoit-Bird and Au 2009)
Collective niche expansion	Increasing size range of resources that can be captured	Hunting larger or higher quality prey	social spiders (Majer et al. 2018, Yip et al. 2008, Powers and Avilés 2007), African wild dogs (Creel and Creel 1995), ant predation (Cerdá and Dejean 2011), Harris' hawks (Bednarz 1988), bacteria (Crespi 2001, Williams et al. 2000), sevengill sharks (Ebert 1991), orcas (Guinet et al. 2000, Baird and Dill 1996), river otters (Blundell et al. 2002)
Collective consumption	Increase the amount of resource consumed per capita	Defending kill from others	hyenas (Lehmann et al. 2017, Smith et al. 2008), coyotes (Bowen 1981), antibiotic production in bacteria (Rigali et al. 2008), primates (Wrangham 1980), resources monopolization in yeast (Fisher and Regenberg 2019, Regenberg et al. 2016), ant cooperative transport (McCreery and Breed 2014, Czaczkes and Ratnieks 2013)
		Slowing diffusion of nutrients	bacteria (Berleman et al. 2008, Rosenberg et al. 1977), budding yeast (Koschwanez et al. 2011)
		Capturing a larger fraction of prey group	bubble-net feeding in humpback whales (Jurasz and Jurasz 1979), ospreys (Greene 1987), leaf-notching moths (Tsubaki and Shiotsu 1982), black-headed gulls (Götmark et al. 1986), blue tang surgeonfish (Foster 1985), orcas (Bigg et al. 1987)
Collective energetics	Decrease rate of energy expenditure	Moving more efficiently	grey mullet (Marras et al. 2015), ducklings paddling on water (Fish 1995), great white pelicans in flight (Weimerskirch et al. 2001), aquatic crustaceans (Ritz 2000)
		Spending less energy on homeostasis	emperor penguins (Ancel et al. 2015), honeybees (Kronenberg and Heller 1982), big brown bats (Willis and Brigham 2007), cavies (Taraborelli and Moreno 2009)
Collective dispersal	Increase probability of successful dispersal	Moving away from current environment faster	Mormon crickets (Berdahl et al. 2018, Romanczuk et al. 2009, Simpson et al. 2006), colonial salps (Sutherland and Weihs 2017), fruiting-body-assisted dispersal in <i>Dictyostelium</i> (Gadagkar and Bonner 1994, Smith et al. 2014) and <i>Myxococcus</i> bacteria (Shimkets 1999), spider mites (Clotuche et al. 2011)
		Accessing collective benefits while dispersing	storks locating thermals (Flack et al. 2018), V-formations in northern bald ibises (Portugal et al. 2014)
		Accessing collective benefits in new environment	ants ( <i>Pogonomyrmex</i> , Johnson 2004; <i>Atta</i> , Mintzer 1987; <i>Lasius</i> , Pull et al. 2013), termites (Matsuura and Nishida 2001), spider mites (Clotuche et al. 2010) founding new colonies

**Figure 1:** Six fundamental resource-related benefits of sociality. For each benefit of sociality, we give a brief description, note specific ways in which the benefit may manifest, and list examples of the benefit across diverse taxa. Rationale for each species' placement is provided in table S2.

### Fundamental Resource-Related Cost of Sociality

*Intragroup competition: individuals in larger groups suffer increased competition for resources.* While the details of intragroup competition differ among species (e.g., finder's share, dominance effects, scramble or contest competition), in general, there will be fewer resources available per capita once captured resources are divided as group size increases.

### Non-Resource-Related Benefits and Costs of Sociality

There are a large number of other effects of sociality that are unrelated to resource acquisition. Such effects include reducing predation risk via several mechanisms (many-eyes hypothesis, Trafalgar or confusion effects, selfish herd principle, dilution; Krause and Ruxton 2002), altering parasite risk (Altizer et al. 2003), affecting reproduction, and more. In short, there are a number of important potential benefits and costs of sociality that are not directly related to resource acquisition, which we combine into a single class ("other mortality").

### Modeling How Benefits of Sociality and Resource Abundance Affect Group Size

That the many resource-related benefits of sociality can be collapsed into just six functionally unique categories suggests that a single model could feasibly incorporate all of the benefits. We developed such a model to examine how the benefits of sociality can cause shifts in group size when resource abundance shifts rapidly. Our model weighs the resource-related benefits of sociality against the cost of resource competition and is essentially a complex cost-benefit analysis, and we deliberately incorporate only the most essential features of groups foraging for resources. By incorporating seven benefits of sociality (the six resource-related benefits plus the generic non-resource-related benefit) and resource competition cost of sociality, the model is already complex. As such, adding other features relevant to certain social species (such as fission-fusion dynamics and dominance hierarchies) would make the model taxon specific but unwieldy. Because of its general framing, this model permits us to draw conclusions that may be applicable to a wide range of taxa but limits our precision with respect to modeling particular species. Nonetheless, our model framework is flexible enough to readily include other features or dynamics relevant to particular species in future work.

Here, we concisely describe the model and depict it schematically in figure 2. Code for the model as well as results are available on Figshare (<https://doi.org/10.6084/m9.figshare.11961879>; Kao et al. 2023). We implemented

the stochastic version of our model described in this section in MATLAB, and we also obtained an analytical solution (see below and app. A).

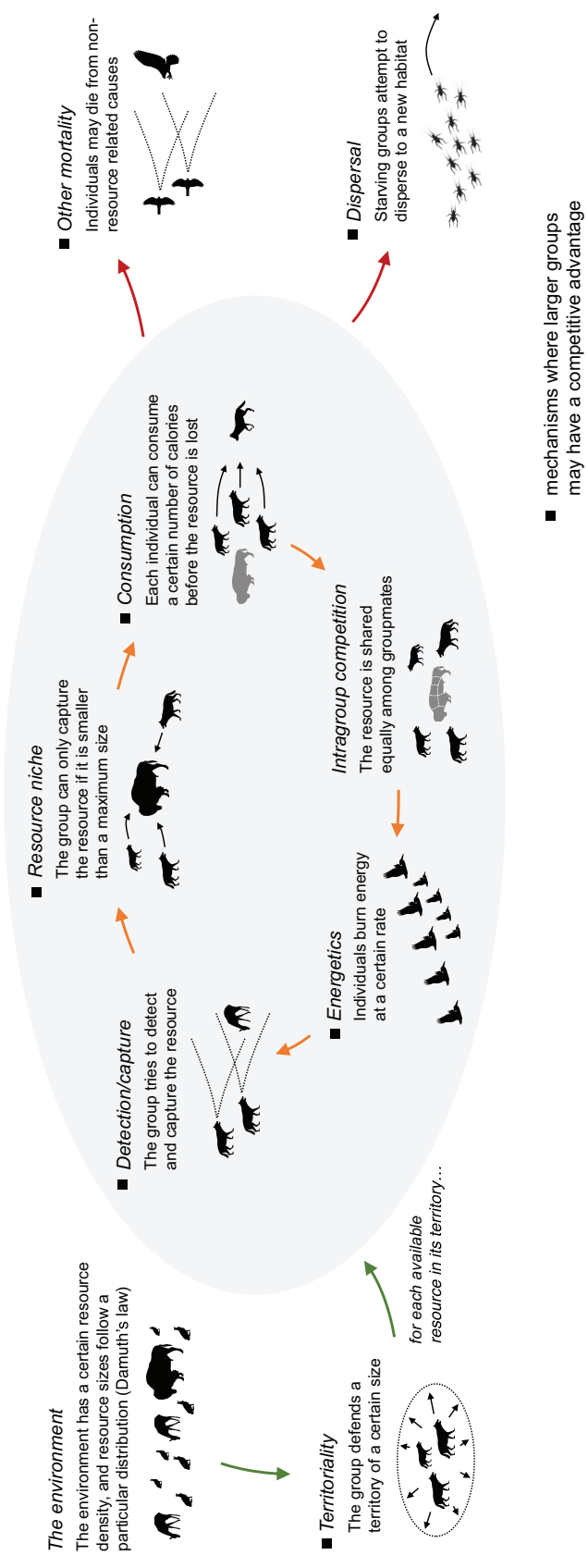
### Model Overview

In our simplified short-term (within-generations) ecological model of social group foraging, a group of size  $M$  exists in an environment containing resources whose dimensionless sizes vary from 0 to  $C_{\max} = 1$  following a power law distribution based on empirical and theoretical work on mass-abundance relationships in nature (i.e., Damuth's law; White et al. 2007; Rossberg et al. 2008). As such, the probability density  $P(C)$  that a resource is a certain size  $C$  is given by  $(1 + \gamma_C)C^{\gamma_C}/C_{\max}^{1+\gamma_C}$ , where we set the exponent to  $\gamma_C = -3/4$  (Damuth 1987). A group is assigned a territory of a certain size, giving it access to a particular number  $\mu$  of those potential resources. To examine the sensitivity of our model to variations from Damuth's law, we also performed simulations with resource sizes following a normal distribution (fig. S1).

Each individual in the group starts with a store of energy,  $c_0$ . Throughout the simulation, the group attempts to detect, capture, and consume each of the  $\mu$  potential resources in its territory. There is some probability,  $p_s$ , that the group successfully detects and captures a particular resource. However, the group can capture resources only within its niche (if  $C \leq C_h$ , where  $C_h$  is the maximum size resource that the group can capture)—the group must ignore the resource if it is too large. If the group successfully captures a particular resource, each individual in the group consumes some portion of the resource, but the group members might not consume the entire resource before it is lost (e.g., to conspecifics, heterospecifics, or the environment). Each individual can consume up to quantity  $c_d$  of the resource before it is lost. However, we assume that groupmates share resources equitably, so that individuals consume a maximum of  $C/M$  if the entire resource is consumed. Therefore, the actual amount of the captured resource that an individual consumes is  $c_c = \min\{c_d, C/M\}$ . If the resource was not detected or captured by the group or was outside of its niche, then  $c_c = 0$  for that resource.

While the group tries to capture the available resources, each individual burns a total of  $c_b$  energy. In addition, there is some probability,  $p_p$ , that an individual dies because of some non-resource-related cause. If the individuals in the group run out of energy (i.e., if  $c_0 + \sum c_c - c_b \leq 0$ ), then the group attempts to disperse to a new habitat; it successfully disperses with some probability,  $p_e$ , and otherwise the individuals in the group die.

Therefore, an individual survives a simulation if (a) it does not die from a non-resource-related cause and does



**Figure 2:** Modeling framework for investigating how the benefits of sociality and resource abundance affect group sizes. We specify an environment containing a certain density of resources (either abundant or scarce); the sizes of the resources follow a power law distribution ("the environment"). A group of organisms has access to the resources within a territory of a certain size ("territoriality"). For each resource in the territory, the group attempts to detect and capture it ("detection/capture") but can only capture it if it is within its dietary niche ("resource niche"). If the group successfully captures a resource, the individuals in the group share the resource but might consume only a fraction of the resource before it is lost ("consumption," "intragroup competition"). Individuals expend energy while searching for resources ("energetics") and may die from non-resource-related causes ("other mortality"). If individuals run out of energy, the group attempts to disperse to a new habitat ("dispersal").

**Box 1: Functional forms of the relationships between group size and parameters associated with each category of sociality benefits implemented in the model**

*Collective territoriality.* Number of accessible resources given by  $\mu = \mu_1 M^{\gamma_t}$ , where  $\mu_1$  is the number of potential resources available to a solitary individual and  $\gamma_t$  is the strength of this social benefit.

*Collective detection/capture.* Probability that the group detects and captures a resource given by  $p_s = 1 - (1 - \alpha_s)^{k_s(M-1)+1}$ , where  $\alpha_s$  is the probability that a solitary individual detects and captures a resource within its niche and  $k_s$  is the strength of this social benefit. This functional form, as well as similar ones below, are based on the perfect many-eyes model (Ward et al. 2011) but modified to allow for different strengths of the social benefit (to match the perfect many-eyes model, we would set  $k_s = 1$ ). This function increases from  $p_s(M = 1) = \alpha_s$  to  $p_s(M = \infty) = 1$ .

*Collective niche expansion.* Maximum accessible resource size given by  $C_h = \alpha_h C_{\max} M^{\gamma_h}$ , where  $\alpha_h$  is the maximum size resource that a solitary individual can capture, as a proportion of  $C_{\max}$ , and  $\gamma_h$  is the strength of this social benefit.

*Collective consumption.* Maximum amount of a captured resource each individual is capable of consuming before the resource is lost, given by  $c_d = \alpha_d C_{\max} M^{\gamma_d}$ , where  $\alpha_d$  is the maximum amount, as a proportion of  $C_{\max}$ , that a solitary individual can consume and  $\gamma_d$  is the strength of this social benefit.

*Collective energetics.* Energy spent by one individual given by  $c_b = c_1((1 - \alpha_b)^{k_b(M-1)+1} + \alpha_b)$ , where  $c_1$  is the amount of energy that a solitary individual burns during the simulation,  $k_b$  is the strength of this social benefit, and  $\alpha_b$  represents the fraction of energy burned by a solitary individual that an individual in an infinitely large group burns. This function decreases from  $c_b(M = 1) = c_1$  to  $c_b(M = \infty) = \alpha_b c_1$  (where  $0 \leq \alpha_b \leq 1$ ).

*Other mortality.* Probability of dying from non-resource-related causes given by  $p_p = \alpha_p^{k_p(M-1)+1}$ , where  $\alpha_p$  is the probability that a solitary individual dies from a non-resource-related cause and  $k_p$  is the strength of this social benefit. This function decreases from  $p_p(M = 1) = \alpha_p$  to  $p_p(M = \infty) = 0$ .

*Collective dispersal.* Probability of surviving after dispersal given by  $p_e = \alpha_e(1 - \alpha_e^{k_e(M-1)})$ , where  $\alpha_e$  is the probability that an infinitely large group successfully disperses and  $k_e$  is the strength of this social benefit. This function increases from  $p_e(M = 1) = 0$  to  $p_e(M = \infty) = \alpha_e$ .

not run out of energy or (b) it does not die from a non-resource-related cause and runs out of energy but successfully disperses.

*How the Different Benefits of Sociality Increase with Group Size*

For each simulation, we “turned on” one of the benefits of sociality, such that larger groups exhibit improved performance in that aspect of the simulation (fig. 2, squares). In particular, depending on which of the seven benefits we turn on, one of the following parameters will be a function of group size  $M$ :  $\mu$  (number of accessible resources, i.e., collective territoriality),  $p_s$  (probability that group detects and captures resource, i.e., collective detection/capture),  $C_h$  (maximum accessible resource size to a given group, i.e., collective niche expansion),  $c_d$  (potential amount of captured resources that are consumed by an individual, i.e., collective consumption),  $c_b$  (energy spent by one individual, i.e., collective energetics),  $p_p$  (probability of dying from non-resource-related causes, i.e., other mortality), or  $p_e$  (probability of surviving after dispersal, i.e., collective dispersal). The specific functions we used are defined in box 1.

*Running the Simulations*

We ran simulations for each mechanism, where the strength of the mechanism was set to 10%, 50%, or 90% of its maximum value (see app. B for details of how we set the maximum values for each mechanism). We set  $\mu_1$  to either 1 or 20 to capture different ecological regimes where resources are relatively rare or common, respectively, although we note that this choice did not strongly affect our conclusions (fig. S2). Note that the two values of  $\mu_1$  do not signify resource scarcity versus abundance (which is implemented as described in the next paragraph) but rather determine the extent to which a particular individual or group may typically rely on each resource item. If  $\mu_1$  is set to 1, the group must consume that resource to survive; with  $\mu_1$  equal to 20, the stakes for each resource item are lower. We set  $\alpha_s$ ,  $\alpha_h$ ,  $\alpha_d$ ,  $\alpha_b$ ,  $\alpha_p$ , and  $\alpha_e$  to .001, .01, .1, .25, .5, .75, .9, .99, or .999. In general, the parameters  $\alpha_b$ ,  $\alpha_p$ , and  $\alpha_e$  (parameters related to energetics, other mortality, and dispersal benefits) affect dynamics only when their respective mechanisms are turned on, since  $\alpha_b$  and  $\alpha_e$  play a role only when those mechanisms are on, and we set  $\alpha_p = 0$  unless that mechanism is turned on.



We calculated the probability that an individual survives a simulation for group sizes ranging from 1 to 100, for both an abundant resource regime and a scarce resource regime. We define the abundant resource regime as the condition where a solitary individual is expected to have exactly 0 energy at the end of the simulation (see app. B for details). The free parameters available to tune this “edge of starvation” are  $c_0$  and  $c_1$  (the amount of energy that an individual starts the simulation with and the amount of energy that a solitary individual burns during the simulation, respectively). We choose to tune  $c_1$  while setting  $c_0 = 1$ . If the edge of starvation (and therefore the abundant resource regime) is given by  $c_1^*$ , then we define the scarce resource regime by setting  $c_1$  to  $sc_1^*$ , where  $s = 1.01$  or  $1.05$ , implying that when resources are scarce, it takes longer (i.e., more energy) for a group to detect each resource.

For each combination of parameter values, we ran 10,000 simulations for each group size ranging from 1 to 100 and computed the optimal group size (defined as that which maximizes survival probability) for both the abundant resources condition and the scarce resources condition. Because our model excludes individual variation, individual survival probability is necessarily equal to group survival probability, except when the other mortality benefit applies, in which case we compute the optimal group size based on the individual survival probability. For the dispersal mechanism, the probability of survival asymptotes to  $\alpha_e$  for large group sizes, so it is difficult to determine the optimal group size in simulations because a wide range of group sizes have survival probabilities close to  $\alpha_e$ . We observe that for this mechanism, as group size increases, the probability of survival appears to either monotonically increase or initially decrease and then increase. Therefore, the optimal group size can only be either  $M = 1$  or  $M = \infty$  (or  $M = 100$  for our simulations). Because of this, we simply observed the survival probability for the two extreme group sizes to determine the optimal group size.

To accurately estimate the optimal group size, we included a set of parameter values in our analyses only if at least one group size, in each of the abundant and scarce conditions, had a survival probability greater than 5% and if none of the group sizes, in both the abundant and scarce conditions, had survival probabilities greater than 95%.

#### *Model Predictions: The Effect of the Sociality Benefit Class on Group Size Shifts*

Depending on which benefit of sociality was present in the simulation, we found that the optimal group size can decrease, increase, or stay the same when resources become scarce. In figure 3A and 3B, we show examples of the optimal group size being smaller under scarce than abundant conditions, and vice versa. In addition to our stochastic

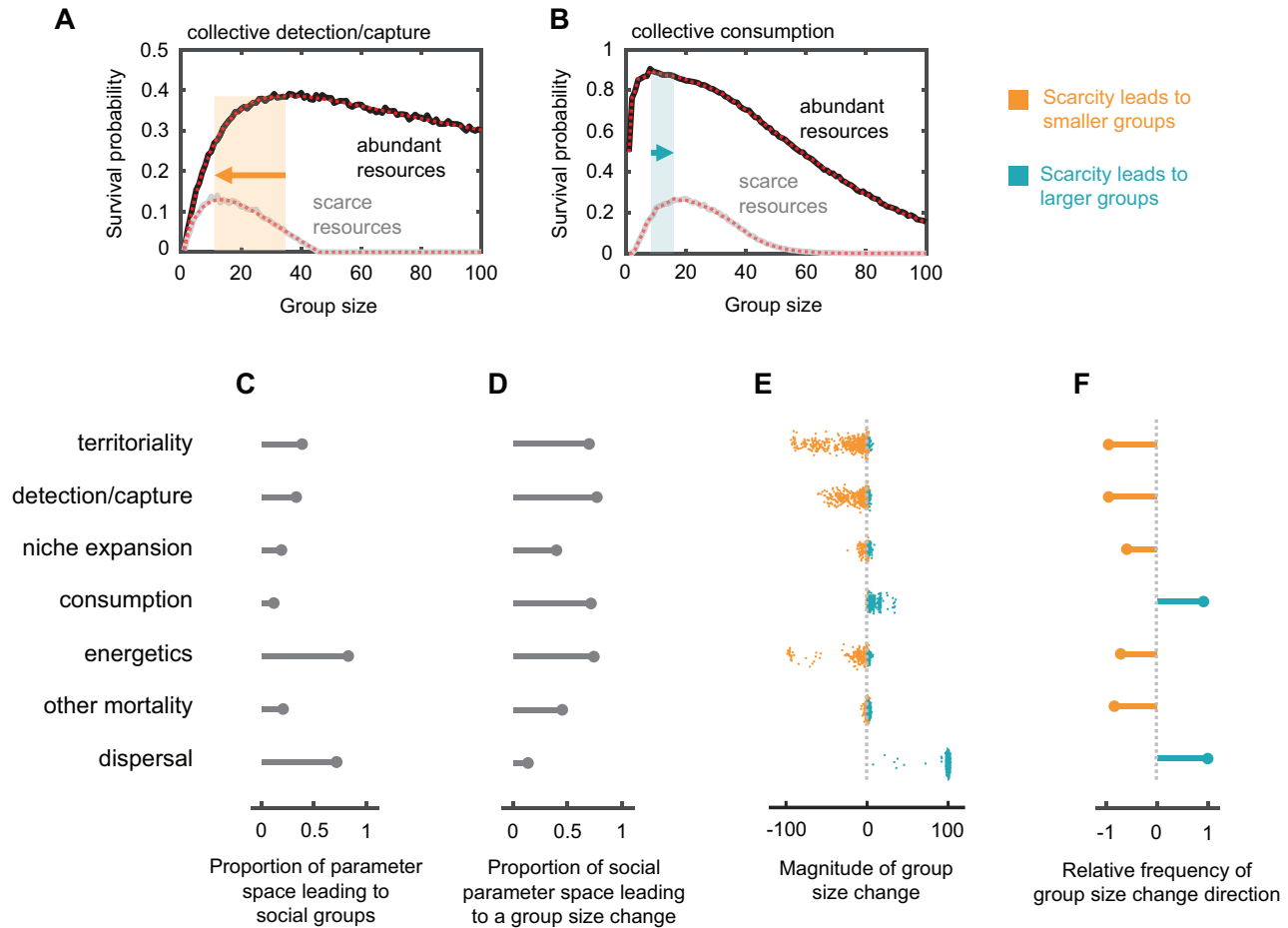
simulations, we developed an analytical solution to our model (exact when the number of resources  $\mu = 1$ ; see app. A), which closely matches our simulation results (fig. 3A, 3B).

Across all of the parameter space, a benefit of sociality permitted the existence of social groups (i.e., survival probability was maximized when the group size  $M > 1$ , for either the abundant resource condition or the scarce resource condition) in 11%–82% of parameter sets, depending on the active social benefit (fig. 3C). Since our aim was to study social species, in subsequent analyses, we focused on those sets of parameter values that permitted social groups, excluding the asocial parameter sets.

Within this restricted parameter space, 13%–76% of parameter sets led to a shift in group size when resource abundance shifted (fig. 3D). The magnitude and direction of group size shifts strongly depended on which benefit of sociality was present (fig. 3E). The territoriality, detection/capture, and energetics mechanisms tended to lead to decreases in group size when resources became scarce (explained in detail in app. C). While the niche expansion and other mortality mechanisms could lead to group size shifts in either direction (fig. 3E), the magnitudes tended to be small (and therefore could be difficult to detect experimentally or observationally in nature). The consumption and dispersal mechanisms tended to lead to group size increases under scarcity (explained in app. C), with collective dispersal leading to very large increases in group size (however, for this mechanism a wide range of group sizes had similar survival rates). Plotting the relative frequency of decreases and increases in group size (fig. 3F) confirms that only the consumption and dispersal benefits robustly cause increases in group size under scarcity. Our results for simulations with resource sizes following a normal distribution, rather than Damuth’s law, are qualitatively very similar (fig. S1), with the main difference in the predictions for the collective consumption benefit. This difference is intuitive because of the fact that collective consumption applies only to very large resources; the effect of this benefit on groups’ response to scarcity therefore depends on how prevalent very large resources are in the environment. Because our main analysis included only two levels of resource abundance (abundant or scarce), we confirmed that groups’ responses to the extent of scarcity are monotonic (app. D). We found no examples of scarcity having nonmonotonic effects on group size.

#### **Empirical Evidence for the Model Predictions**

We returned to the literature to examine the extent to which existing data support, or contradict, our theoretical predictions. On the basis of the quantitative results in figure 3,



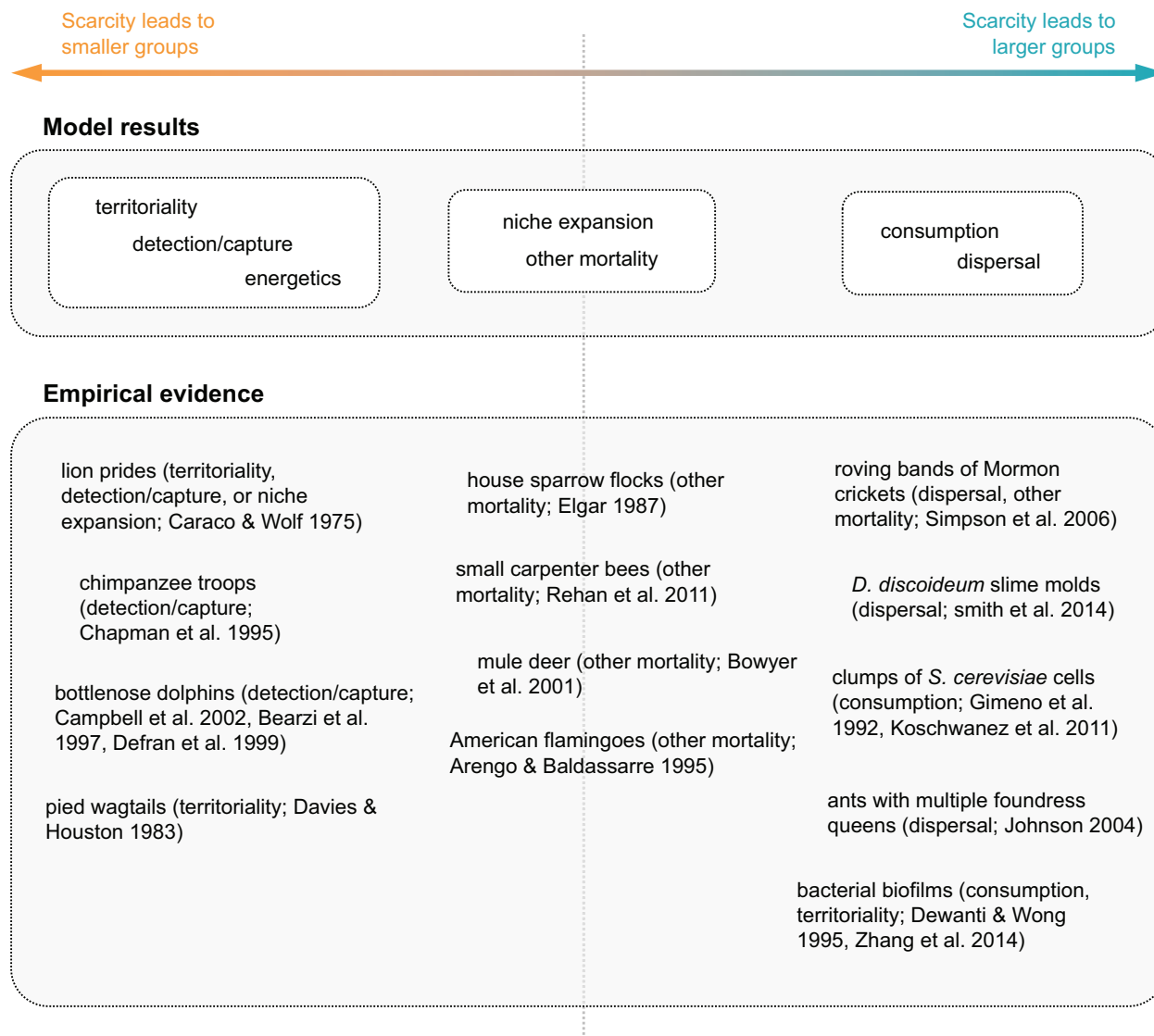
**Figure 3:** Group size changes depend on the underlying benefit of sociality. *A*, Resource scarcity can lead to decreases in the optimal group size. Collective detection/capture is the dominant benefit, with parameters  $\mu_1 = 1$ ,  $k_s = 0.1k_{s_{\max}}$ ,  $s = 1.01$ ,  $\alpha_s = .01$ ,  $\alpha_h = .5$ , and  $\alpha_d = .999$ . Black and gray lines show results from simulations (mean of 10,000 repetitions) for the abundant and scarce resource conditions, respectively, while the red and pink lines show the analytical solution. *B*, Resource scarcity can also lead to increases in optimal group size. Collective consumption is the dominant benefit, with parameters  $\mu_1 = 20$ ,  $\gamma_d = 0.5\gamma_{\max}$ ,  $s = 1.01$ ,  $\alpha_s = .5$ ,  $\alpha_h = .25$ , and  $\alpha_d = .001$ . *C*, Proportion of parameter space where the optimal group size was greater than one for either resource condition. *D*, Proportion of social parameter space (i.e., the fraction of parameter space shown in *C*) that leads to a change in group size. *E*, Scatterplot of the resulting group size shift for parameter sets that led to a shift. *F*, Relative frequencies of the shift direction for parameter sets that led to a group size shift (a value of  $-1$  indicates that all shifts caused by scarcity were decreases, a value of  $1$  indicates that all were increases). Code and data underlying figure 3 are available on Figshare (<https://doi.org/10.6084/m9.figshare.11961879>; Kao et al. 2023).

we partitioned the seven benefits of sociality (six resource-related categories plus the other mortality category) into three groups: those that tend to lead to decreases, increases, or only very small changes in group sizes when resources become scarce (fig. 4, “model results”).

#### Literature Survey

To examine how well existing evidence supports these coarse model predictions, we conducted an additional literature search. We focused on finding taxa with both known

changes in group size under short-term resource abundance shifts and a known or widely hypothesized reason for the change (fig. 4, “empirical evidence”). Our methodology was very similar to that for the first literature review. We found only a small number of taxa that satisfied both requirements (i.e., a documented change in group size under short-term changes in resource availability with agreement among experts for a particular mechanism). All of these taxa are either included in figure 4 or discussed below as examples with less clear evidence. This search was also not meant to be exhaustive and was unbiased, as decisions



**Figure 4:** Comparing our model predictions to existing empirical data. The model results, shown in figure 3C–3F, lead to coarse classifications of the benefits of sociality based on their general tendency to produce decreases, increases, or only minor shifts in group size when resources become scarce. Existing empirical evidence, while relatively scant, tends to agree with our model predictions. We note that this comparison is preliminary, since even for the species that we list in this figure, the dominant benefit of sociality is not known with certainty.

about inclusion were made without regard for whether the results fit our predictions.

#### *Evidence Aligns with Model Predictions*

For species with relatively strong evidence of which benefits dominate, we found substantial agreement between empirical examples and our model predictions (fig. 4, “empirical evidence”). For example, there is evidence that lion prides (Caraco and Wolf 1975), chimpanzee troops (Chapman et al. 1995), bottlenose dolphin pods (Campbell et al. 2002), and

pied wagtail flocks (Davies and Houston 1983) are smaller when resources are scarce. Previous work suggests that these species benefit particularly from collective territoriality, collective detection/capture, and collective niche expansion. Our model predicts that collective territoriality and collective detection/capture typically lead to smaller groups under scarcity (but that collective niche expansion should lead to only small decreases in group sizes under scarcity).

Other species increase their group size under scarcity. Large bands of Mormon crickets are more likely to discover new habitats (collective dispersal) but may also benefit from

predator avoidance (other mortality; Simpson et al. 2006). Slime molds, such as *Dictyostelium discoideum*, aggregate into a social slug when resources become scarce and form a spore-carrying fruiting body (collective dispersal; Smith et al. 2014). Bacteria can form biofilms (Dewanti and Wong 1995; Zhang et al. 2014), and the yeast *Saccharomyces cerevisiae* can form clumps (Gimeno et al. 1992; Koschwanez et al. 2011) when nutrients are scarce, which absorb more of a resource's nutrients and/or cooperatively produce digestive enzymes (collective consumption). For some species of ants, new colonies started by multiple foundress queens are more likely to survive than colonies with single queens (collective dispersal; Johnson 2004). Our model predicts that collective dispersal and collective consumption do lead to larger groups under scarcity. Indeed, some of the species benefiting from collective dispersal exhibit the extremely large increases in group size predicted in our model, such as Mormon crickets and locusts that transition from solitary individuals to vast swarms.

Still other species have been shown to not change their group size significantly when resource abundances change. For example, house sparrow flocks remained the same size regardless of the feeder size presented to them (Elgar 1987), social nesting in small carpenter bees did not depend on nest site availability or foraging opportunity (Rehan et al. 2011), mule deer group sizes were consistent regardless of the patch size of habitat or availability of water (Bowyer et al. 2001), and the average flock size of American flamingos did not depend on food abundance (Arengo and Baldassarre 1995). For all of these examples, it is presumed that these species form groups to decrease their risk of predation—our model predicts that the other mortality collective benefit should not lead to changes in group size as resource abundance shifts.

For other species, the underlying driver of sociality is less well resolved. For example, finches and monk parakeets form larger flocks when resources are scarce (Cody 1971; South and Pruett-Jones 2000). These groups may benefit from collective sensing/capture, but alternatively large groups may simply reflect aggregation at fewer food patches. Hyenas were shown to decrease their group size under scarcity, with several hypothesized mechanisms driving sociality, including collective capture and collective consumption (Smith et al. 2008), and it is not known which, if any, may dominate. See table S1 for examples across taxa where group sizes have been measured across different resource abundances.

While existing empirical data generally support our model predictions, we stress that this comparison is preliminary and certainly not exhaustive, as the dominant driver of sociality is generally not known with certainty. Experiments specifically designed to test our model predictions are therefore necessary.

## Discussion

Contrary to the general expectation that decreased resource availability should lead to smaller groups (e.g., Preddiger et al. 2014), there are many species for which groups remain stable or even increase in size under scarcity (table S1). We hypothesized that differing key benefits of sociality may account for these divergent responses to scarcity, and we explored this hypothesis by developing a conceptual framework for understanding how different classes of sociality benefits interact with changes in resource abundance. Through a literature review, we collated a wide variety of resource-related benefits across taxa and discovered that these benefits can be condensed into just six classes with fundamentally different functional forms (fig. 1). These classes motivated the development of our model of groups acquiring resources (fig. 2), which was able to reproduce the full range of responses to scarcity in nature in both stochastic and analytic implementations. Specifically, our model revealed that the direction and magnitude of group size changes due to declines in resource abundance are strongly dependent on the underlying key benefit of sociality (fig. 3). This allowed us to partition the benefits into three groups: those predicted to lead to smaller, larger, or similar-sized groups under scarcity (fig. 4). Although currently limited, existing data on a variety of species broadly support our model predictions.

Organizing the complex array of resource-related benefits of sociality proposed for various organisms into six functionally distinct categories proved intrinsically insightful, because it allowed us to draw hitherto unrecognized parallels across diverse taxa. For example, we now realize that both groups of yeast slowing the diffusion of nutrients (Koschwanez et al. 2011) and groups of hyenas defending a carcass from competitors (Smith et al. 2008) benefit from collective consumption (i.e., increasing the fraction of a captured resource that can be consumed). Historically, the search for a general understanding of the ecological and social context of group living has been particularly challenging, in part because sociality is so widespread taxonomically, as the specific benefits, costs, contexts, and even lexicons of sociality are system specific (Rubenstein and Abbot 2017). Our classification of resource-related benefits into categories that are relevant across the diversity of life is a first step toward a unified understanding of sociality.

Our study is conceptually related to Shen et al. (2017), which divides benefits of sociality into two categories: resource defense benefits and collective action benefits. The former does not increase the amount of resources accessible to the group (the per capita resource allotment decreases monotonically as a function of group size), while the latter does (the per capita resource allotment can increase, to a certain extent, with group size). While that

study was unable to distinguish among collective action benefits, our study reveals fundamental classes of collective action benefits and predicts different responses to scarcity. In addition, because of the flexibility of our model framework (particularly by changing the strength of the benefit), we can simulate scenarios where the per capita resource allotment increases or decreases as a function of group size for a particular range of group sizes. In general, an increase in per capita resources improves an individual's probability of survival, leading to a larger optimal group size, and vice versa.

Furthermore, our model provides clear predictions for expected shifts in optimal group size under scarcity, depending on which is the main benefit that is “turned on.” All of our six categories of benefits make it easier for larger groups to acquire the resources they need, yet they differ substantially in the resulting direction and magnitude of predicted group size changes under short-term resource shifts (fig. 3). These differences were apparent despite our very broad parameter space—which one may have expected would wash out differences between the different sociality benefits. This indicates that changes in group size in real species may contain strong signals of the most important benefits driving the maintenance of sociality. For example, while groups benefiting from collective territoriality frequently shrink in size when resources become scarce, groups benefiting from collective dispersal tend to get much larger. We explored the reasons for these differences in appendix C. For instance, the collective dispersal benefit causes larger groups under scarcity because scarcity leads to more starvation-induced dispersal attempts, so the effect of this benefit is stronger under scarcity. Likewise, collective consumption is also stronger under scarcity. Collective consumption provides a benefit only with resources that are too large to consume immediately. In our simulations, these large resources became crucial for survival under scarcity, thereby increasing the strength of the benefit compared with abundant resource conditions, when individuals need to consume only a modest amount of each resource. Thus, collective consumption, like collective dispersal, causes scarcity-induced increases in group size. See appendix C for detailed explanations of the mechanisms behind these and other benefit categories.

For the sake of tractability, we made many simplifying assumptions in our model. While these simplifications limit our ability to make specific predictions about particular species, they were crucial in attempting what is, to our knowledge, the first comprehensive accounting of the diversity of resource-related benefits of sociality in a single framework. As we described in “Scope,” we focused only on the benefits of sociality directly related to the acquisition and expenditure of resources, with all of the myriad other non-resource-related benefits of sociality aggregated

into a single category. Many various costs and benefits of sociality are implicitly included in this other mortality category, such as those associated with predation risk and reproduction. Indeed, predation risk and reproduction, in particular, are themselves broad categories of costs and benefits, and it may be valuable in future work to apply an approach similar to that presented here to these broad categories, dissecting them into functionally distinct consequences of sociality. For example, perhaps some of the many identified mechanisms decreasing the predation risk to social animals (e.g., the many-eyes effect, confusion effect, mobbing, dilution of risk) are actually functionally equivalent to each other. Similarly, it may be useful to gather the many reproduction-related benefits of sociality (e.g., increased mating opportunities and/or choice, alloparental food provisioning, and/or offspring guarding) into functionally distinct categories.

Additional simplifying assumptions of our framework include the fact that we considered the effects of only one benefit category at a time, while multiple types of benefits are likely important in many cases—examining how our benefit classes interact would be an interesting and potentially fruitful area of future work. We also made assumptions about how resources are distributed in the environment and how they decline under scarce conditions, and we simulated only two potential mass-abundance relationships for resources (figs. 2, S2). We assumed that all of the mechanisms, except intragroup competition, function as benefits of sociality, rather than costs. We omitted intergroup competition, interspecies interactions (except through the consumption mechanism), demographic structures such as assortment based on kinship, and strategies besides dispersal to stave off starvation. We recognize the importance of all of these dynamics for certain social species and that many of these dynamics have enjoyed considerable research attention. Our goal was to add to this literature a new, complementary approach by focusing on the relationship between resource-related benefits of sociality and changes in group size when resource abundance shifts.

Furthermore, our model assumes that all individuals are identical within a group and split resources equally, excluding individual variation and intragroup dynamics (e.g., dominance hierarchies, finder's shares, division of labor). Individuals in real groups may gain different proportions of captured resources, and resource scarcity may impact certain group members more than others (e.g., males vs. females; Chapman et al. 1995; Hartwell et al. 2021). Some individuals may “cheat,” gaining more than their share or saving energy by avoiding contributing to a collective benefit. Such dynamics may have different effects on the different benefits of sociality, causing cooperation to collapse more easily for some benefits. Thus, an important direction of future work will be to incorporate heterogeneity



within groups. Our current model does consider stochastic effects (such as probabilistic resource capture, survival, and dispersal), which can be interpreted as resulting from small individual differences within each group, but investigating how the different benefits of sociality interact within a multilevel selection framework will be important for gaining a fuller understanding of how sociality evolves and is influenced by ecological context. Such an extension to the model, including groups interacting with each other, could also explicitly uncover Allee effects, which surely exist in the interactions between the benefits of sociality and the cost of intragroup competition that we investigated.

We also assumed that observed group sizes in nature should correlate with optimal group size. This requires individual behavior to be plastic on short timescales, such that group size can change adaptively to changing resource conditions. This plasticity is a typical assumption of fission-fusion models (e.g., Guerra et al. 2020), yet some groups lack this plasticity. In these cases, other measures could serve as proxies for optimal group size, such as stress hormones or body condition of individuals across groups of different sizes (Pride 2005; Markham et al. 2015; Dantzer et al. 2017), changes in the social network structure (Henzi et al. 2009; Foster et al. 2012), or the degree of investment in social behaviors such as grooming (Chapman and Chapman 1999). Group sizes may increase not because of individuals joining the group but because of reproduction of members of the group and the offspring remaining in the group for some period of time. Because these offspring are by definition related to other group members, the optimal group size, when incorporating kin effects, may be different from what our model predicts (Shen et al. 2017). However, in general, the mechanics of how groups change in size are less relevant to the predictions of our model, as long as the group size can change at a similar timescale as the change in resource abundance.

Even when group size is plastic, group sizes may deviate from the predicted optimal. For example, groups may more closely match the stable, rather than optimal, size (i.e., the group size for which the probability of survival is the same as that for a solitary individual; Giraldeau 1988). Even when considering the stable group size, however, it is likely that the direction and magnitude of group size shift in response to scarcity will be consistent with our results reported here. Our model predictions may also be less relevant for aggregations with other constraints on size, such as those with a limited number of food patches or nesting grounds or groups that shrink during resource scarcity because of the mortality of some individuals. Additionally, actual group sizes may not match a given individual's desired group size because group size is an emergent property of the preferences of all of the individuals (Guerra et al. 2020). For these reasons, care needs to be taken to understand the context of

the natural history of the species under study before applying our model framework to make predictions about how group sizes should shift when resource abundance shifts.

Our model also focuses specifically on how group sizes shift when they experience scarce resource availability. This was achieved by setting an individual in the abundant regime at the edge of starvation and then setting the scarce regime to be even harsher than that. We focused on this scarce regime partly because our measure of fitness was survival probability, which requires a meaningful probability of death to compare across groups. It is possible that different predictions would arise when considering scenarios with truly abundant resource availability (such as during mast years), but other fitness measures would need to be used, such as fat stores or brood size. Our model could be adapted to examine these other ecologically relevant regimes.

While we must be careful in predicting shifts in group size for particular species, it may still be valuable to make such predictions, especially in the context of anthropogenic impacts and global climate change. Studies predict that shrinking habitats and climate change will be devastating to a wide range of taxa and lead to mass extinctions (Román-Palacios and Wiens 2020). For social species that are threatened, it is important to understand how the changing environment will shape behavior and how this will influence survival. In particular, climate change is predicted to substantially impact resource abundances in many habitats (because of increased fires, droughts, and other causes) and may lead to unnaturally severe scarcity events. Understanding how particular benefits of sociality may be affected by such events, and how species at risk may respond, will allow us to better form strategies to mitigate their negative effects. Climate change may also offer opportunities to further develop and test our model and approach, as its attendant resource abundance shifts may serve as natural experiments allowing researchers to observe how a variety of species respond under these scenarios (e.g., Chapman and Valenta 2015).

We aggregated results of all of our simulations across a wide range of parameter values, which allowed us to capture, coarsely, the lifestyles of diverse organisms and environments. In principle, researchers could generate more precise, targeted predictions for particular species by running simulations within a narrower parameter space. After doing so, one may be able to substantially reduce the list of likely drivers of sociality by simply knowing that the species is social or knowing how group sizes shift when resources become scarce. Given all of the complexity of social behavior, discussed above, that we necessarily omitted from our model, it would currently be challenging to make such inferences with confidence. However, this is a valuable area of future research because understanding the selection pressures that cause organisms to become, and remain, social is one of the major questions in biology.

How responsive organisms are to shifts in resources may depend on how stable or unstable resources were during their evolutionary past. In some cases, species may even be adapted to extreme situations, when selection is strongest, rather than the “typical” environment (e.g., Grant and Grant 2002). Sensitivity to shifting resources and plasticity in group size and social behavior clearly varies across species, but there is evidence to suggest that it can even vary within species, particularly when populations occupy different environments or when group size is assessed at different timescales (e.g., see spider and colobus monkeys, where multiple directions of group size shift have been observed in the same species; table S1). Even within a group, the relative selection pressures may change with resource abundance: when food is abundant, non-resource-related benefits of sociality may more strongly dictate the size of the group, but when food is more scarce, resource-related benefits may become dominant. In our model analysis, we discarded sets of parameter values where the probability of survival was uniformly high or low for all group sizes, since this made it impossible to determine the optimal group size; however, this subset of parameter space may be useful to determine ecological contexts where resource-related benefits may exert more or less selection pressure relative to non-resource-related benefits.

Despite the inherent cost of increased resource competition, a great many organisms live in groups, enjoying diverse benefits that overcome the costs of competition. Our classification of benefits into six functionally unique categories permits a cross-comparison of the drivers of sociality across taxa, and our modeling framework demonstrates that functionally distinct benefits lead to diverging predictions for group size shifts under scarcity—predictions that align with empirical observations. Thus, our framework helps explain why groups in some species get larger, rather than smaller, under scarcity and moves us closer to a unified understanding of sociality across taxa.

#### Acknowledgments

We thank Andrew Berdahl for contributing ideas that stimulated initial discussions for this project. A.B.K. was supported by a Baird Scholarship from the Santa Fe Institute, and A.B.K. and J.G. were supported by an Omidyar Fellowship from the Santa Fe Institute. A.K.H., J.-G.Y., F.P.S., R.A.O., and H.F.M. were supported by a James S. McDonnell Postdoctoral Fellowship Award. D.B. gratefully acknowledges financial support from National Science Foundation grant DMR-1608211. The James S. McDonnell Foundation and the Santa Fe Institute additionally funded meetings and a working group grant for this work. The authors declare no competing interests.

#### Statement of Authorship

A.B.K. conceived of the study. A.K.H., H.F.M., A.B.K., F.P.S., and R.A.O. performed the literature review to identify the fundamental drivers of sociality. A.K.H., H.F.M., and R.A.O. performed the literature review to compare the model predictions to existing empirical evidence. All authors contributed to the conceptual development of the model. A.B.K., F.P.S., J.G., J.-G.Y., and D.B. wrote simulation code, and F.P.S. and A.B.K. ran the simulations and generated the figures. J.-G.Y., D.B., and F.P.S. developed the analytical solution to the model. A.K.H., H.F.M., A.B.K., and F.P.S. performed the literature review to create the supplemental tables. A.B.K., H.F.M., A.K.H., F.P.S., J.-G.Y., and R.A.O. drafted the manuscript. All authors edited the manuscript and gave final approval for publication.

#### Data and Code Availability

Data and code associated with our model are available on Figshare (<https://doi.org/10.6084/m9.figshare.11961879>; Kao et al. 2023). Code files are in formats for MATLAB (stochastic implementation) and Mathematica (analytic implementation).

#### Literature Cited

- Alexander, R. D. 1974. The evolution of social behavior. *Annual Review of Ecology and Systematics* 5:325–383.
- Altizer, S., C. L. Nunn, P. H. Thrall, J. L. Gittleman, J. Antonovics, A. A. Cunningham, A. P. Dobson, et al. 2003. Social organization and parasite risk in mammals: integrating theory and empirical studies. *Annual Review of Ecology, Evolution, and Systematics* 34:517–547.
- Ancel, A., C. Gilbert, N. Poulin, M. Beaulieu, and B. Thierry. 2015. New insights into the huddling dynamics of emperor penguins. *Animal Behaviour* 110:91–98.
- Arengo, F., and G. A. Baldassarre. 1995. Effects of food density on the behavior and distribution of nonbreeding American flamingos in Yucatan, Mexico. *Condor* 97:325–334.
- Baird, R. W., and L. M. Dill. 1996. Ecological and social determinants of group size in transient killer whales. *Behavioral Ecology* 7:408–416.
- Barnard, C. J., and R. M. Sibly. 1981. Producers and scroungers: a general model and its application to captive flocks of house sparrows. *Animal Behaviour* 29:543–550.
- Bazazi, S., P. Romanczuk, S. Thomas, L. Schimansky-Geier, J. J. Hale, G. A. Miller, G. A. Sword, S. J. Simpson, and I. D. Couzin. 2011. Nutritional state and collective motion: from individuals to mass migration. *Proceedings of the Royal Society B* 278:356–363.
- Bednarz, J. C. 1988. Cooperative hunting in Harris’ hawks (*Parabuteo unicinctus*). *Science* 239:1525–1527.
- Benoit-Bird, K. J., and W. W. L. Au. 2009. Cooperative prey herding by the pelagic dolphin, *Stenella longirostris*. *Journal of the Acoustical Society of America* 125:125–137.

- Berdahl, A. M., A. B. Kao, A. Flack, P. A. H. Westley, E. A. Codling, I. D. Couzin, A. I. Dell, and D. Biro. 2018. Collective animal navigation and migratory culture: from theoretical models to empirical evidence. *Philosophical Transactions of the Royal Society B* 373:20170009.
- Berleman, J. E., J. Scott, T. Chumley, and J. R. Kirby. 2008. Predatation behavior in *Myxococcus xanthus*. *Proceedings of the National Academy of Sciences of the USA* 105:17127–17132.
- Bigg, M. A., G. M. Ellis, J. K. B. Ford, and K. C. Balcomb. 1987. Killer whales: a study of their identification, genealogy, and natural history in British Columbia and Washington State. Phantom, Nanaimo, Canada.
- Bilde, T., K. S. Coates, K. Birkhofer, T. Bird, A. A. Maklakov, Y. Lubin, and L. Aviles. 2007. Survival benefits select for group living in a social spider despite reproductive costs. *Journal of Evolutionary Biology* 20:2412–2426.
- Blundell, G. M., M. Ben-David, and R. T. Bowyer. 2002. Sociality in river otters: cooperative foraging or reproductive strategies? *Behavioral Ecology* 13:134–141.
- Boesch, C., and H. Boesch. 1989. Hunting behavior of wild chimpanzees in the Taï National Park. *American Journal of Physical Anthropology* 78:547–573.
- Bowen, W. D. 1981. Variation in coyote social organization: the influence of prey size. *Canadian Journal of Zoology* 59:639–652.
- Bowyer, R. T., D. R. McCullough, and G. E. Belovsky. 2001. Causes and consequences of sociality in mule deer. *Alces* 37:371–402.
- Brandl, S. J., and D. R. Bellwood. 2015. Coordinated vigilance provides evidence for direct reciprocity in coral reef fishes. *Scientific Reports* 5:14556.
- Bshary, R., A. Hohner, K. Ait-el-Djoudi, and H. Fricke. 2006. Interspecific communicative and coordinated hunting between groupers and giant moray eels in the Red Sea. *PLoS Biology* 4:2393–2398.
- Campbell, G. S., B. A. Bilgre, and R. H. Defran. 2002. Bottlenose dolphins (*Tursiops truncatus*) in Turneffe Atoll, Belize: occurrence, site fidelity, group size, and abundance. *Aquatic Mammals* 28:170–180.
- Caraco, T., and L. L. Wolf. 1975. Ecological determinants of group sizes in foraging lions. *American Naturalist* 109:343–352.
- Carr, G. M., and D. W. Macdonald. 1986. The sociality of solitary foragers: a model based on resource dispersion. *Animal Behaviour* 34:1540–1549.
- Carrascal, L. M., and J. L. Tellería. 1990. Flock size of birds wintering in a cultivated area: influence of vegetation structure and type of diet. *Ekologia Polska* 38:201–210.
- Cerdá, X., and A. Dejean. 2011. Predation by ants on arthropods and other animals. Pages 39–78 in C. Polidori, ed. *Predation in Hymenoptera: an evolutionary perspective*. Transworld Research Network, Kerala, India.
- Chapman, C. A., and L. J. Chapman. 1999. Implications of small scale variation in ecological conditions for the diet and density of red colobus monkeys. *Primates* 40:215–231.
- Chapman, C. A., L. J. Chapman, and R. W. Wrangham. 1995. Ecological constraints on group size: an analysis of spider monkey and chimpanzee subgroups. *Behavioral Ecology and Sociobiology* 36:59–70.
- Chapman, C. A., and K. Valenta. 2015. Costs and benefits of group living are neither simple nor linear. *Proceedings of the National Academy of Sciences of the USA* 112:14751–14752.
- Clotuche, G., A. C. Mailleux, J. L. Deneubourg, G. J. Le Goff, T. Hance, and C. Detrain. 2010. Group effect on fertility, survival and silk production in the web spinner *Tetranychus urticae* (Acari: Tetranychidae) during colony foundation. *Behaviour* 147:1169–1184.
- Clotuche, G., A.-C. Mailleux, A. A. Fernández, J.-L. Deneubourg, C. Detrain, and T. Hance. 2011. The formation of collective silk balls in the spider mite *Tetranychus urticae* Koch. *PLoS ONE* 6: e18854.
- Cody, M. 1971. Finch flocks in the Mohave Desert. *Theoretical Population Biology* 2:142–158.
- Creel, S., and N. M. Creel. 1995. Communal hunting and pack size in African wild dogs, *Lycaon pictus*. *Animal Behaviour* 50:1325–1339.
- Crespi, B. J. 2001. The evolution of social behavior in microorganisms. *Trends in Ecology and Evolution* 16:178–183.
- Cresswell, W. 1994. Flocking is an effective anti-predation strategy in redshanks, *Tringa totanus*. *Animal Behaviour* 47:433–442.
- Czaczes, T. J., and F. L. W. Ratnieks. 2013. Cooperative transport in ants (Hymenoptera: Formicidae) and elsewhere. *Myrmecological News* 18:1–11.
- Damuth, J. 1987. Interspecific allometry of population density in mammals and other animals: the independence of body mass and population energy-use. *Biological Journal of the Linnean Society* 31:193–246.
- Dantzer, B., N. C. Bennett, and T. H. Clutton-Brock. 2017. Social conflict and costs of cooperation in meerkats are reflected in measures of stress hormones. *Behavioral Ecology* 28:1131–1141.
- Davies, N. B., and A. I. Houston. 1983. Time allocation between territories and flocks and owner-satellite conflict in foraging pied wagtails, *Motacilla alba*. *Journal of Animal Ecology* 52:621–634.
- Despland, E., and A. Le Huu. 2007. Pros and cons of group living in the forest tent caterpillar: separating the roles of silk and of grouping. *Entomologia Experimentalis et Applicata* 122:181–189.
- Dewanti, R., and A. C. L. Wong. 1995. Influence of culture conditions on biofilm formation by *Escherichia coli* O157:H7. *International Journal of Food Microbiology* 26:147–164.
- Ebensperger, L. A., M. J. Hurtado, and R. Ramos-Jiliberto. 2006. Vigilance and collective detection of predators in degus (*Octodon degus*). *Ethology* 112:879–887.
- Ebert, D. A. 1991. Observations on the predatory behaviour of the sevengill shark *Notorynchus cepedianus*. *South African Journal of Marine Science* 11:455–465.
- Elgar, M. A. 1987. Food intake rate and resource availability: flocking decisions in house sparrows. *Animal Behaviour* 35:1168–1176.
- Emlen, S. T., and L. W. Oring. 1977. Ecology, sexual selection, and the evolution of mating systems. *Science* 197:215–223.
- Fernández, G. J., A. F. Capurro, and J. C. Reboreda. 2003. Effect of group size on individual and collective vigilance in greater rheas. *Ethology* 109:413–425.
- Fernández-Juricic, E., G. Beauchamp, and B. Bastain. 2007. Group-size and distance-to-neighbour effects on feeding and vigilance in brown-headed cowbirds. *Animal Behaviour* 73:771–778.
- Fish, F. E. 1995. Kinematics of ducklings swimming in formation: consequences of position. *Journal of Experimental Zoology* 273:1–11.
- Fisher, R. M., and B. Regenber. 2019. Multicellular group formation in *Saccharomyces cerevisiae*. *Proceedings of the Royal Society B* 286:20191098.
- Flack, A., M. Nagy, W. Fiedler, I. D. Couzin, and M. Wikelski. 2018. From local collective behavior to global migratory patterns in white storks. *Science* 360:911–914.

- Foster, E. A., D. W. Franks, L. J. Morrell, K. C. Balcomb, K. M. Parsons, A. van Ginneken, and D. P. Croft. 2012. Social network correlates of food availability in an endangered population of killer whales, *Orcinus orca*. *Animal Behaviour* 83:731–736.
- Foster, S. A. 1985. Group foraging by a coral reef fish: a mechanism for gaining access to defended resources. *Animal Behaviour* 33:782–792.
- Fraleigh, P. C., and J. C. Burnham. 1988. Myxococcal predation on cyanobacterial populations: nutrient effects. *Limnology and Oceanography* 33:476–483.
- Fronhofer, E. A., J. Liebig, O. Mitesser, and H. J. Poethke. 2018. Eusociality outcompetes egalitarian and solitary strategies when resources are limited and reproduction is costly. *Ecology and Evolution* 8:12953–12964.
- Gadagkar, R., and J. Bonner. 1994. Social insects and social amoebae. *Journal of Biosciences* 19:219–245.
- Gimeno, C. J., P. O. Ljungdahl, C. A. Styles, and G. R. Fink. 1992. Unipolar cell divisions in the yeast *S. cerevisiae* lead to filamentous growth: regulation by starvation and RAS. *Cell* 68:1077–1090.
- Giraldeau, L.-A. 1988. The stable group and the determinants of foraging group size. Pages 33–53 in C. N. Slobodchikoff, ed. *The ecology of social behavior*. Academic Press, San Diego, CA.
- Grant, P. R., and B. R. Grant. 2002. Unpredictable evolution in a 30-year study of Darwin's finches. *Science* 296:707–711.
- Greene, E. 1987. Individuals in an osprey colony discriminate between high and low quality information. *Nature* 329:239–241.
- Götmark, F., D. W. Winkler, and M. Andersson. 1986. Flock-feeding on fish schools increases individual success in gulls. *Nature* 319:589–591.
- Guerra, A. S., A. B. Kao, D. J. McCauley, and A. M. Berdahl. 2020. Fisheries-induced selection against schooling behaviour in marine fishes. *Proceedings of the Royal Society B* 287:20201752.
- Guinet, C., L. G. Barrett-Lennard, and B. Loyer. 2000. Coordinated attack behavior and prey sharing by killer whales at Crozet archipelago: strategies for feeding on negatively-buoyant prey. *Marine Mammal Science* 16:829–834.
- Hardie, S. M., and H. M. Buchanan-Smith. 1997. Vigilance in single- and mixed-species groups of tamarins (*Saguinus labiatus* and *Saguinus fuscicollis*). *International Journal of Primatology* 18:217–234.
- Hartwell, K. S., H. Notman, U. Kalbitzer, C. A. Chapman, and M. M. Pavelka. 2021. Fruit availability has a complex relationship with fission-fusion dynamics in spider monkeys. *Primates* 62:165–175.
- Hector, D. P. 1986. Cooperative hunting and its relationship to foraging success and prey size in an avian predator. *Ethology* 73:247–257.
- Helms Cahan, S., D. T. Blumstein, L. Sundström, J. Liebig, and A. Griffin. 2002. Social trajectories and the evolution of social behavior. *Oikos* 96:206–216.
- Henzi, S. P., D. Lussea, T. Weingrill, C. P. Van Schaik, and L. Barrett. 2009. Cyclicity in the structure of female baboon social networks. *Behavioral Ecology and Sociobiology* 63:1015–1021.
- Herrera, E. A., and D. W. Macdonald. 1989. Resource utilization and territoriality in group-living capybaras (*Hydrochoerus hydrochaeris*). *Journal of Animal Ecology* 58:667–679.
- Horn, H. S. 1968. The adaptive significance of colonial nesting in the Brewer's blackbird (*Euphagus cyanocephalus*). *Ecology* 49:682–694.
- Ioannou, C. C., V. Guttal, I. D. Couzin. 2012. Predatory fish select for coordinated collective motion in virtual prey. *Science* 337:1212–1215.
- Johnson, D. D. P., R. Kays, P. G. Blackwell, and D. W. Macdonald. 2002. Does the resource dispersion hypothesis explain group living? *Trends in Ecology and Evolution* 17:563–570.
- Johnson, R. A. 2004. Colony founding by pleometrosis in the semiclaustral seed-harvester ant *Pogonomyrmex californicus* (Hymenoptera: Formicidae). *Animal Behaviour* 68:1189–1200.
- Jurasz, C. M., and V. P. Jurasz. 1979. Feeding modes of the humpback whale, *Megaptera novaeangliae*, in southeast Alaska. *Scientific Reports of the Whales Research Institute* 31:69–83.
- Kao, A. B., A. K. Hund, F. P. Santos, J.-G. Young, D. Bhat, J. Garland, R. A. Oomen, and H. F. McCreery. 2023. Data from: Opposing responses to scarcity emerge from functionally unique sociality drivers. *American Naturalist*, Figshare, <http://doi.org/10.6084/m9.figshare.11961879>.
- Keane, R., and J. Berleman. 2016. The predatory life cycle of *Myxococcus xanthus*. *Microbiology* 162:1–11.
- Korb, J., and J. Heinze. 2016. Major hurdles for the evolution of sociality. *Annual Review of Entomology* 61:297–316.
- Koschwanez, J. H., K. R. Foster, and A. W. Murray. 2011. Sucrose utilization in budding yeast as a model for the origin of undifferentiated multicellularity. *PLoS Biology* 9:e1001122.
- Krause, J., and G. D. Ruxton. 2002. *Living in groups*. Oxford University Press, Oxford.
- Kronenberg, F., and H. C. Heller. 1982. Colonial thermoregulation in honey bees (*Apis mellifera*). *Journal of Comparative Physiology B* 148:65–76.
- Lamprecht, J. 1981. The function of social hunting in larger terrestrial carnivores. *Mammal Review* 11:169–179.
- Lang, S. D. J., and D. R. Farine. 2017. A multidimensional framework for studying social predation strategies. *Nature Ecology and Evolution* 1:1230–1239.
- Langen, T. A., and S. L. Vehrencamp. 1998. Ecological factors affecting group and territory size in white-throated magpie-jays. *Auk* 115:327–339.
- Lehmann, K. D., T. M. Montgomery, S. M. MacLachlan, J. M. Parker, O. S. Spagnuolo, K. J. VandeWetering, P. S. Bills, and K. E. Holekamp. 2017. Lions, hyenas and mobs (oh my!). *Current Zoology* 63:313–322.
- Lönstedt, O. M., M. C. O. Ferrari, and D. P. Chivers. 2014. Lionfish predators use flared fin displays to initiate cooperative hunting. *Biology Letters* 10:20140281.
- Lott, D. F. 1991. Intraspecific variation in the social systems of wild vertebrates. *Behaviour* 88:266–325.
- Lowen, C., and R. I. M. Dunbar. 1994. Territory size and defendability in primates. *Behavioral Ecology and Sociobiology* 35:347–354.
- Macdonald, D. W. 1983. The ecology of carnivore social behaviour. *Nature* 301:379–384.
- Majer, M., C. Holm, Y. Lubin, and T. Bilde. 2018. Cooperative foraging expands dietary niche but does not offset intra-group competition for resources in social spiders. *Scientific Reports* 8:11828.
- Markham, A. C., L. R. Gesquiere, S. C. Alberts, and J. Altmann. 2015. Optimal group size in a highly social mammal. *Proceedings of the National Academy of Sciences of the USA* 112:14882–14887.
- Marras, S., S. S. Killen, J. Lindström, D. J. McKenzie, J. F. Steffensen, and P. Domenici. 2015. Fish swimming in schools save energy regardless of their spatial position. *Behavioral Ecology and Sociobiology* 69:219–226.
- Matsuura, K., and T. Nishida. 2001. Comparison of colony foundation success between sexual pairs and female asexual units in



- the termite *Reticulitermes speratus* (Isoptera: Rhinotermitidae). *Population Ecology* 43:119–124.
- Mayer, C., and G. Pasinelli. 2013. New support for an old hypothesis: density affects extra-pair paternity. *Ecology and Evolution* 3:694–705.
- McCreery, H. F., and M. D. Breed. 2014. Cooperative transport in ants: a review of proximate mechanisms. *Insectes Sociaux* 61:99–110.
- Mintzer, A. C. 1987. Primary polygyny in the ant *Atta texana*: number and weight of females and colony foundation success in the laboratory. *Insectes Sociaux* 34:108–117.
- Mosser, A., and C. Packer. 2009. Group territoriality and the benefits of sociality in the African lion, *Panthera leo*. *Animal Behaviour* 78:359–370.
- Nunn, C. L., P. H. Thrall, K. Stewart, and A. H. Harcourt. 2008. Emerging infectious diseases and animal social systems. *Evolutionary Ecology* 22:519–543.
- Orians, G. H. 1969. On the evolution of mating systems in birds and mammals. *American Naturalist* 103:589–603.
- Packer, C., and L. Rutan. 1988. The evolution of cooperative hunting. *American Naturalist* 132:159–198.
- Packer, C., D. Scheel, and A. E. Pusey. 1990. Why lions form groups: food is not enough. *American Naturalist* 136:1–19.
- Palmer, T. M. 2004. Wars of attrition: colony size determines competitive outcomes in a guild of African acacia ants. *Animal Behaviour* 68:993–1004.
- Pitcher, T. J., A. E. Magurran, and I. J. Winfield. 1982. Fish in larger shoals find food faster. *Behavioral Ecology and Sociobiology* 10:149–151.
- Portugal, S. J., T. Y. Hubel, J. Fritz, S. Heese, D. Trobe, B. Voelkl, S. Hailes, A. M. Wilson, and J. R. Usherwood. 2014. Upwash exploitation and downwash avoidance by flap phasing in ibis formation flight. *Nature* 505:399–402.
- Powers, K. S., and L. Avilés. 2007. The role of prey size and abundance in the geographical distribution of spider sociality. *Journal of Animal Ecology* 76:995–1003.
- Prediger, S., B. Volland, and B. Herrmann. 2014. Resource scarcity and antisocial behavior. *Journal of Public Economics* 119:1–9.
- Pride, R. E. 2005. Optimal group size and seasonal stress in ring-tailed lemurs (*Lemur catta*). *Behavioral Ecology* 16:550–560.
- Pride, R. E., D. Felantsoa, T. M. Randriamboavonjy, and R. Randriambelona. 2006. Resource defense in *Lemur catta*: the importance of group size. Pages 280–232 in A. Jolly, R. W. Sussman, N. Koyama, and H. Rasamimanana, eds. *Ringtailed lemur biology. Developments in Primatology: Progress and Prospect*. Springer, Boston.
- Pruitt, J. N., A. Berdahl, C. Riehl, N. Pinter-Wollman, H. V. Moeller, E. G. Pringle, L. M. Aplin, et al. 2018. Social tipping points in animal societies. *Proceedings of the Royal Society B* 285:20181282.
- Pull, C. D., W. O. H. Hughes, and M. J. F. Brown. 2013. Tolerating an infection: an indirect benefit of co-founding queen associations in the ant *Lasius niger*. *Naturwissenschaften* 100:1125–1136.
- Rehan, S. M., M. P. Schwarz, and M. H. Richards. 2011. Fitness consequences of ecological constraints and implications for the evolution of sociality in an incipiently social bee. *Biological Journal of the Linnean Society* 103:57–67.
- Regenberg, B., K. E. Hanghøj, K. S. Andersen, and J. J. Boomsma. 2016. Clonal yeast biofilms can reap competitive advantages through cell differentiation without being obligatorily multicellular. *Proceedings of the Royal Society B* 283:20161303.
- Rigali, S., F. Titgemeyer, S. Barends, S. Mulder, A. W. Thomae, D. A. Hopwood, and G. P. van Wezel. 2008. Feast or famine: the global regulator DasR links nutrient stress to antibiotic production by *Streptomyces*. *EMBO Reports* 9:670–675.
- Ritz, D. A. 2000. Is social aggregation in aquatic crustaceans a strategy to conserve energy? *Canadian Journal of Fisheries and Aquatic Sciences* 57:59–67.
- Romanczuk, P., I. D. Couzin, and L. Schimansky-Geier. 2009. Collective motion due to individual escape and pursuit response. *Physical Review Letters* 102:010602.
- Román-Palacios, C., and J. J. Wiens. 2020. Recent responses to climate change reveal the drivers of species extinction and survival. *Proceedings of the National Academy of Sciences of the USA* 117:4211–4217.
- Rosenberg, E., K. H. Keller, and M. Dworkin. 1977. Cell density dependent growth of *Myxococcus xanthus* on casein. *Journal of Bacteriology* 129:770–777.
- Rosser, A. G., R. Ishii, T. Amemiya, and K. Itoh. 2008. The top-down mechanism for body-mass-abundance scaling. *Ecology* 89:567–580.
- Rubenstein, D. R., and P. Abbot. 2017. *Comparative social evolution*. Cambridge University Press, Cambridge.
- Shen, S. F., S. T. Emlen, W. D. Koenig, and D. R. Rubenstein. 2017. The ecology of cooperative breeding behaviour. *Ecology Letters* 20:708–720.
- Shimkets, L. J. 1999. Intercellular signalling during fruiting-body development of *Myxococcus xanthus*. *Annual Reviews in Microbiology* 53:525–549.
- Silk, J. B. 2007. The adaptive value of sociality in mammalian groups. *Philosophical Transactions of the Royal Society B* 362:539–559.
- Simpson, S. J., G. A. Sword, P. D. Lorch, and I. D. Couzin. 2006. Cannibal crickets on a forced march for protein and salt. *Proceedings of the National Academy of Sciences of the USA* 103:4152–4156.
- Smith, J., D. C. Queller, and J. E. Strassmann. 2014. Fruiting bodies of the social amoeba *Dictyostelium discoideum* increase spore transport by *Drosophila*. *BMC Ecology and Evolution* 14:105.
- Smith, J. E., J. M. Kolowski, K. E. Graham, S. E. Dawes, and K. E. Holekamp. 2008. Social and ecological determinants of fission-fusion dynamics in the spotted hyaena. *Animal Behaviour* 76:619–636.
- Snijders, L., R. H. J. M. Kurvers, S. Krause, I. W. Ramnarine, and J. Krause. 2018. Individual- and population-level drivers of consistent foraging success across environments. *Nature Ecology and Evolution* 2:1610–1618.
- Solari, C. A., R. E. Michod, and R. E. Goldstein. 2008. *Volvox barberi*, the fastest swimmer of the Volvocales (Chlorophyceae). *Journal of Phycology* 44:1395–1398.
- South, J., and S. Pruett-Jones. 2000. Patterns of flock size, diet, and vigilance of naturalized monk parakeets in Hyde Park, Chicago. *Condor* 102:848–854.
- Stander, P. E., and S. D. Albon. 1993. Hunting success of lions in a semi-arid environment. *Symposia of the Zoological Society of London* 65:127–143.
- Steenbeek, R., and C. P. van Schaik. 2001. Competition and group size in Thomas's langurs (*Presbytis thomasi*): the folivore paradox revisited. *Behavioral Ecology and Sociobiology* 49:100–110.



- Sumpter, D. J. 2010. *Collective animal behavior*. Princeton University Press, Princeton, NJ.
- Sutherland, K. R., and D. Weihs. 2017. Hydrodynamic advantages of swimming by salp chains. *Journal of the Royal Society Interface* 14:20170298.
- Taraborelli, P., and P. Moreno. 2009. Comparing composition of social groups, mating system and social behaviour in two populations of *Micvocavia australis*. *Mammalian Biology* 74:15–24.
- Tsubaki, Y., and Y. Shiotsu. 1982. Group feeding as a strategy for exploiting food resources in the burnet moth *Pryeria sinica*. *Oecologia* 55:12–20.
- Valeix, M., A. J. Loveridge, and D. W. Macdonald. 2012. Influence of prey dispersion on territory and group size of African lions: a test of the resource dispersion hypothesis. *Ecology* 93:2490–2496.
- Van Orsdol, K. G., J. P. Hanby, and J. D. Bygott. 1985. Ecological correlates of lion *Panthera leo* social organization. *Journal of Zoology London* 206:97–112.
- Ward, A. J. W., J. E. Herbert-Read, D. J. T. Sumpter, and J. Krause. 2011. Fast and accurate decisions through collective vigilance in fish shoals. *Proceedings of the National Academy of Sciences of the USA* 108:2312–2315.
- Weimerskirch, H., J. Martin, Y. Clerquin, P. Alexandre, and S. Jiraskova. 2001. Energy saving in flight formation. *Nature* 413:697–698.
- White, E. P., S. K. Ernest, A. J. Kerkhoff, and B. J. Enquist. 2007. Relationships between body size and abundance in ecology. *Trends Ecology and Evolution* 22:323–330.
- Williams, P., M. Camara, A. Hardman, S. Swift, D. Milton, V. J. Hope, K. Winzer, B. Middleton, D. I. Pritchard, and B. W. Bycroft. 2000. Quorum sensing and the population-dependent control of virulence. *Philosophical Transactions of the Royal Society B* 355:667–680.
- Willis, C. K. R., and R. M. Brigham. 2007. Social thermoregulation exerts more influence than microclimate on forest roost preferences by a cavity-dwelling bat. *Behavioral Ecology and Sociobiology* 62:97–108.
- Wong, B. B. M., and U. Candolin. 2015. Behavioral responses to changing environments. *Behavioral Ecology* 26:665–673.
- Wrangham, R. W. 1980. An ecological model of female-bonded primate groups. *Behaviour* 75:262–300.
- Yip, E. C., K. S. Powers, and L. Avilés. 2008. Cooperative capture of large prey solves scaling challenge faced by spider societies. *Proceedings of the National Academy of Sciences of the USA* 105:11818–11822.
- Zhang, W., A. Seminara, M. Suaris, M. P. Brenner, D. A. Weitz, and T. E. Angelini. 2014. Nutrient depletion in *Bacillus subtilis* biofilms triggers matrix production. *New Journal of Physics* 16:015028.
- Brandl, R., M. Hacker, R. K. N. Bagine, and M. Kaib. 2001. Geographic variation of polygyny in the termite *Macrotermes michaelseni* (Sjöstedt). *Insectes Sociaux* 48:134–137.
- Brashares, J. S., and P. Arcese. 2002. Role of forage, habitat and predation in the behavioural plasticity of a small African antelope. *Journal of Animal Ecology* 71:626–638.
- Brotons, L., and S. Herrando. 2003. Effect of increased food abundance near forest edges on flocking patterns of coal tit *Parus ater* winter groups in mountain coniferous forests. *Bird Study* 50:106–111.
- Bull, N. J., and M. P. Schwarz. 1996. The habitat saturation hypothesis and sociality in an allodapine bee: cooperative nesting is not “making the best of a bad situation.” *Behavioral Ecology and Sociobiology* 39:267–274.
- Chapman, C. A. 1990. Ecological constraints on group size in three species of Neotropical primates. *Folia Primatologica* 55: 1–9.
- Chapman, C. A., L. J. Chapman, and L. Lefebvre. 1989. Variability in parrot flock size: possible functions of communal roosts. *Condor* 91:842–847.
- Chaverri, G., and E. H. Gillam. 2010. Cooperative signaling behavior of roost location in a leaf-roosting bat. *Communicative and Integrative Biology* 3:599–601.
- Davies, N. B., and A. I. Houston. 1981. Owners and satellites: the economics of territory defence in the pied wagtail, *Motacilla alba*. *Journal of Animal Ecology* 50:157–180.
- Doran, D. 1997. Influence of seasonality on activity patterns, feeding behavior, ranging, and grouping patterns in Tai chimpanzees. *International Journal of Primatology* 18:183–206.
- Dunbar, R. I. M. 1987. Habitat quality, population dynamics, and group composition in colobus monkeys (*Colobus guereza*). *International Journal of Primatology* 8:299–329.
- Ebensperger, L. A., F. Pérez de Arce, S. Abades, and L. D. Hayes. 2016. Limited and fitness-neutral effects of resource heterogeneity on sociality in a communally rearing rodent. *Journal of Mammalogy* 97:1125–1135.
- Halat, Z., D. K. N. Dechmann, M. Zegarek, A. E. J. Visser, and I. Ruczyński. 2018. Sociality and insect abundance affect duration of nocturnal activity of male parti-colored bats. *Journal of Mammalogy* 99:1503–1509.
- Harris, T. R., C. A. Chapman, and S. L. Monfort. 2010. Small folivorous primate groups exhibit behavioral and physiological effects of food scarcity. *Behavioral Ecology* 21:46–56.
- Helms Cahan, S., and K. R. Helms. 2012. Relatedness does not explain geographic variation in queen cooperation in the seed-harvester ant *Messor pergandei*. *Insectes Sociaux* 59:579–585.
- Hoare, D. J., I. D. Couzin, J. G. J. Godin, and J. Krause. 2004. Context-dependent group size choice in fish. *Animal Behaviour* 67:155–164.
- Huynh, T. T., D. McDougald, J. Klebensberger, B. Al Qarni, N. Barraud, S. A. Rice, S. Kjelleberg, and D. Schleheck. 2012. Glucose starvation-induced dispersal of *Pseudomonas aeruginosa* biofilms is cAMP and energy dependent. *PLoS ONE* 7:e42874.
- Isbell, L. A. 2012. Re-evaluating the ecological constraints model with red colobus monkeys (*Procolobus rufomitratu tephrosceles*). *Behaviour* 149:493–529.
- Kagata, H., and T. Ohgushi. 2002. Clutch size adjustment of a leaf-mining moth (Lyonetiidae: Lepidoptera) in response to resource availability. *Annals of the Entomological Society of America* 95:213–217.

### References Cited Only in the Online Enhancements

- Asensio, N., A. H. Korstjens, and F. Aureli. 2009. Fissioning minimizes ranging costs in spider monkeys: a multiple-level approach. *Behavioral Ecology and Sociobiology* 63:649–659.
- Baden, A. L., T. H. Webster, and J. M. Kamilar. 2016. Resource seasonality and reproduction predict fission-fusion dynamics in black-and-white ruffed lemurs (*Varecia variegata*). *American Journal of Primatology* 78:256–279.
- Bernstein, R. A. 1975. Foraging strategies of ants in response to variable food density. *Ecology* 56:213–219.

- Karczmarski, L., V. G. Cockcroft, and A. McLachlan. 1999. Group size and seasonal pattern of occurrence of humpback dolphins *Sousa chinensis* in Algoa Bay, South Africa. *South African Journal of Marine Science* 21:89–97.
- Kawaguchi, S., R. King, R. Meijers, J. E. Osborn, K. M. Swadling, D. A. Ritz, and S. Nicol. 2010. An experimental aquarium for observing the schooling behaviour of Antarctic krill (*Euphausia superba*). *Deep Sea Research Part II: Topical Studies in Oceanography* 57:683–692.
- Kelly, B., G. E. Carrizo, J. Edwards-Hicks, D. E. Sanin, M. A. Stanczak, C. Priesnitz, L. J. Flachsmann, et al. 2021. Sulfur sequestration promotes multicellularity during nutrient limitation. *Nature* 591:471–476.
- Kinnaird, M. F., T. G. O'Brien, and S. Suryadi. 1996. Population fluctuation in Sulawesi red-knobbed hornbills: tracking figs in space and time. *Auk* 113:431–440.
- Koppik, M., A. Thiel, and T. S. Hoffmeister. 2014. Adaptive decision making or differential mortality: what causes offspring emergence in a gregarious parasitoid? *Entomologia Experimentalis et Applicata* 150:208–216.
- Krause, J. 1993. The influence of hunger on shoal size choice by three-spined sticklebacks, *Gasterosteus aculeatus*. *Journal of Fish Biology* 43:775–780.
- Kushlan, J. A. 1981. Resource use strategies of wading birds. *Wilson Bulletin* 93:145–163.
- Lawson, G. L., D. L. Kramer, and W. Hunte. 1999. Size-related habitat use and schooling behavior in two species of surgeonfish (*Acanthurus bahianus* and *A. coeruleus*) on a fringing reef in Barbados, West Indies. *Environmental Biology of Fishes* 54:19–33.
- Majer, M., J.-C. Svenning, and T. Bilde. 2015. Habitat productivity predicts the global distribution of social spiders. *Frontiers in Ecology and Evolution* 3:101.
- Randall, J. A., K. Rogovin, P. G. Parker, and J. A. Eimes. 2005. Flexible social structure of a desert rodent, *Rhombomys opimus*: philopatry, kinship, and ecological constraints. *Behavioral Ecology* 16:961–973.
- Rimbach, R., A. Link, A. Montes-Rojas, A. Di Fiore, M. Heistermann, and E. W. Heymann. 2014. Behavioral and physiological responses to fruit availability of spider monkeys ranging in a small forest fragment. *American Journal of Primatology* 76:1049–1061.
- Rodewald, P. G., and M. C. Brittingham. 2002. Habitat use and behavior of mixed species landbird flocks during fall migration. *Wilson Bulletin* 114:87–98.
- Schaffner, C. M., L. Rebecchini, G. Ramos-Fernandez, L. G. Vick, and F. Aureli. 2012. Spider monkeys (*Ateles geoffroyi yucatanensis*) cope with the negative consequences of hurricanes through changes in diet, activity budget, and fission-fusion dynamics. *International Journal of Primatology* 33:922–936.
- Seddon, P. J., and Y. van Heezik. 1996. Seasonal changes in Houbara bustard *Chlamydotis undulata macqueenii* numbers in Harrat Al Harrah, Saudi Arabia: implications for managing a remnant population. *Biological Conservation* 75:139–146.
- Skinner, J. D., R. J. Van Aarde, and R. A. Goss. 1995. Space and resource use by brown hyenas *Hyaena brunnea* in the Namib Desert. *Journal of Zoology* 237:123–131.
- Smith-Aguilar, S. E., G. Ramos-Fernández, and W. M. Getz. 2016. Seasonal changes in socio-spatial structure in a group of free-living spider monkeys (*Ateles geoffroyi*). *PLoS ONE* 11:e0157228.
- Strand, S. W., and W. M. Hamner. 1990. Schooling behavior of Antarctic krill (*Euphausia superba*) in laboratory aquaria: reactions to chemical and visual stimuli. *Marine Biology* 106:355–359.
- Struhsaker, T. T., A. R. Marshall, K. Detwiler, K. Siex, C. Ehardt, D. D. Lisbjerg, and T. M. Butynski. 2004. Demographic variation among Udzungwa red colobus in relation to gross ecological and sociological parameters. *International Journal of Primatology* 25:615–658.
- Sugardjito, J., I. J. A. te Boekhorst, and J. A. R. A. M. Van Hooff. 1987. Ecological constraints on the grouping of wild orangutans (*Pongo pygmaeus*) in the Gunung Leuser National Park, Sumatra, Indonesia. *International Journal of Primatology* 8:17–41.
- Yang, L., L. Zhou, and Y. Song. 2015. The effects of food abundance and disturbance on foraging flock patterns of the wintering hooded crane (*Grus monacha*). *Avian Research* 6:15.

Associate Editor: Michael J. Sheehan  
Editor: Erol Akçay



A subset of the authors of this article working on the initial version of the modeling framework during a working group meeting in Tesuque, New Mexico, February 3–7, 2019, supported by the Santa Fe Institute. Photo by Amanda Hund.