

Changes in group size during resource shifts reveal drivers of sociality across the tree of life

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ABSTRACT

From biofilms to whale pods, organisms have repeatedly converged on sociality as a strategy to improve individual fitness. Yet, it remains challenging to identify the most important drivers—and by extension, the evolutionary mechanisms—of sociality for particular species. Here, we present a conceptual framework, literature review, and model demonstrating that the direction and magnitude of the response of group size to sudden resource shifts provides a strong indication of the underlying drivers of sociality. We catalog six functionally distinct mechanisms related to the acquisition of resources, and we model these mechanisms' effects on the survival of individuals foraging in groups. We find that whether, and to what degree, optimal group size increases, decreases, or remains constant when resource abundance declines depends strongly on the dominant mechanism. Existing empirical data support our model predictions, and we demonstrate how our framework can be used to predict the dominant social benefit for particular species. Together, our framework and results show that a single easily measurable characteristic, namely, group size under different resource abundances, can illuminate the potential drivers of sociality across the tree of life.

Key words

social behavior, resource abundance, resource scarcity, evolution, optimal group size, cooperation

Introduction

Living in a group can benefit an organism in numerous and diverse ways^{1–4}. Sociality may improve an organism's caloric intake^{5–8}, reduce the costs of maintaining homeostasis^{9–11}, decrease predation risk^{12–15}, facilitate the discovery or defense of higher quality habitats or breeding sites^{16–18}, increase the probability of finding a mate or opportunities for extra-pair copulations^{4,19,20}, or increase the survival probability of offspring^{18,21,22}. However, there are also many potential costs of group living, including increased competition over resources, disease risk⁴, and probability of infanticide^{23,24}.

A large body of literature explores how particular costs and benefits may affect group size and other social metrics^{25–30}, yet it remains challenging to identify the most important drivers of sociality in particular species. For a given species, a subset of the potential benefits and costs will tend to dominate, and the balance of their magnitudes will determine the overall selection pressure for an organism to be social or asocial (as well as the typical group size)^{31–33}. Knowledge of the underlying drivers of sociality is crucial not only for understanding the present distribution of social species and group sizes across taxa, but also for understanding the major evolutionary pathways by which sociality has arisen³⁴ (*i.e.*, whether sociality has generally been driven by a subset of potential benefits, with secondary benefits accruing subsequently), as well as the future of social species in the face of emerging natural and anthropogenic threats^{35–39}.

32 In practice, measuring the selection pressures driving sociality is difficult. It may require performing one or more
33 experiments for each potential benefit of sociality, and the magnitude of a benefit may vary nonlinearly with group size and
34 across different environmental contexts^{22, 25, 27, 29, 40–42}. As a result, it is likely infeasible to comprehensively measure all of the
35 selection pressures governing sociality for any species. Instead, studies typically isolate and study only one of the proximate
36 mechanisms at a time. Studying a mechanism in isolation may allow researchers to determine whether that mechanism offers a
37 measurable benefit (or cost) to group living, but cannot provide insight into its magnitude relative to other potential benefits and
38 costs. Therefore, this strategy is unlikely to reveal the dominant drivers of sociality.

39 Here, we demonstrate a new approach to the problem of determining the drivers of sociality, using literature reviews, a new
40 conceptual framework, and stochastic and analytic models. In nature, when the abundance of resources (*e.g.*, food) shifts over
41 relatively short time scales⁴³, the mean group size has been empirically observed to shrink for some species⁴⁴, increase for
42 others⁴⁵, and remain constant for yet other species. We hypothesize that these differences in the direction in which group sizes
43 shift when resources become scarce may be due to differences in the dominant driver of sociality across those species^{46, 47}. If
44 true, then observing changes in group size when resource abundance shifts could be a relatively simple method to generate a
45 shortlist of likely drivers of sociality for a given species. Further experiments could then target those specific candidate drivers,
46 in order to identify the dominant driver of sociality for particular species, and across taxa. Because resource availability is
47 relatively easy to alter in the lab and group size easy to measure, this may be an experimentally tractable strategy to rapidly
48 identify the dominant drivers of sociality.

49 Results

50 The fundamental resource-related benefits and costs of sociality

51 We first surveyed the literature and compiled a list of potential benefits of sociality, focusing on those related to gaining and
52 consuming resources. We took a broad definition of “sociality” to include any group-living organism in a wide range of taxa,
53 including bacteria, protists, fungi, arthropods, fish, birds, and mammals. Despite myriad resource-related benefits described
54 across taxa in the literature⁴⁸, we found that they could be condensed into a small set of functionally distinct classes. In total,
55 we identified six fundamental benefits of sociality related to gaining or using resources (Table 1). We also recorded a wide
56 range of non-resource-related benefits and costs of sociality, but we collapsed them into a single class, despite their variety,
57 because they are generally indistinguishable from one another when studying how group size changes under shifting resource
58 abundance.

59 Fundamental resource-related benefits of sociality

60 Collective territoriality: Larger groups are able to secure access to more resources. This describes organisms that can
occupy larger territories, or those that can travel further as a group in order to explore a larger area. For example, larger
groups of capybaras have larger and higher-quality home ranges⁴⁹, while larger *Volvox* colonies can move farther in the
water column to exploit a larger productive area⁵⁴.

61 Collective detection/capture: Larger groups detect and capture a resource with higher probability. This benefit may
occur because larger groups have a higher probability of detecting a resource (*e.g.*, individuals in larger groups spend
less time looking for predators due to “shared vigilance,” allowing them to devote more time to foraging) or of capturing
a detected resource. For example, degus spend less time individually on vigilance and more time foraging when in
groups⁵⁷, goldfish in larger shoals spend less time foraging before discovering a prey item⁶¹, and *Myxococcus* bacteria
more efficiently predate on cyanobacteria at higher densities⁷⁰.

62 Collective niche expansion: Larger groups can successfully capture larger or higher-quality resources. This benefit
expands the dietary niche of the social species by giving members of large groups access to novel resources, rather
than simply increasing the probability of capturing a resource that is also accessible to smaller groups (collective
sensing/capture). This includes social spiders that use collective web structures to capture larger prey^{7, 72, 73}, and some
pathogenic bacteria that suppress their virulence until a quorum is reached, in order to overcome a host’s immune
responses^{77, 78}.

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 ⁴⁹ , white-throated magpie-jays ⁵⁰ , coyote packs ⁵¹ , acacia ants ⁵² , chimpanzees ⁵³ , <i>Volvox</i> colonies ⁵⁴ , ring-tailed lemurs ⁶
Collective detection/capture	Increase probability of capturing a resource	Spending less time looking for predators	mule deer ⁵⁵ , greater rheas ⁵⁶ , degus ⁵⁷ , brown-headed cowbirds ⁵⁸ , rabbitfishes ⁵⁹ , tamarins ⁶⁰
		Detecting resources with higher probability	goldfish ⁶¹ , forest tent caterpillars ⁶² , mixed bird flocks ⁶³ , Brewer's blackbirds ⁶⁴ , guppies ⁶⁵
		Capturing resources with higher probability	zebra lionfish ⁸ , aplomado falcons ⁶⁶ , lions ⁶⁷ , groupers and giant moray eels ⁶⁸ , chimpanzees ⁶⁹ , bacteria ⁷⁰ , spinner dolphins ⁷¹
Collective niche expansion	Increasing size range of resources that can be captured	Hunting larger or higher quality prey	social spiders ^{7,72,73} , African wild dogs ⁷⁴ , ant predation ⁷⁵ , Harris' hawks ⁷⁶ , bacteria ^{77,78} , sevengill sharks ⁷⁹ , orcas ^{80,81} , river otters ⁸²
Collective consumption	Increase the amount of resource consumed per capita	Defending kill from others	hyenas ^{44,83} , coyotes ⁵ , antibiotic production in bacteria ⁸⁴ , primates ⁴⁷ , resources monopolization in yeast ⁸⁵ , ant cooperative transport ^{86,87}
		Slowing diffusion of nutrients	bacteria ⁸⁸ , budding yeast ⁸⁹
		Capturing a larger fraction of prey group	bubble-net feeding in humpback whales ⁹⁰ , ospreys ⁹¹ , leaf-notching moths ⁹² , black-headed gulls ⁹³ , blue tang surgeonfish ⁹⁴ , bacteria ⁹⁵ , orcas ⁹⁶
Collective energetics	Decrease rate of energy expenditure	Moving more efficiently	grey mullet ⁹⁷ , ducklings paddling on water ⁹⁸ , great white pelicans in flight ⁹⁹ , aquatic crustaceans ¹⁰⁰
		Spending less energy on homeostasis	emperor penguins ¹⁰¹ , honeybees ¹⁰² , big brown bats ¹⁰³ , cavies ¹⁰⁴
Collective dispersal	Increase probability of successful dispersal	Moving away from current environment faster	Mormon crickets ¹⁰⁵⁻¹⁰⁷ , colonial salps ¹⁰⁸ , fruiting-body-assisted dispersal in <i>Dictyostelium</i> ¹⁰⁹ and <i>Myxobacteria</i> ¹¹⁰ , spider mites ¹¹¹
		Accessing collective benefits while dispersing	storks locating thermals ¹¹² , V-formations in northern bald ibises ¹¹³
		Accessing collective benefits in new environment	ants (<i>Pogonomyrmex</i> ¹¹⁴ , <i>Atta</i> ¹¹⁵ , <i>Lasius</i> ¹¹⁶), termites ¹¹⁷ , spider mites ¹¹⁸ founding new colonies

Table 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 in different taxa, and list several examples of the benefit across diverse taxa. In addition to these six resource-related benefits, in our model we include the net effect of all non-resource-related benefits of sociality as a single benefit.

Collective consumption: Individuals in larger groups can consume more, per capita, of a captured resource before it is lost. Resources may be lost by being stolen by conspecifics or heterospecifics, or by environmental forces. Larger groups, therefore, may be able to better defend resources from others, as with coyotes⁵, or ants that utilize cooperative transport, carrying large resources to the nest, thus removing them from competition^{86,87}. Alternatively, collective feeding of a resource comprised of many components can permit the consumption of a larger fraction of that resource, such as biofilms that encapsulate a resource and slow the diffusion of nutrients^{88,89}, or humpback whales that use bubble nets to feed on a school of fish⁹⁰.

64 Collective energetics: Individuals in larger groups expend less energy, on average, per unit time. This benefit may be due to aerodynamic or hydrodynamic benefits, such as with great white pelicans, which have reduced energy expenditure while flying in a V-formation⁹⁹. Other social animals are better able to thermoregulate in a large group, such as emperor penguins¹⁰¹ and honeybees¹⁰², lowering the energetic costs of maintaining homeostasis.

65 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 Mormon crickets that move more ballistically as a swarm^{105–107} and slime molds that self-assemble into a dispersal stalk¹⁰⁹. Alternatively, larger groups may disperse more successfully by accessing one or more of the other collective benefits when traveling (such as storks saving energy by collectively sensing air thermals¹¹²) or when they arrive at their new habitat (such as some ant species that exhibit increased survival of new colonies when multiple queens found nests together^{114–116}).

66 **Fundamental resource-related cost of sociality**

67 Intragroup competition: Individuals in larger groups suffer increased competition for resources. While the details of intragroup competition differ among species (*e.g.*, the size of the finder's share, whether dominant individuals claim a larger share, whether group mates are subject to scramble or contest competition), in general there will be fewer resources available per capita as group size increases.

68 **Non-resource-related benefits and costs of sociality**

69 In addition to these fundamental resource-related benefits and costs of sociality, there are a large number of other effects of sociality that are unrelated to resource acquisition. Such benefits include avoiding predation by detecting predators more reliably (the “many eyes” hypothesis), evading predators more effectively (“Trafalgar” or “confusion” effects), shunting risk onto groupmates (the “selfish herd” principle), and diluting the overall risk of predation⁴. Sociality may also affect the probability of acquiring mates (such as in leks¹¹⁹, and harems¹²⁰), increase fitness via cooperative breeding^{121,122}, decrease fitness via inbreeding¹²³, and alter parasite risk^{124–128}. In short, there are a large number of potential benefits and costs of sociality that are not directly related to resource acquisition, which we combine into a single class (*other mortality*).

70 All of the sociality mechanisms described here, resource-related or not, may in principle result in net benefits or costs for some species and contexts. For example, the probability of capturing prey may shrink as group size increases if the prey can more easily detect a larger group. For simplicity, we assume that competition represents a cost of sociality and, for all other mechanisms, we focus on the net benefits of sociality.

74 **Modeling how benefits of sociality and resource abundance affect group sizes**

75 With this understanding of the fundamental benefits of sociality, we can investigate how these benefits may impact group size when resource abundance shifts. To do so, we introduce a general model of a group foraging for resources, which we briefly describe qualitatively here, depict schematically in Figure 1, and describe quantitatively in *Methods: Detailed description of the model framework*.

76 In the model, a group exists in an environment containing resources whose sizes follow a power-law distribution, based on empirical and theoretical work on mass-abundance relationships in nature^{129–131} (Figure 1, *the environment*). Consequently, during a simulation a group typically has access to many small resources and few large resources. A group is assigned a territory of a certain size, giving it access to a particular number of potential resources (Figure 1, *territoriality*).

77 At the start of the simulation, each individual in the group has a store of energy. During the simulation, the group attempts to detect, capture, and consume each of the potential resources. There is some probability that the group successfully detects and captures a particular resource (Figure 1, *detection/capture*); however, the group is limited to those resources that are within its niche (Figure 1, *resource niche*). If a resource has been successfully captured, each individual in the group extracts some energy from it, based on how much can be consumed before it is lost (Figure 1, *consumption*), and assuming that individuals in the group share resources equally (Figure 1, *intragroup competition*). As the group tries to capture and consume the available resources, each individual burns a certain amount of energy (Figure 1, *energetics*), and there is some probability that an individual dies due to a non-resource-related cause (Figure 1, *other mortality*). If the individuals in the group run out of energy during the simulation, then the group attempts to disperse to a new habitat; it successfully disperses with some probability and otherwise the individuals in the group die (Figure 1, *dispersal*). Therefore, an individual survives a simulation if 1) it does not die from a non-resource-related cause and does not run out of energy, or 2) it does not die from a non-resource-related cause and runs out of energy but successfully disperses.

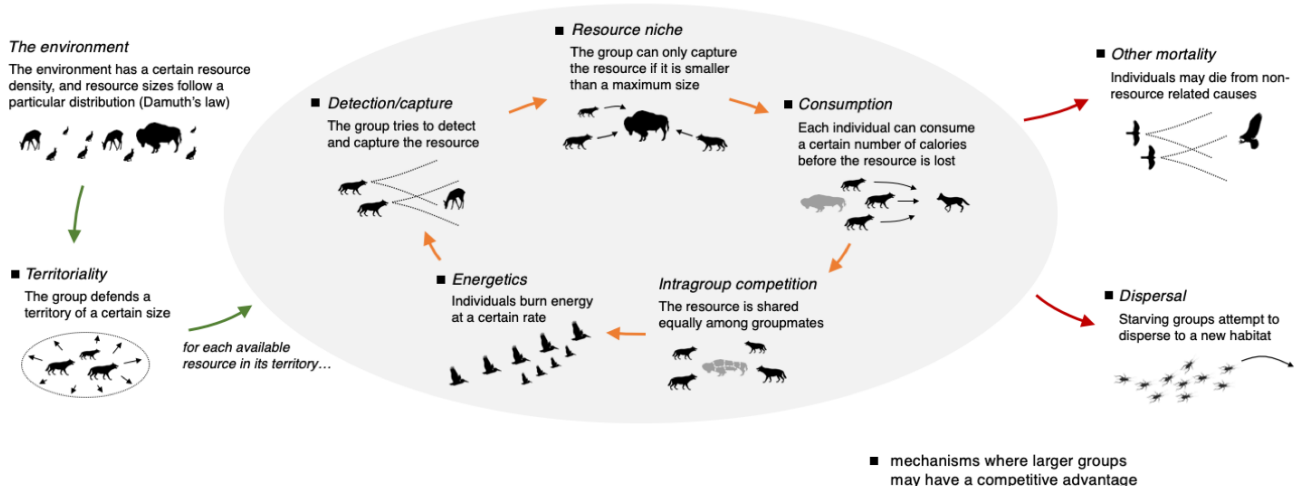


Figure 1. Modeling framework for investigating the effects of the benefits of sociality and resource abundance on group sizes. We specify an environment, which consists of a particular resource density and a power-law resource mass-abundance relationship. A group is allocated a territory of a certain size, which provides it access to a certain number of potential resources. The group then tries to detect, capture, and consume each resource in its territory, spending energy in the process. If the individuals in the group run out of energy, then the group attempts to disperse to a new habitat. During a simulation, individuals may also die from non-resource-related causes. The probability of surviving a simulation, as a function of group size, the dominant benefit of sociality, and resource abundance, is recorded. Although mammals or birds are typically used here as an illustration of different parts of the model framework, we stress that this framework can be used to model a wide variety of taxa.

95 For each simulation, we “turned on” one of the potential benefits of sociality, such that larger groups exhibit improved
 96 performance in that aspect of the simulation (Figure 1, black squares). We ran simulations at different group sizes, and
 97 across a wide range of all of the free parameters of the model, turning on each of the benefits individually (for simplicity and
 98 interpretability, we did not consider multiple potential benefits acting in concert, though our model could be used to perform
 99 such analyses in the future). For each combination of parameter values, we ran 10,000 simulations for each group size ranging
 100 from 1 to 100 and computed the optimal group size that maximized survival probability, for both an “abundant resources”
 101 condition and a “scarce resources” condition (*Methods: Computing the optimal group size*).

102 The effect of the sociality benefit class on group size shifts

103 Depending on which benefit of sociality was present in the simulation, we found that the optimal group size can decrease,
 104 increase, or stay the same when resources become scarce. In Figure 2A, we show illustrative examples of the optimal group
 105 size decreasing (when the collective detection/capture benefit of sociality was present) and increasing (when the collective
 106 consumption benefit of sociality was present). In addition to our stochastic simulations, we also developed an analytical
 107 solution to our model (exact when the number of resources $\mu = 1$, see *Methods: Analytical solution*), which closely matches
 108 our simulation results (Figure 2A).

109 Across all of parameter space, a given benefit of sociality led to social groups (*i.e.*, survival probability was maximized
 110 when $M > 1$, for either the abundant or scarce resource condition), in 11 to 82% of sets of parameter values, depending on the
 111 active social benefit (Figure 2B). In subsequent analyses, we focused on those sets of parameter values that permitted social
 112 groups, since our aim was to study social, rather than asocial, species.

113 Within this restricted region of parameter space, between 13 to 76% of sets of parameter values led to a shift in group size
 114 when resource abundance shifted (Figure 2C), with the territoriality, detection/capture, consumption, and energetics benefits
 115 most frequently leading to shifts in group size. Furthermore, the magnitude and direction of group size shifts strongly depended
 116 on which benefit of sociality was present (Figure 2D). The territoriality and detection/capture mechanisms tended to lead to
 117 decreases in group size when resources became scarce, with a wide range of magnitudes, depending on the parameter values. By
 118 contrast, the energetics mechanism also generally resulted in decreases in group size under scarcity, but the magnitudes tended

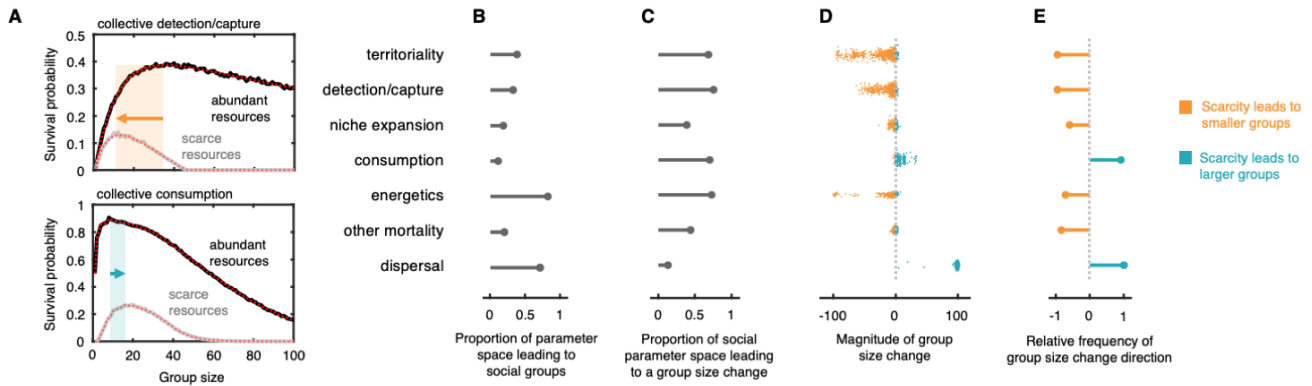


Figure 2. The benefits of sociality can cause either increases or decreases in group size when resources become scarce.

A. Resource scarcity can lead to decreases (top) or increases (bottom) in the optimal group size, depending on the dominant benefit of sociality and the parameters of the environment. In the top panel, collective detection/capture is the dominant benefit, with parameters $\mu = 1$, $k_s = 0.1k_{s,max}$, $s = 1.01$, $\alpha_s = 0.01$, $\alpha_h = 0.5$, and $\alpha_d = 0.999$, while in the bottom panel, collective consumption is the dominant benefit, with parameters $\mu = 20$, $\gamma_d = 0.5\gamma_{max}$, $s = 1.01$, $\alpha_s = 0.5$, $\alpha_h = 0.25$, and $\alpha_d = 0.001$ (see *Methods: Detailed description of the model framework* for parameter definitions). Black and grey 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 for the same parameter values as in the simulations. **B.** The proportion of parameter space where the optimal group size was greater than 1 for either the abundant or the scarce resource condition, for each benefit of sociality. **C.** The proportion of social parameter space (i.e., the fraction of parameter space shown in B) that leads to a change in group size. **D.** Scatter plot of the resulting group size shift for those sets of parameter values that led to a group size shift (orange points indicate that group size decreases when resources are scarce, blue points indicate that group size increases when resources are scarce; a small amount of jitter was added in both the horizontal and vertical directions to more clearly visualize the data points). **E.** The relative frequencies of the shift direction for those sets of parameter values that led to a group size shift (a value of -1 indicates that all group size shifts were decreases in group size when resources are scarce, +1 indicates that all group size shifts were increases in group size when resources are scarce).

119 to be either small or large. While the niche expansion and other mortality mechanisms could lead to either decreases or increases
 120 in group size, the magnitudes of these shifts tended to be small (and therefore possibly difficult to detect in experiments). The
 121 consumption and dispersal mechanisms tended to lead to group size increases under scarcity, with collective dispersal leading
 122 to very large increases in group size (however, for this mechanism a wide range of group sizes had nearly identical survival
 123 rates, so group size changes in nature or in experiments may be smaller than shown in Figure 2D; see *Methods: Computing the*
 124 *optimal group size*). We further quantify group size shifts under scarcity by plotting the relative frequency of decreases and
 125 increases in group size (Figure 2E), confirming that the consumption and dispersal benefits are the only two that robustly cause
 126 increases in group size under scarcity, while all of the other benefits tend to lead to decreases in group size (though with widely
 127 varying magnitudes).

128 Empirical evidence for the model predictions

129 We returned to the literature to examine the extent to which existing data support, or contradict, our theoretical predictions.
 130 Based on the quantitative results in Figure 2, we partitioned the seven benefits of sociality into three groups: those that tend to
 131 lead to decreases (territoriality, detection/capture, and energetics), increases (consumption and dispersal), or only very small
 132 changes in group sizes (niche expansion and other mortality) when resources become scarce (Figure 3, “Model results”). The
 133 fact that the seven benefits of sociality evenly partition into these three groups suggests that a single measurement (direction
 134 of group size shift under scarcity) can be a highly informative indicator of the dominant driver of sociality for a species by
 135 efficiently selecting a subset of the possible benefits. We then looked for empirical evidence of group size shifts when resource
 136 abundance shifts.

137 While existing data are relatively scant, we found a high degree of agreement between empirical examples and our model
 138 predictions (Figure 3, “Empirical data”). For example, there is evidence that lion prides¹³², chimpanzee troops¹³³, bottlenose

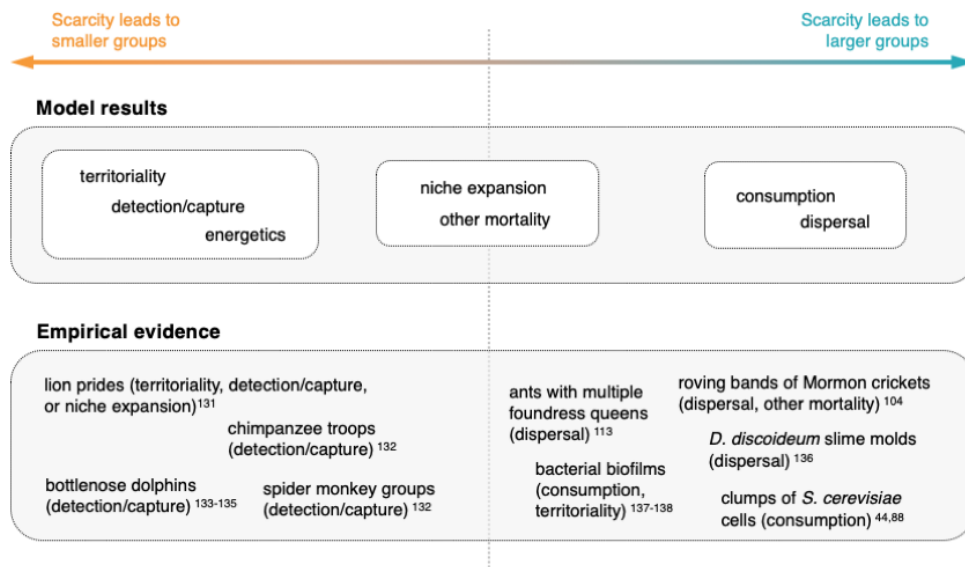


Figure 3. Comparing our model predictions to existing empirical data. The model results, shown in Figure 2B-E, lead to broad classifications of the benefits of sociality based on their general tendency to produce either decreases, increases, or only minor shifts in group size when resources become scarce. Existing empirical evidence, while relatively scant, tend 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.

139 dolphin pods^{134–136}, and spider monkey troops¹³³ are smaller when resources are scarce. The most plausible benefit of sociality
 140 for these species, as previously established from empirical data, is that group living improves the ability of individuals to
 141 capture prey or other resources, whether due to improved detection or capture of resources, increased territory size, or ability to
 142 capture larger resources.

143 By contrast, several species are known to increase their group size under scarcity. Large bands of Mormon crickets likely
 144 have an improved ability to discover new habitats (dispersal), but may also benefit from improved predator avoidance (other
 145 mortality)¹⁰⁵. Slime molds, such as *Dictyostelium discoideum*, switch from a solitary to a social phase when food is scarce,
 146 dispersing via spores within an aggregate fruiting body (dispersal)¹³⁷. For some species of ants, new colonies comprising
 147 multiple foundress queens are more likely to survive than single queens (dispersal)¹¹⁴. Bacteria can form biofilms^{138, 139} and the
 148 yeast *Saccharomyces cerevisiae* can form clumps^{45, 89} when nutrients are scarce, which absorb more of a resource's nutrients
 149 and/or cooperatively produce digestive enzymes (consumption). Some of the species likely benefiting from collective dispersal
 150 exhibit the extremely large increases in group size that we observed in our model, such as Mormon crickets and locusts that
 151 transition from solitary individuals to vast swarms.

152 For other species, group size shifts when resource abundance shifts but with less clear evidence of the driver of sociality.
 153 For example, finches and monk parakeets form larger flocks when resources are scarce^{140, 141}. These groups may benefit
 154 from improved information gathering and sharing (collective sensing/capture), but alternatively large groups may form simply
 155 due to aggregation at a smaller number of available food patches. Similarly, many gram-negative bacteria form biofilms
 156 only in nutrient-rich media and detach when nutrients become scarce, although the function of the biofilm is not known with
 157 certainty¹⁴². Hyenas were shown to decrease their group size under scarcity, with hypothesized mechanisms driving sociality
 158 including collective capture, collective consumption, and improved infant safety⁴⁴.

159 While existing empirical data generally support our model predictions, we stress that this comparison is preliminary, as the
 160 dominant driver of sociality is not known with certainty for any species. For many species, there are multiple social mechanisms
 161 hypothesized to significantly affect individual fitness. In Figure 3, we listed species for which the set of possible mechanisms is
 162 reasonably small, or for which there is greater confidence among researchers about which is the dominant driver of sociality.
 163 We did not list in Figure 3 species with evidence of group size shifts under scarcity but with less known about the underlying
 164 drivers.

165 Experiments specifically designed to test our model predictions are necessary. A simple such test would be to change
166 resource availability while keeping other aspects of the environment constant (such as patchiness), recording any changes in
167 group size. Our model can produce a reduced subset of potential drivers of sociality based on the group size shift, and these
168 potential drivers can be individually tested to measure the associated selection pressure. Our model predicts that at least one of
169 these potential drivers will exhibit a substantially stronger effect compared to the other possible drivers of sociality.

170 **Generating predictions for particular species**

171 In the analyses above, we aggregated the results of all of our simulations, which were conducted across a wide range of
172 parameter values (see *Methods: Detailed description of the model framework*). We deliberately selected a wide range in order
173 to capture the lifestyles of diverse organisms and environments across the tree of life. However, researchers wanting to identify
174 the dominant driver of sociality for a particular species will likely have some knowledge of the specific region of parameter
175 space that it inhabits. If so, then our model could be run within that specific region of parameter space and more targeted
176 predictions could be generated for that species.

177 Here, we demonstrate how our model framework could be used to create a shortlist of likely drivers of sociality for particular
178 species. To avoid making unsubstantiated assumptions about any real biological species, we showcase how to apply our
179 framework to two mythological creatures: dragons and unicorns (Figure 4A,D). We assume that dragons are carnivorous,
180 large, fierce, can fly, and can breathe fire. By contrast, unicorns are herbivorous, smaller, timid, live in forests, and we assume
181 that their horns result mainly from sexual selection and are not effective defensive tools. Based on these traits, we identified
182 hypothetical parameter ranges for both species, as a researcher would do for their focal real species—see *Methods: Dragon and*
183 *unicorn analyses* for a complete explanation of our chosen parameters for these examples.

184 We can narrow down the list of likely drivers of sociality for dragons and unicorns even without collecting any additional
185 data, simply by knowing that these two species are social and reside in particular regions of parameter space. Within the dragon
186 region of parameter space, our model predicts that collective consumption and other mortality benefits can never lead to social
187 groups (optimal group size > 1) regardless of resource abundance (Figure 4B). Since we presume that dragons can be found in
188 groups (because we are asking why dragons are social), we can eliminate these benefits as likely sociality drivers. For unicorns,
189 on the other hand, we can eliminate only collective consumption with this logic (Figure 4E).

190 To narrow the list of potential drivers even further, we took a likelihood approach. Supposing a researcher observes
191 how group size changes when resources become scarce, we can assign a probability that each of the potential benefits of
192 sociality resulted in the observed outcome. In other words, if we observe a decrease (or increase or no change) in dragon
193 group size when resources become scarce, what proportion of simulations resulting in decreases were caused by each potential
194 benefit? Considering only the easily-measurable direction, rather than the magnitude, of group size shifts, we highlight those
195 mechanisms that had a probability greater than 0.1 of generating the given group size shift. In the case of a decrease in group
196 size for dragons, for example, our model predicts that collective territoriality and collective detection/capture are the most likely
197 drivers of sociality (orange dots and squares in Figure 4C). If no change in group size is measured, collective energetics and
198 collective dispersal are the most likely drivers (grey dots and squares). The model predicts that increases in group size should
199 not be observed in the region of parameter space that dragons reside, regardless of the driver of sociality (blue dots in Figure
200 4C). If unicorn groups decrease in group size under scarcity, our model highlights four potential drivers of sociality: collective
201 territoriality, collective detection/capture, collective niche expansion, and other mortality (orange dots and squares in Figure
202 4F). However, consistent with Figure 2, for collective niche expansion and other mortality we expect only small decreases in
203 group size, which may be more difficult to measure in practice. An increase in group size would suggest the collective dispersal
204 mechanism as the dominant driver of sociality (blue dots and squares), while no change in group size highlights the collective
205 niche expansion, collective energetics, and collective dispersal mechanisms (grey dots and squares in Figure 4F).

206 Overall, these results demonstrate how predictions can differ depending on the region of parameter space in which a species
207 resides. Simply by knowing that the species under study is social, or additionally, knowing how group sizes shift when resources
208 become scarce, one can dramatically reduce the list of likely drivers of sociality. Researchers could then test the remaining
209 sociality drivers to identify the main drivers of sociality for that species.

210 **Discussion**

211 We described here a novel conceptual framework—applicable across diverse taxa, from bacteria to large mammals—to study
212 how a variety of potential benefits of sociality can affect group size (Figure 1). While there are a large number of potential

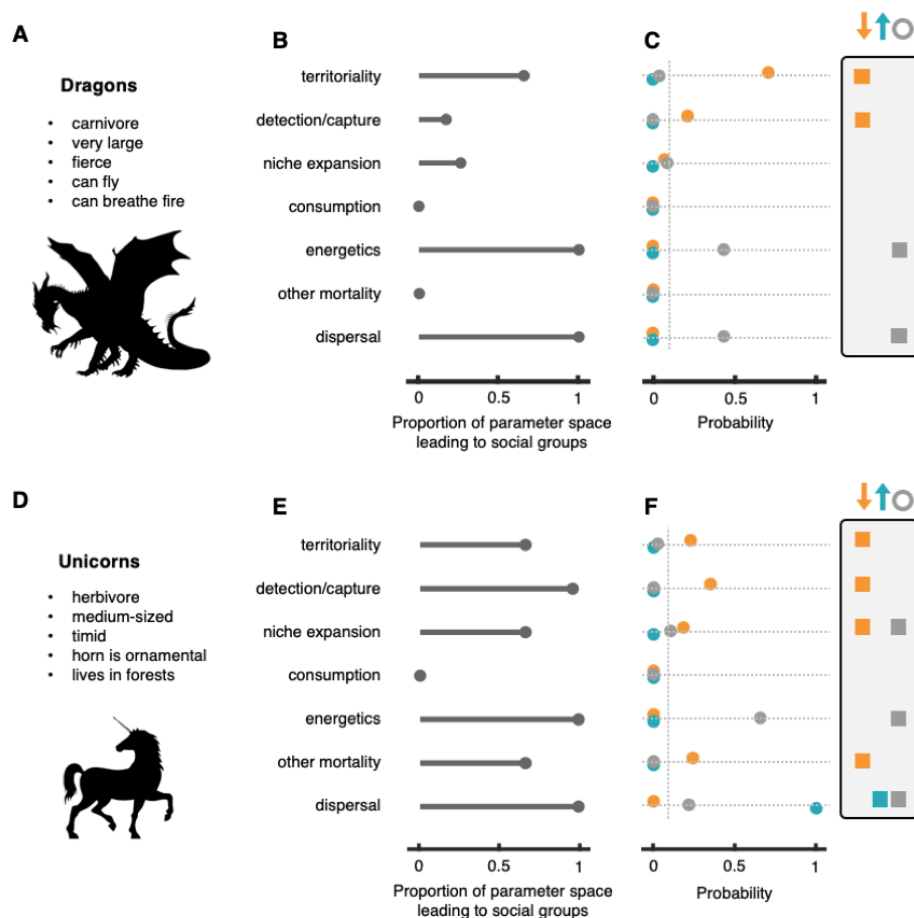


Figure 4. Model predictions may be taxon-dependent. We apply our model to two mythological creatures, dragons and unicorns. **A.** Dragons are large, can fly, and can breathe fire. **B.** The proportion of dragon parameter space where the optimal group size was greater than 1 for either the abundant or the scarce resource condition, for each benefit of sociality. **C.** The probability that observed group size changes arise from each benefit type. The x-axis shows the proportion of scarcity-caused group size decreases (in orange), increases (in blue), and simulations with no change (in grey) attributable to each benefit type, for the dragon parameter space. Inset at right highlight benefits that surpass 0.1 probability of driving a given result. Parameters are described in *Methods: Detailed description of the model framework*, and the dragon parameter space for these analyses was estimated as described in *Methods: Dragon and unicorn analysis*. **D.** Unicorns are medium-sized, timid, and have only ornamental horns. **E.** The proportion of unicorn parameter space where the optimal group size was greater than 1 for either the abundant or the scarce resource condition. **F.** The probability that observed group size changes arise from each benefit type for the unicorn parameter space.

213 benefits related to gaining resources, our analysis condensed these benefits into six classes with fundamentally different
 214 functional forms (Table 1). Stochastic simulations of our model of groups acquiring resources, and its analytic solution, revealed
 215 that the direction and magnitude of group size changes due to declines in resource abundance are strongly dependent on which
 216 benefit is the underlying driver of sociality (Figure 2). This allowed us to partition the benefits of sociality into three groups:
 217 those that tend to lead to smaller groups under scarcity (collective territoriality, collective detection/capture, and collective
 218 energetics), those that tend to lead to little or no change in group size (collective niche expansion, other mortality), and those
 219 that tend to lead to larger groups under scarcity (collective consumption, collective dispersal) (Figure 3). Although currently
 220 limited, existing data on a variety of species appear to broadly support our model predictions. Finally, we demonstrated how a
 221 researcher could apply our framework to particular species and how the model can make different predictions depending on the
 222 relevant parameter space for that species (Figure 4).

223 Our approach of taking a bird's eye view of all resource-related benefits of sociality across taxa necessitated making

224 simplifying assumptions. We implicitly assume that resources are randomly distributed in the environment and can only
225 shift in abundance, that available resources follow a particular mass-abundance relationship, and that the abundance of all
226 resources declines uniformly under scarce conditions. In real habitats, resources can also vary in patchiness, may follow
227 different mass-abundance relationships, and the abundance of resources may decline nonuniformly (*e.g.*, large resources may
228 be more or less resilient during droughts). Furthermore, resources may shift not only in abundance but also in frequency and
229 predictability. We also do not model intragroup dynamics (*e.g.*, dominance hierarchies, finder's shares, division of labor, etc.),
230 intergroup competition, interspecies interactions, demographic structures, and other strategies besides dispersal to stave off
231 starvation. In our model, we assumed that all of the mechanisms, except intragroup competition, function as potential benefits
232 of sociality, rather than potential costs. Despite—and because of—these simplifications, our model highlights fundamental
233 dynamics governing group size across species. Nonetheless, our model framework is general enough to accommodate these
234 additional features if they are particularly important to a species of interest.

235 An important direction for future research is to apply our modeling framework to understand how multiple benefits of
236 sociality may interact with each other. Many social species are likely to benefit from multiple mechanisms, such as collective
237 territoriality, collective detection/capture, and collective niche expansion. These may combine nonlinearly to promote sociality
238 and affect group size shifts and may alter our predictions of what group sizes we expect to observe in nature.

239 Importantly, our framework reveals that group size shifts under changes in resource availability can be an insightful clue
240 about the underlying driver of sociality. Rather than performing separate experiments on each possible benefit of sociality
241 (*i.e.*, the many proximate forms, some of which are listed in Table 1), we argue that simply observing group size changes can
242 substantially reduce the set of likely drivers of sociality. This experiment is often tractable and cost-effective to perform in the
243 lab. In this work, we reported changes in optimal group size, but some groups may have a relatively fixed group size, and may
244 not adjust over the course of a typical experiment. In such cases, researchers could use proxies for optimal group size, such as
245 levels of stress hormones in groups of different sizes⁶. Comparative phylogenetic approaches, such as correlating group size to
246 typical habitat conditions, could also be fruitful for taxa with relatively fixed group sizes, for which we expect changes to occur
247 on evolutionary timescales.

248 Knowing the major drivers of sociality across species is crucial to a comparative understanding of how sociality evolves
249 across diverse biological systems¹⁴³, as well as anticipating the resilience of social species when facing environmental change.
250 For example, we observe a possible correlation between organism size and group size change, or likely sociality driver (Figure
251 3); future research on this correlation could explore its implications for the evolution of sociality and social resilience. Our
252 model framework demonstrated that the different benefits of sociality differ in their propensity to generate social groups (Figure
253 2B). Improving our understanding of which benefits underlie sociality among extant species will allow us to test whether some
254 benefits tend to drive the evolution of sociality, with other benefits accruing secondarily. In addition, this framework could be
255 applied at the sub-organismal level, potentially explaining the group sizes of cellular aggregations such as sperm cells^{144, 145},
256 erythrocytes and platelets^{146–148}, and some immune cells^{149–151}. Taking a high-level view of sociality across the tree of life,
257 while abstracting away many of the finer details, may therefore be a powerful approach towards a deeper understanding of one
258 of the major evolutionary transitions.

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264 Andrew Berdahl contributed ideas (particularly on the ballistic motion of locust swarms) that stimulated initial discussions for
265 this project.

266 **Data availability**

267 We will publish the data and code associated with our model upon publication.

268 Author contributions

269 ABK conceived of the study. AKH, HFM, ABK, FPS, and RAO performed the literature review to identify the fundamental
270 drivers of sociality. AKH, HFM, and RAO performed the literature review to compare the model predictions to existing
271 empirical evidence. All authors contributed to the conceptual development of the model. ABK, FPS, JG, J-GY, and DB and
272 wrote simulation code, and ABK ran the simulations and generated the figures. J-GY, DB, and FPS developed the analytical
273 solution to the model. ABK, HFM, AKH, FPS, J-GY, and RAO drafted the manuscript. All authors edited the manuscript and
274 gave final approval for publication.

275 Methods

276 Detailed description of the model framework

277 First, we specify the resource environment within which the group forages. The environment contains a certain density of
278 resources; these resources vary in size from 0 to $C_{max} = 1$, and the probability density $P(C)$ that a resource is a certain size C
279 is given by $(1 + \gamma_C)C^{\gamma_C} / C_{max}^{1+\gamma_C}$, where we set the exponent to $\gamma_C = -3/4$, following existing empirical and theoretical work on
280 mass-abundance relationships in nature, known as Damuth's law^{129–131}. A group is assigned a territory, the area of which is
281 proportional to the number of potential resources, μ , that the group can access during the simulation.

282 Each individual in a group of size M begins with c_0 energy. During the simulation, the group attempts to detect, capture,
283 and consume each of the μ potential resources. There is some probability p_s that the group successfully detects and captures
284 that resource. However, the group can capture a resource only if it is within its niche, *i.e.*, $C \leq C_h$, where C_h is the maximum
285 size resource that the group can capture; the group must ignore the resource if it is too large. If the resource has been
286 successfully captured, then each individual in the group consumes some portion of the resource. Each individual can potentially
287 consume c_d of the resource before it is lost (*e.g.*, to conspecifics, heterospecifics, or the environment). However, because we
288 assume that groupmates share resources equitably, individuals can each consume a maximum of C/M of the resource (*i.e.*,
289 if the entire resource is consumed). Therefore, the actual amount of the captured resource that an individual consumes is
290 $c_c = \min\{c_d, C/M\}$; if the resource was not detected and captured, or was outside of its niche, then $c_c = 0$ for that resource.

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

295 Therefore, an individual survives a simulation if 1) it does not die from a non-resource-related cause and does not run out of
296 energy, or 2) it does not die from a non-resource-related cause and runs out of energy but successfully disperses.

297 For a given simulation, we “turned on” one of the potential benefits of sociality; depending on which mechanism is turned
298 on, the magnitude of one of μ , p_s , C_h , c_d , c_b , p_p , or p_e will be a function of group size M . We used generic functions to model
299 how these variables change with M :

300 Collective territoriality: $\mu = \mu_1 M^{\gamma_t}$, where μ_1 is the number of potential resources available to a solitary individual, and γ_t
301 is the strength of this social benefit.

302 Collective detection/capture: $p_s = 1 - (1 - \alpha_s)^{k_s(M-1)+1}$, where α_s is the probability that a solitary individual detects and
303 captures a resource within its niche, and k_s is the strength of this social benefit. This functional form, as well as similar ones
304 below, are based on the “perfect many eyes” scenario¹⁵², but modified to allow for different strengths of the social benefit; this
305 function increases from $p_s(M = 1) = \alpha_s$ to $p_s(M = \infty) = 1$.

306 Collective niche expansion: $C_h = \alpha_h C_{max} M^{\gamma_h}$, where α_h is the maximum size resource that a solitary individual can capture,
307 as a proportion of C_{max} , and γ_h is the strength of this social benefit.

308 Collective consumption: $c_d = \alpha_d C_{max} M^{\gamma_d}$, where α_d is the amount of a captured resource, as a proportion of C_{max} , that a
309 solitary individual can consume before the resource is lost, and γ_d is the strength of this social benefit.

310 Collective energetics: $c_b = c_1((1 - \alpha_b)^{k_b(M-1)+1} + \alpha_b)$ where c_1 is the amount of energy that a solitary individual burns
311 during the simulation, k_b is the strength of this social benefit, and α_b represents the fraction of energy burned by a solitary
312 individual that an individual in an infinitely large group burns. This function decreases from $c_b(M = 1) = c_1$ to $c_b(M = \infty) =$
313 $\alpha_b c_1$ (where $0 \leq \alpha_b \leq 1$).

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

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

318 We set maximum values of the strengths of the social benefits, typically such that the benefit can only grow sublinearly with
 319 group size, with some exceptions (see *Methods: Limits on the strength of the social benefits*), and ran simulations for each
 320 mechanism, where the strength of the mechanism was set to 10%, 50%, or 90% of its maximum value. We set μ_1 to either 1 or
 321 20 to capture different ecological regimes (where, respectively, resources are relatively rare or common), and α_s , α_h , α_d , α_b ,
 322 α_p , and α_e to 0.001, 0.01, 0.1, 0.25, 0.5, 0.75, 0.9, 0.99, or 0.999. In general, the parameters α_b , α_p , and α_e affect dynamics
 323 only when their respective mechanisms are turned on, since α_b and α_e play a role only when those mechanisms are on, and we
 324 set $\alpha_p = 0$ unless that mechanism is turned on.

325 We calculated the probability that an individual survives a simulation for group sizes ranging from 1 to 100, for both an
 326 “abundant resource” regime and a “scarce resource” regime. We define the abundant resource regime as the condition where a
 327 solitary individual is expected to have exactly 0 energy at the end of the simulation (see *Methods: Calculating the “edge of*
 328 *starvation”*). The free parameters available to tune this “edge of starvation” are c_0 and c_1 . We choose to use c_1 , while setting c_0
 329 to 1. If the edge of starvation (and therefore the abundant resource regime) is given by c_1^* , then we define the scarce resource
 330 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)
 331 for a group to detect each resource. For each combination of parameter values, we ran 10,000 simulations for each group
 332 size and computed the optimal group size for both the abundant and scarce resource conditions (see *Methods: Computing*
 333 *the optimal group size*). In our analyses, we only included a set of parameter values if at least one group size, in each of the
 334 abundant and scarce conditions, had a survival probability greater than 5%, and if none of the group sizes, in both the abundant
 335 and scarce conditions, had survival probabilities greater than 95%, in order to accurately estimate the optimal group size.

336 Limits on the strength of the social benefits

337 We typically assume that the benefits of sociality increase sublinearly with group size. For the collective territoriality, collective
 338 niche expansion, and collective consumption mechanisms, we simply set $\gamma_{max} = 1$, $\gamma_{hmax} = 1$, and $\gamma_{dmax} = 1$. For other mortality,
 339 we need $p_p(M = 2) \geq p_p(M = 1)/2$, so that $k_{pmax} = \log(1/2)/\log(\alpha_p)$.

340 We define the criteria for the sensing/detection, energetics, and dispersal mechanisms somewhat differently because the
 341 sublinear accrual of benefits cannot be defined for these mechanisms. Instead, for these mechanisms, we assume that groups
 342 of size 2 ($M = 2$) have, at best, a performance halfway between a solitary individual and an infinitely large group. For
 343 the sensing/detection mechanism, we have $p_s(M = 2) \leq (1 + \alpha_s)/2$, which gives us $k_{smax} = \log(1/2)/\log(1 - \alpha_s)$. For the
 344 energetics mechanism, we have $c_b(M = 2) \geq c_1(1 + \alpha_b)/2$, so that $k_{bmax} = \log((1 - \alpha_b)/2)/\log(1 - \alpha_b) - 1$. For the dispersal
 345 mechanism, we have $p_e(M = 2) \leq \alpha_e/2$, so that $k_{emax} = \log(1/2)/\log(\alpha_e)$.

346 Calculating the “edge of starvation”

347 We define the “edge of starvation” as an environment where a solitary individual in the abundant resources condition has, on
 348 average, exactly 0 energy stores at the end of the simulation.

349 To calculate this, we first calculate the mean energy that a solitary individual extracts from a potential resource. The
 350 probability that a resource is of size C is $(1 + \gamma_C)C^{\gamma_C}/C_{max}^{1+\gamma_C}$, where we set $C_{max} = 1$ and $\gamma_C = -3/4$. There are two conditions
 351 to consider: 1) where $\alpha_h \leq \alpha_d$, and 2) where $\alpha_h > \alpha_d$. For condition (1), a solitary individual can entirely consume any resource
 352 that it captures, so we just need to find the expected size of resources ranging in size from 0 to α_h :

$$\langle C \rangle = \int_0^{\alpha_h} \frac{C(1 + \gamma_C)C^{\gamma_C}}{C_{max}^{1+\gamma_C}} dC = \left(\frac{1 + \gamma_C}{2 + \gamma_C} \right) \frac{\alpha_h^{2+\gamma_C}}{C_{max}^{1+\gamma_C}}$$

353 For condition (2), a solitary individual can entirely consume a resource it captures if its size $C \leq \alpha_d$ but only consumes α_d
 354 of the resource if $C > \alpha_d$; the mean energy consumed in this case is:

$$\langle C \rangle = \int_0^{\alpha_d} \frac{C(1 + \gamma_C)C^{\gamma_C}}{C_{max}^{1+\gamma_C}} dC + \int_{\alpha_d}^{\alpha_h} \frac{\alpha_d(1 + \gamma_C)C^{\gamma_C}}{C_{max}^{1+\gamma_C}} dC = \left(\frac{\alpha_d}{C_{max}^{1+\gamma_C}} \right) \left(\alpha_h^{1+\gamma_C} - \frac{\alpha_d^{1+\gamma_C}}{2 + \gamma_C} \right)$$

355 The mean total energy gained in a simulation by a solitary individual is $C_{total} = \mu_1 \alpha_s \langle C \rangle$. For the solitary individual to
 356 have 0 energy at the end of the simulation, we need $c_0 + C_{total} - c_1 = 0$.

357 **Computing the optimal group size**

358 For all of the mechanisms except the dispersal mechanism, we simply locate the group size, for each of the abundant and
 359 scarce resource conditions, that maximizes the probability of survival. For the dispersal mechanism, the probability of survival
 360 asymptotes to α_e for large group sizes, so it is difficult to determine the optimal group size in simulations because a wide
 361 range of group sizes have survival probabilities close to α_e . We observe that, for this mechanism, as group size increases, the
 362 probability of survival appears to either monotonically increase, or initially decrease and then increase. Therefore, the optimal
 363 group size can only either be $M = 1$ or $M = \infty$ (or $M = 100$ for our simulations). Therefore, we simply observed the survival
 364 probability for the two extreme group sizes to determine the optimal group size.

365 **Analytical solution**

Here, we assume $C_{max} > C_h$. Let us use $P_c(x; M)$ as the probability that an individual consumes exactly x calories when in a
 group size M , and $F_c(x; M)$ as the probability function of $P_c(x; M)$ —*i.e.*, the probability that an individual consumes x calories
 or less ($F_c(x; M) = P_c(X \leq x; M)$). Altogether, we may write the survival probability of an individual, $S(M)$, as

$$S(M) = (1 - p_p(M))(1 - F_c(c_b - c_0; M)(1 - p_e(M))).$$

366 That is, an individual survives if it does not die from non-resource-related causes (with probability $1 - p_p(M)$) and it does
 367 not die of starvation, which we can calculate as the reciprocal of the probability of starvation—given by the probability that the
 368 caloric intake is insufficient ($F_c(c_b - c_0; M)$)—times the probability of unsuccessful dispersal $1 - p_e(M)$. As before, $c_b(M)$
 369 denotes the energy that individuals burn and $c_0 = 1$ represents the initial energy level—an individual has insufficient energy
 370 to survive when consuming less than $c_b - c_0$. While $p_p(M)$ and $p_e(M)$ are directly set by model parameters (see *Methods:*
 371 *Detailed description of the model framework*), $F_c(x; M)$ is not; it is instead an emergent quantity of the model, which we now
 372 derive. To simplify the notation, we will omit arguments M , and simply refer to p_p , p_e , c_b , C_h , c_d , and $F_c(x)$.

373 **One prey scenario ($\mu_1 = 1$ and $\gamma_i = 0$)**

First, we note that an individual obtains no resources at all when 1) the available prey is larger than the niche size C_h or 2) even
 if its size is within reach, when the prey is not detected or captured. The probability of obtaining 0 resources is therefore given
 by

$$g(M) + (1 - g(M))(1 - p_s) = 1 + p_s(g(M) - 1),$$

374 where $g(M)$ is the probability that prey has size higher than C_h , $g(M) = 1 - \int_0^{C_h} P(x) dx = 1 - C_h^{\gamma_c+1} / C_{max}^{\gamma_c+1}$ and p_s is the capture
 375 probability.

Second, the probability of capturing prey, yet consuming x or less out of it, is given by $f_C(x) = \int_0^x P_c(x) dx$, where $P_c(x)$ is
 the probability of consuming exactly x calories. Note that the prey captured is divided by the group (with size M) before being
 consumed. As a result, the probability of consuming y calories, $P_c(y)$, can be derived from the probability of capturing a prey
 worth x calories $P(x) = (1 + \gamma_c)x^{\gamma_c} / C_{max}^{1+\gamma_c}$, after the change of variable $y = x/M$, yielding $y^{-1} = h(x) = xM$. Accounting for
 the Jacobian involved in the change of variable, this results in $P_c(x) = P(h(x))h'(x) = P(xM)M$. The probability of consuming
 less than x of a captured resource, $f_C(x; M)$, thus reads

$$f_C(x; M) = \int_0^x P(zM)M dz = (xM)^{\gamma_c+1} / C_{max}^{1+\gamma_c}.$$

We can now write down the probability of consuming less than x calories, $F_c(x)$. It is given by 1) the probability of failing
 to capture any resource plus 2) the probability of capturing a resource yet consuming less than x ($0 \leq x < \frac{C_h}{M}$) out of it:

$$F_c(x; M) = 1 + p_s(g(M) - 1) + p_s f_C(x) = 1 + p_s(g(M) - 1 + f_C(x)).$$

Finally, we complement the probability function above to account for consumption limitation due to the collective consumption
 mechanism. If $c_d M > C_h$ (**scenario 1**), collective consumption does not play any role: it would only affect the level of energy
 intake for prey larger than the threshold imposed by the niche constraint. If $c_d M < C_h$ (**scenario 2**) and $x > c_d$, however,
 collective consumption—rather than resource competition—limits energy intake. This means that a prey can be so large that it
 cannot be fully consumed by the group. If this is the case, then an individual always consumes c_d or less, such that $F_c(x)$ is
 given by

$$F_c(x) = \begin{cases} 1 + p_s(g(M) - 1 + f_C(x)) & \text{if } x < c_d \\ 1 & \text{if } x \geq c_d \end{cases}.$$

To summarize, the probability of survival is given by

$$S(M) = (1 - p_p)(1 - F_c(c_b - c_0)(1 - p_e)),$$

where under **scenario 1** ($c_d M > C_h$) the probability function of resource consumed is given by

$$F_c(x; M) = 1 + p_s \left[\left(\frac{xM}{C_{max}} \right)^{\gamma_c+1} - \left(\frac{C_h}{C_{max}} \right)^{\gamma_c+1} \right],$$

and, under **scenario 2** ($c_d M < C_h$), the probability function of resource consumed is given by

$$F_c(x; M) = \begin{cases} 1 + p_s \left[\left(\frac{xM}{C_{max}} \right)^{\gamma_c+1} - \left(\frac{C_h}{C_{max}} \right)^{\gamma_c+1} \right] & \text{if } x \leq c_d \\ 1 & \text{if } x > c_d \end{cases}.$$

Multiple prey scenario ($\mu_1 > 1$ or $\gamma_i > 0$)

When more than one resource is available, calculating $F_c(x)$ requires calculating the probability that consuming a combination of several resources leads to insufficient energy. Given the highly heterogeneous distribution of resource sizes assumed, such calculation involves a combinatorial problem hard to solve analytically. Nonetheless, it is possible to compute $F_c(x)$ numerically, when multiple resources exist. We can use the inverse transform sampling method to sample random values from a distribution of caloric gains per resource. Random values of caloric gain can be sampled by 1) sampling random values from a standard uniform distribution ($y \sim U(0, 1)$) and 2) calculating $F_c^{-1}(y)$, where $F_c^{-1}(y)$ is the inverse of function $F_c(x)$ (i.e., the CDF function of $P_c(x)$, the probability of consuming x —defined above). Considering the two scenarios already mentioned, we have, for **scenario 1** ($c_d M > C_h$),

$$F_c^{-1}(y; M) = \begin{cases} 0 & \text{if } y \in [0, F_c(0)] \\ \frac{C_{max}}{M} \left(\frac{y-1+p_s C_h^{\gamma_c+1}}{p_s} \right)^{1/(\gamma_c+1)} & \text{if } y \in [F_c(0), 1] \end{cases}.$$

Note that $F_c(x)$ is only defined in the interval $x \in [0, \frac{C_h}{M}]$, thereby $F_c^{-1}(y)$ is defined for $y \in [F_c(0), F_c(\frac{C_h}{M})]$, where $F_c(0) = 1 - p_s (\frac{C_h}{C_{max}})^{\gamma_c+1}$ and $F_c(\frac{C_h}{M}) = 1$. Following a similar reasoning, for **scenario 2** ($c_d M < C_h$) we have:

$$F_c^{-1}(y; M) = \begin{cases} 0 & \text{if } y \in [0, F_c(0)] \\ \frac{C_{max}}{M} \left(\frac{y-1+p_s C_h^{\gamma_c+1}}{p_s} \right)^{1/(\gamma_c+1)} & \text{if } y \in [F_c(0), F_c(c_d)] \\ \alpha_d M^{\gamma_d} & \text{if } y \in [F_c(c_d), 1] \end{cases}.$$

Where $F_c(c_d) = 1 + p_s \left[\left(\frac{c_d M}{C_{max}} \right)^{\gamma_c+1} - \left(\frac{C_h}{C_{max}} \right)^{\gamma_c+1} \right]$. Using $F_c^{-1}(y)$, we can now calculate the probability of getting insufficient energy by taking the average (over many trials, N) of sampling μ values of energy intake, using $F_c^{-1}(y)$ and each time sampling y from a uniform standard distribution. This way, a numerical approximation of $F_c(x; M)$ —which we denote by $\overline{F}_c(x; M)$ —is given by

$$\overline{F}_c(x; M) = \frac{1}{N} \sum_{i=1}^N \theta \left(\sum_{j=1}^{\mu} F_c^{-1}(y \sim U(0, 1); M) - x \right),$$

where $\theta(x) = 1$ if $x \geq 0$ and $\theta(x) = 0$ otherwise. $\overline{F}_c(x; M)$ can be directly used in the probability of survival, $S(M)$, defined above. We used $N = 10,000$ in Figure 2A and $N = 1,000$ in Figure 4.

Dragon and unicorn analyses

Based on the supernatural histories of dragons and unicorns, we posited ranges for the parameters μ_1 , α_s , α_h , α_d , α_b , α_p , and α_e for the two species. We assume that dragons eat large meals relatively infrequently, so we set $\mu_1 = 1$. When dragons do hunt we assume they detect prey relatively easily since they can fly, and that their fierceness allows them to capture even large prey solitarily—though not the very largest potential prey in their environment. We therefore restricted both the individual

385 detection/capture parameter (α_s) and the niche or maximum size parameter (α_h) for dragons to between 0.5-0.7. Likewise, we
386 also use a relatively high range of 0.5-0.7 for the individual consumption parameter (α_d) for dragons, as their fire-breathing
387 abilities mean that they can cook their food, to better extract nutrients and delay rot. We fixed α_b at 0.4, as dragons can take
388 advantage to some degree of aerodynamic drafting while flying in groups, α_p at 0.3, as dragons' extremely low predation risk
389 reduces other mortality overall, and α_e at 0.8, as dragons' flight makes them excellent dispersers. The last three parameters
390 were fixed at specific values, rather than ranges, for both dragons and unicorns, so that all of the mechanisms took up the same
391 volume of parameter space and could be directly compared with each other.

392 While one may expect unicorns' powers to help them find resources, we assume their magical horn does not aid in foraging,
393 specifically. We set $\mu_1 = 1$ for unicorns, as they typically will not encounter more than one patch of grass at a time. Unicorns
394 are notoriously skittish, so we assume that they spend a large portion of their time on anti-predator vigilance, leaving less time
395 for foraging. Therefore, we restrict α_s to between 0.1-0.3. We also restrict α_h and α_d to 0.1-0.3, as their herbivorous diet means
396 that even their largest meals are relatively low in calories, and they can consume only a small fraction of a grass patch they find.
397 We fixed α_b at 0.8, as unicorns derive no strong group benefit in terms of energetics, α_p at 0.5, because, while they are cryptic,
398 they are susceptible to predators, and α_e at 0.2, as unicorns are known for rarely leaving the relative safety of their natal forest,
399 thus making successful dispersal unlikely.

400 We used the analytical solution for this analysis, and uniformly sampled the region of parameter space for each species at a
401 resolution of 0.01 for each parameter, recording whether the optimal group size decreased, increased, or did not change, when
402 resources became scarce. For Figures 4C and F, we removed results for which the optimal group size was 1 for both conditions
403 (because we are interested in the social behavior of these two species). Then, given a particular hypothetical experimental
404 result (*i.e.*, decrease, increase, or no change), we calculated the proportion of results arising from each of the seven benefits of
405 sociality.

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