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Adaptive collective foraging in groups with conflicting nutritional needs

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Collective foraging, based on positive feedback and quorum responses, is believed to improve the foraging efficiency of animals. Nutritional models suggest that social information transfer increases the ability of foragers with closely aligned nutritional needs to find nutrients and maintain a balanced diet. However, whether or not collective foraging is adaptive in a heterogeneous group composed of individuals with differing nutritional needs is virtually unexplored. Here we develop an evolutionary agent-based model using concepts of nutritional ecology to address this knowledge gap. Our aim was to evaluate how collective foraging, mediated by social retention on foods, can improve nutrient balancing in individuals with different requirements. The model suggests that in groups where inter-individual nutritional needs are unimodally distributed, high levels of collective foraging yield optimal individual fitness by reducing search times that result from moving between nutritionally imbalanced foods. However, where nutritional needs are highly bimodal (e.g. where the requirements of males and females differ) collective foraging is selected against, leading to group fission. In this case, additional mechanisms such as assortative interactions can coevolve to allow collective foraging by subgroups

of individuals with aligned requirements. Our findings indicate that collective foraging is an efficient strategy for nutrient regulation in animals inhabiting complex nutritional environments and exhibiting a range of social forms.

1. Introduction

Many species live in heterogeneous environments in which essential resources are patchily distributed. Foraging decisions, which have a large impact on fitness, can be especially complex, leading some animals to exploit social information emanating from their conspecifics in locating and selecting foods [1,2]. In gregarious animals, such as many insects, fish, birds and ungulates, social information transfer may result in collective foraging decisions whereby all (or most) individuals in the group decide to exploit the same food resource from several available alternatives [3–5]. Typically, these collective dynamics are driven by positive feedback and quorum responses, whereby the probability of an individual choosing a resource varies positively and nonlinearly with the number of individuals already exploiting that resource [4,6]. Through these processes, groups often make faster and/or more accurate decisions than isolated animals, a phenomenon known as swarm intelligence [4,6]. To date, research on collective foraging behaviour has largely focused on identifying the mechanisms that underpin collective decision-making. However, little is known about the evolutionary roots of this widespread phenomenon [7].

Insightful data come from studies on insects, which exemplify how relatively simple social interactions, such as social retention on, or attraction to, foods based on the number of conspecifics already exploiting that food, can impact the foraging decisions and efficiency of individuals [6,8–10]. Informal comparisons of experimental data suggest that the fitness benefits of collective foraging depend on a subtle interplay between the strength of social effects in a species and the availability of resources in their environment. For instance, studies on domiciliary cockroaches (*Blattella germanica*) illustrate how the number of conspecifics already feeding on a food can influence the choice of an individual, with larger groups being more likely to attract new recruits [11,12]. It is hypothesized that this simple mechanism provides an individual cockroach with an honest signal about the quantity and/or quality of a food source enabling grouped cockroaches to make more accurate decisions than isolated conspecifics [12]. By contrast, experiments in tent caterpillars (*Malacosoma disstria*) indicate that the strength of social retention may compromise the quality of nutritional decisions, which individuals alone make with some accuracy [13]. These differential findings highlight an interesting potential trade-off between group foraging, which may increase the efficiency of individual decision-making, and the specific nutritional needs of the individual.

Conceptual progressions in nutrition research show that foraging decisions are intrinsically complicated by the fact that individuals must take into account their needs for multiple nutrients, which may be contained in differing amounts and ratios in those foods available [14]. Ultimately studies on the evolution of collective foraging decisions must capture the complex multidimensional nature of nutrition, rather than solely focusing on the acquisition of a single resource (e.g. energy [15]). Recently, Lihoreau *et al.* [16] developed an agent-based model (ABM) derived from nutritional geometry, a state-space modelling framework for conceptualizing the nutritional decisions of animals (figure 1*a* and box 1) [14,17,18] to explore the efficiency of collective foraging in complex multi-nutrient environments. Their model suggests that an optimal level of social retention (termed K_{soc}), whereby foragers are more likely to remain on and eat from heavily occupied food sources, improves the nutritional performance of individuals. This simple form of information transfer is sufficient to enable individuals to efficiently comprise a balanced diet from individually imbalanced, but collectively complementary, foods [18]. While this is an important first step, this approach overlooks inter-individual variation in nutritional requirements, which is likely to be present in most animal groups (cf. [15]). A recent meta-analysis exemplifies the probable ubiquity of such variability in species from different trophic levels and a wide range of taxonomic groups [24]. In part, this variation may be readily predictable based on phenotype, for example if the nutrient requirements of an individual vary with age or sex [14,25]. However, even where groups of individuals appear to be outwardly homogeneous, as for instance in a cohort of same sex individuals, heterogeneity in other traits such as metabolic rate may result in variance in nutritional requirements [24]. Given that the nutritional needs of all individuals in a group may never be perfectly aligned, does collective foraging still improve the foraging efficiency of individuals?

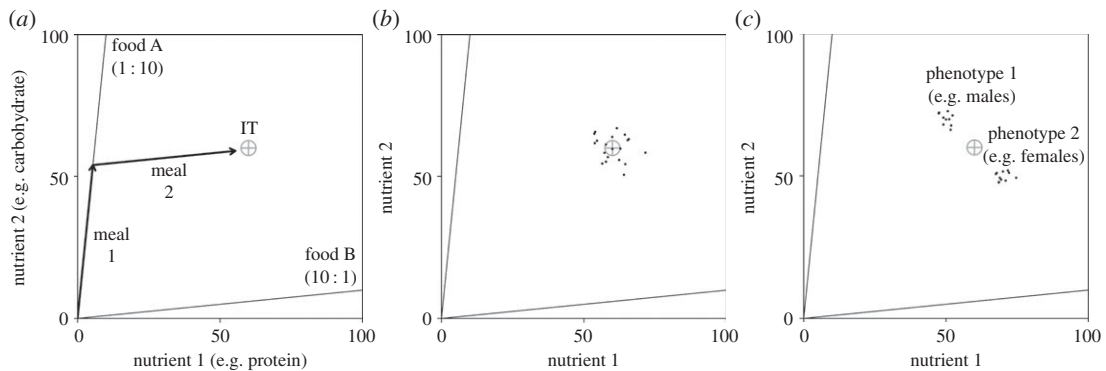


Figure 1. Nutritional geometry models. (a) Nutritional geometry (see box 1) model for two nutrients, e.g. protein on the x -axis and carbohydrate on the y -axis. In this example, the individuals' requirements are given by a single coordinate known as the intake target (IT; grey cross hair). The environment contains two foods. Food A is rich in carbohydrate (10 parts to each part protein) and food B is rich in protein. An individual has been able to move its nutritional state (NS) towards the IT, by eating food A for meal 1 and food B for meal 2 (sequence of black arrows). (b) While a single IT may adequately represent the mean requirements of all individuals in a group (grey cross hair), in reality there is likely to be within-group variance, with each individual having its own IT (for a hypothetical group of 20 individuals given here by black points). (c) In some instances, variance in nutritional requirements may be predictable. For example, if the group is composed of individuals with two phenotypes with distinct nutritional requirements (e.g. male and female), individual ITs (black points) may be bimodally distributed in two subgroups around an overall mean (grey cross hair).

Box 1. Key principles of nutritional geometry.

Nutritional geometry is a state-based modelling approach for studying the nutritional strategies of animals, based on graphic representations of individuals, their nutritional requirements, foods and the interactions thereof in a geometric space [14,17,18]. Over recent years, this conceptual framework has become increasingly used to study how animals regulate their acquisition of multiple nutrients simultaneously, and how this varies across feeding guilds, trophic levels and taxonomic groups. In the most basic nutritional geometry models, two nutrients (such as the macronutrients protein and carbohydrate) are depicted in a two-dimensional Cartesian coordinate system forming a nutrient space (see example in figure 1a). An individual's nutritional state (NS) is denoted by its (x, y) coordinates, and moves through the nutrient space when foods are eaten. Foods are radials projecting through the nutrient space at angles from the origin determined by the ratio of the component nutrients contained (nutritional rails; figure 1a). The nutritional requirements of an individual are given by a single coordinate or a broader region within the nutrient space known as the intake target (IT, figure 1a) [14]. Multiple ITs may maximize different life-history traits in the same individual (e.g. maximize growth, reproduction or longevity [19,20]). However, evolutionary theory and experimental evidence suggest that animals evolve strategies that attempt to reach the IT that maximizes overall evolutionary fitness [14,19,21,22]. While most previous nutritional geometry models have assumed that a single IT would maximize the fitness of all individuals within a group or population (e.g. [23]), it is becoming increasingly clear that inter-individual variation in ITs is abundant (figure 1b) [24]. In the relatively homogeneous groups, this variation may be captured by a unimodal distribution of individual ITs surrounding the group mean IT (figure 1b). In more heterogeneous groups, these ITs may have discrete distributions, separating the group into distinct subgroups, as for example, in the case of sex-specific nutritional needs where the ITs of mixed-sex groups may be bimodally distributed (figure 1c).

Here we explored the costs and benefits of collective foraging for nutrient balancing in groups with increasing levels of inter-individual variance in nutritional requirements. We have developed a nutritional geometry focused ABM in which we assigned each agent an individual value of the group retention parameter K_{SOC} . Allowing K_{SOC} to mutate across generations, we then used an evolutionary

algorithm to explore how ecological and nutritional aspects of the environment affect optimal levels of group retention. Among those factors explored, we tested how aspects of inter-individual variation in nutrient needs interact with the composition and number of foods available to govern the degree of K_{soc} that optimizes an individual's ability to meet its nutritional requirements.

2. Material and methods

2.1. Agent-based model overview

All models were coded and simulation experiments performed in the ABM programming environment Netlogo 5.1 [26]. Model data were analysed and plotted in the statistical programming environment *R* v. 3.1.2 [27]. Below, we describe our model using the overview, design and details format as is now widely adopted for ABMs [28–30]. All Netlogo code can be found in the electronic supplementary material, S2 'Netlogo Code'.

2.1.1. Purpose

The ABMs have been programmed to evaluate how within-group heterogeneity affects the efficacy of social retention as a mechanism to improve individual foraging in a complex nutritional environment. Previous models suggest that a relatively high level of social retention is optimal when all individuals have equal needs [15,16]. Here, we use an evolutionary algorithm to explore how this optimal level of social retention varies with inter-individual variation in nutrient requirements.

2.1.2. Entities, states, variables and scales

The ABM is made up of individuals and their environment. The environment is a two-dimensional Cartesian coordinate system representing the space available for two nutrients (i.e. figure 1*a*; implemented as in Senior *et al.* [23]). Each individual's nutritional state (NS; all parameters and variables are summarized in table 1) is given by its (x, y) coordinates. An individual's fitness (F) is maximized when its NS reaches its intake target (IT; figure 1*a,b*). Individuals are given a fixed period to reach their IT before the next generation begins, and generations are non-overlapping. The group has a mean IT of (μ_x, μ_y) and we alter the distribution of individual ITs around this mean. An individual's NS moves as it eats. There are N_{food} foods in the environment, each defined by a nutritional rail: a radial projecting through the nutrient space at an angle corresponding to the nutrient balance (V) of that food (figure 1*a*). That is, increasing N_{food} increases the diversity of foods, but not their total abundance. Individuals can only eat one food at a time and thus their NS moves in parallel to the nutritional rail for the food consumed (figure 1*a*). After eating an amount of a food (φ), an individual may seek an alternative, based on its own nutritional requirements and the number of other individuals consuming that food. The importance ascribed to these two factors is governed by a social retention parameter, K_{soc} , which evolves. The higher the value of K_{soc} , the lower the probability an individual will leave a popular food. We assume that foods can be patchily distributed in space and that there is a travel time (T) associated with moving between foods; we have explored the effects of different values of this time-cost on the evolution of K_{soc} . The distribution of individual ITs is governed by σ_{IT} and B (B is a fixed global parameter which governs the degree of bimodality in ITs; table 1, figure 1*c*). We also explored variation in ability to consume food, φ , although no effects were observed (see electronic supplementary material, S1 and figure S1). The model runs for 1000 generations with K_{soc} values randomly mutating at each generation, and F governing an individual's representation in the subsequent generation. Note that our aim is not to precisely mimic evolution by natural selection but to explore optimal levels of K_{soc} under different environments and levels of group heterogeneity.

2.1.3. Process overview and scheduling

On each iteration of the ABM, the following three processes occur (detailed below, and in figure 2*a*): (i) 'Find Food', where those individuals not located on a food find one; (ii) 'Eat', where individuals located on a food eat some of it (i.e. move their NS through the environment); and (iii) 'Leave Food', where individuals may decide to leave a food on which they are feeding to seek an alternative. A new generation begins after 500 iterations. Data on the evolution of K_{soc} are recorded after 1000 generations.

Table 1. All model parameters and variables, their notation, level of operation and values (s.d. = standard deviation).

variable/parameter	notation	level	description	value
nutritional state	NS	individual	an individual's nutritional state, as tracked by its (x, y) position in the nutrient space	variable (x, y)
fitness	F	individual	an individual's fitness, which is a function of the Euclidean distance between an individual's NS and its IT	variable (equation (2.5))
intake target	IT	individual	an individual's IT is the (x, y) coordinate in the nutrient space that maximizes F	variable (x, y)
group mean IT	(μ_x, μ_y)	global	the mean IT (i.e. requirements) of the group for the nutrients on x - and y -axes	(500, 500)
number of foods	N_{food}	global	the number of food types (i.e. food rails) present in environment	2, 3 or 4
nutrient balance	V	global	the amount of y -axis nutrient present within a food, relative to each part of the x -axis nutrient (e.g. carbohydrate to protein in figure 1a)	0.0625, 0.251, 4 and 16
capacity to eat food	φ	individual	the maximum amount of food that an individual can eat on one time step	2; see [25]
social retention	K_{soc}	individual	the degree to which an individual takes into account the popularity of a food, when evaluating whether to seek an alternative	variable and evolvable
time-cost	T	global	the time-cost associated with finding an alternative food	0–4
standard deviation in IT	σ_{IT}	global	the s.d. in ITs (inter-individual)	0–75
bimodality	B	global	the degree of bimodality in ITs (see equations (2.1) and (2.2))	0–0.5
deviation from the mean IT	ε	individual	the amount that an individual's IT deviates from the group mean	random-normal with mean = 0, s.d. = σ_{IT}
distance to the IT	D	individual	the Euclidean distance between an individual's NS and their IT	variable
ideal food rail	α_{ideal}	individual	the angle in radians of the ideal food rail connecting an individual's NS with their IT	variable
food 'popularity'	P	individual	the proportion of the group located on the same food as a given individual	variable
assortative interactions	A_{int}	individual	a binary variable denoting whether an individual is able to discriminate between and interact with conspecifics on the basis of their nutritional needs (1), or not (0)	0 or 1

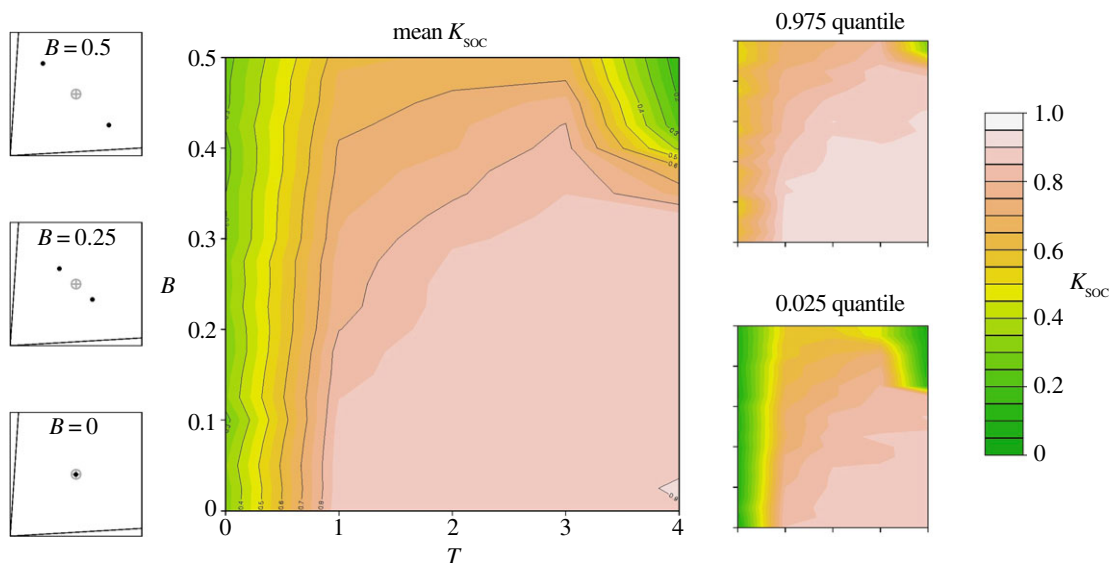


Figure 5. Bimodality in nutrient requirements in a two-food environment and the evolution of collective foraging. Heat maps representing the effects of covarying B and T on the mean level of K_{soc} after 1000 generations, in a two-food environment (0.025–0.975 quantile given on the right). Shown on the left is a nutritional geometry depiction of model settings, including the nutritional value of food rails (V), the mean intake target (grey cross hair) and individual intake targets (black points), distributed around the group mean with a given B (see table 1 for all parameters and variables).

individuals prior to making a foraging decision, we also assume that individuals with $A_{\text{int}} = 1$ take an additional iteration to locate a food source (i.e. the time-cost of moving between foods = $T + A_{\text{int}}$).

We found that where A_{int} could evolve, the constraints that B had on the evolution of K_{soc} were overcome. For example, in a two-food environment with high T and high B (4 and 0.5, respectively), and where A_{int} and K_{soc} can coevolve, K_{soc} evolved to around 0.9 (figure 6a). This result contrasts with the evolved K_{soc} of 0.2 obtained under equivalent model setting where A_{int} could not evolve (figure 4). We also found selection for A_{int} , despite the associated cost. Where B and T are high, A_{int} evolved to be around 0.9 on average, but was selected against in all other areas of the parameter space (figure 6b). Thus, time-costs associated with foraging as well as distinct bimodality in nutrient requirements may select for the evolution of assortative foraging, whereby groups segregate into subgroups of individuals with similar nutritional needs. See the electronic supplementary material, S3, figures S4 and S5, for equivalent results in three- and four-food environments.

4. Discussion

Many animals, from insects to mammals, make collective decisions that enhance the speed and/or accuracy of individual choices [5,31,32]. While previous studies show how collective foraging enables individuals to select the richest or the largest available food resources in their environment [8–10], little is known about whether and how individuals can also collectively regulate their acquisition of vital nutrients from multiple imbalanced foods [15,16]. Our evolutionary model, based on concepts of nutritional geometry, indicates that collective foraging is often an efficient strategy for nutrient balancing, even in groups of individuals with different needs.

4.1. Collective foraging is adaptive in heterogeneous groups

In cases where nutrient intake must be balanced from complementary foods and there is a time-cost to foraging, our model shows that social retention is an effective mechanism for preventing individuals from over-investing in the time spent foraging. This prediction remained true in a number of instances where the specific requirements of individuals actually varied, only appearing to be suboptimal when the group contained an incredibly high degree of bimodality (i.e. figure 5). However, the presence of a food that met the mean requirements of the group (i.e. a food rail passing through the mean group IT) interacted with the distribution of ITs to determine optimal levels of social retention. When such a food was present and intra-group variation in ITs was low, social retention was only weakly

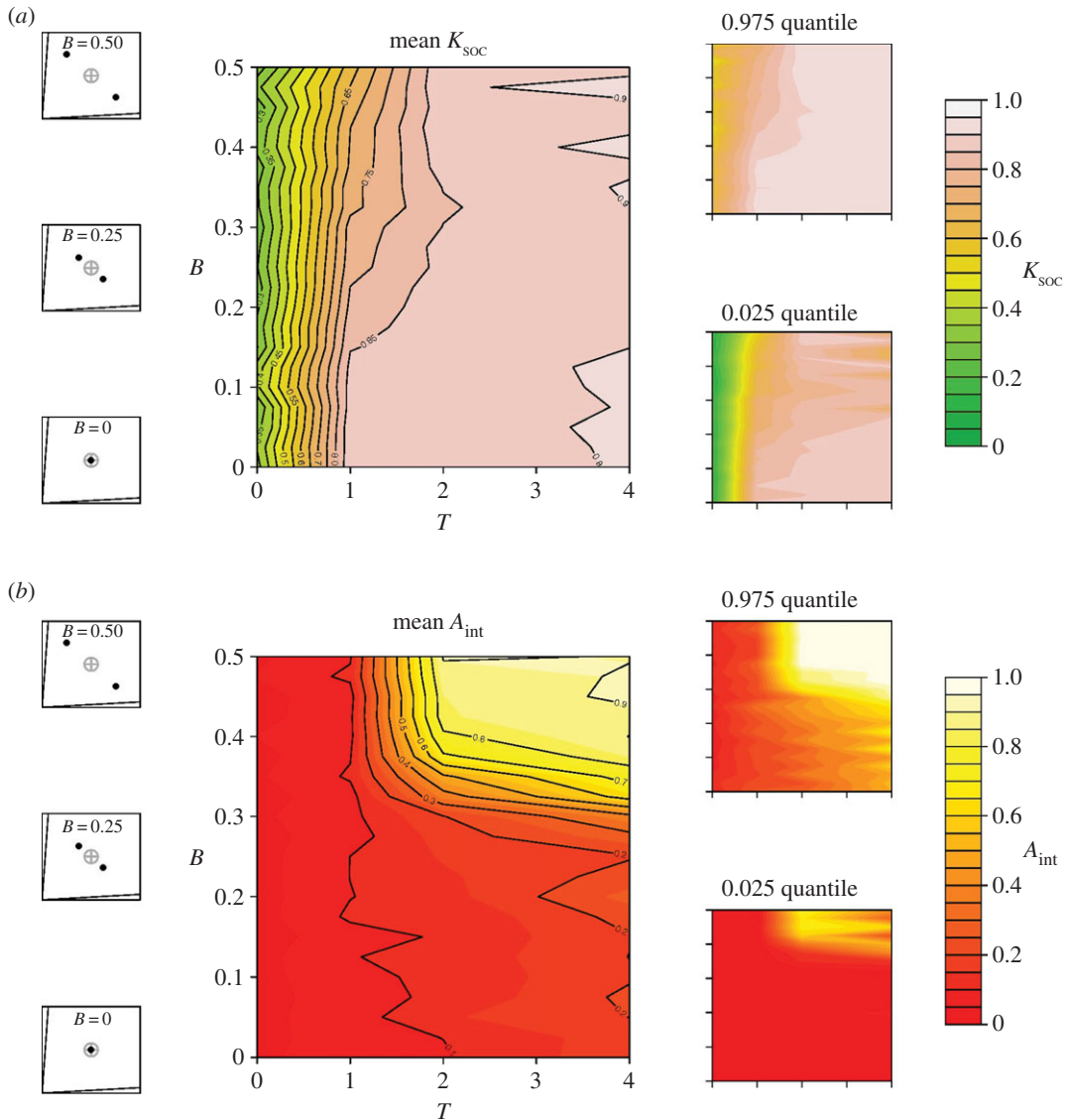


Figure 6. Bimodality in nutritional requirements and the co-evolution of collective foraging and assortative interactions. Heat maps represent the effects of covarying B and T on the mean (0.025–0.975 quantile given on the right) level of (a) K_{soc} and (b) A_{int} after 1000 generations, when the two traits are allowed to co-evolve in a two-food environment (i.e. equivalent of figure 4). Shown on the left is a nutritional geometry depiction of model settings, including the nutritional value of food rails (V), the mean intake target (grey cross hair) and individual intake targets (black points), distributed around the group mean with a given B (see table 1 for all parameters and variables).

selected for, despite costs associated with foraging. Surprisingly, in this environment, increasing inter-individual variance around a single mean (and therefore increasing potential conflict of interest between individuals) selected for stronger social retention (i.e. figure 4b). Here, collective foraging caused individuals to converge on a food that would meet their needs approximately, rather than over-investing (in terms of foraging time) in attempting to accurately cater to the idiosyncrasies of their own dietary requirements. Ecological scenarios such as those identified by our model may help explain how group retention can evolve to be so strong that it effectively traps individuals on nutritionally imbalanced foods, overriding their own nutritional needs, such as has been observed in the forest-tent caterpillar [13], where experimental conditions do not necessarily match natural nutritional environments.

Given the above, we can make a number of predictions about where organisms might, or might not, be expected to display collective foraging based on simple mechanisms of group retention. Namely, our model states that social retention becomes maladaptive under three circumstances: (i) where there is no cost associated with nutrient balancing (e.g. foods are nutritionally balanced or not patchily distributed); (ii) when the environment becomes increasingly complex (large numbers of different types

of foods patchily distributed), and individuals are too sparsely scattered across patches to effectively aggregate; and (iii) when the group has a highly bimodal distribution of requirements. Accordingly, we may expect organisms that inhabit stable environments falling under one, or more, of the above categories not to display social retention, whereas in the reciprocal environment the trait should evolve. Testing such a prediction would necessitate cross-taxa comparative study. However, in organisms that live in fluctuating environments, we might expect individuals to update and adapt their use of social information in response to environmental change [2,33]. For such species, nutritional geometry provides an experimental framework with which to evaluate the use of social information for nutrient balancing. Foods with known nutritional composition can be created, allowing one to manipulate the composition and distribution of foods in the environment [14]. In addition, if the species does not intrinsically contain individuals with differing nutritional needs it may be possible to experimentally modify the distribution of inter-individual requirements by manipulating individual NS (e.g. feeding individuals with differing foods prior to the trial).

4.2. Assortative foraging and group heterogeneity

In the extreme case where inter-individual variance has a highly discrete (multimodal) distribution, for instance, when groups are composed of distinct subsets of individuals with divergent needs, social retention tended to be selected against. Bimodal distributions of ITs may be common in mixed groups composed of males and females. Such observations have been made, for example, in field crickets (*Teleogryllus commodus*) [25] and fruit flies (*Drosophila melanogaster*) [34,35], where females maximize their reproductive fitness on diets richer in protein than males. Our results suggest that where the differences between sexes in nutritional requirements are large, collective foraging may be selected against. However, the constraints that sex-specificity in nutritional requirements place on the evolution of group foraging are easily overcome if individuals interact in an assortative manner, for instance by preferentially following individuals of the same sex rather than the group as a whole.

Sexual segregation of foraging groups has been observed in taxa ranging from marine and terrestrial mammals to fish [36–38]. Numerous competing hypotheses have been proposed to explain this behaviour [38], and comparative analyses restricted to large herbivores have provided perhaps the best insights. A leading hypothesis, termed the ‘forage selection’, or ‘nutritional needs’ hypothesis, explicitly states that sexual segregation results from differential dietary requirements of the sexes [37]. While support from comparative studies for this hypothesis has been mixed [37,39], data have focused on looking for differences in ‘diet-quality’ (e.g. nitrogen content) between males and females, rather than differences in diet composition *per se* (i.e. required ratios and amounts of nutrients, or ITs). Our model suggests that bimodality in nutritional requirements, in combination with selective pressures that favour collective foraging (e.g. time-costs associated with foraging), can lead to the emergence of such sexual segregation.

4.3. Collective nutrient regulation and the evolution of group complexity

It has long been suggested that nutritional constraints, such as limited access to key nutrients, may promote the evolution of cooperation and division of labour in animal groups [40–42]. However, the lack of a conceptual framework for testing these hypotheses has long hampered such research. Our theoretical exploration of the costs and benefits of social retention across multiple levels of group heterogeneities suggests that nutritional factors such as spatial/temporal distribution of foods and individual nutrient requirements are potential drivers of the evolution of collective foraging. Recently, it has been proposed that levels of intra-group variance in ITs and NSs may become greater with increasing degrees of social complexities, as one moves from forming temporary aggregations to living in permanent and fully eusocial colonies that forage from a central sedentary location [15]. Group living may increase inter-individual variance in requirements because of the simultaneous effects of competition over nutrient acquisition, age structures or differential parental nourishment, all of which are associated with cooperation and division of labour [43–45]. Ultimately, these factors may lead to the evolution of highly integrated social groups containing multiple classes of individuals with discrete ITs, as for instance the different castes of individuals that characterize the colonies of eusocial insects (e.g. ants, bees, wasps, termites) [46]. Although not its primary aim, our model predicts an evolutionary relationship between group heterogeneity (as measured by inter-individual variance in ITs) and social interactions (collective foraging) that is modulated by the nutritional environment (nutrient balance of available foods), partially supporting the above hypothesis.

Our results further suggest that collective foraging is not selected for in groups composed of individuals with highly divergent nutritional needs (i.e. bimodal distribution of ITs). However, this does not necessarily mean that intra-group variance is incompatible with sociality. As we have shown, in such species, additional mechanisms can evolve to mitigate the costs of collective foraging. For instance, eusocial insects have evolved sophisticated collective regulatory behaviour whereby a subset of individuals (the foragers) attempts to collect amounts and balances of nutrients that address the divergent nutritional needs of all colony members. In these advanced societies, foragers are able to gather foods that meet the high protein requirements of larvae and the queens, as well as the other adults that are more reliant on carbohydrates, based on a complex system of nutritional feedback between colony members [47–51].

4.4. Further development and conclusions

Our model, derived from nutritional geometry, provides a theoretical platform for exploring the costs and benefits of collective foraging in complex nutritional environments. A major advantage of this approach is that it generates specific predictions that can be empirically tested using well-established experimental designs from nutritional geometry [18]. Using this framework, it is possible to combine behavioural observations of groups of interacting animals feeding on chemically defined diets and to correlate individual nutrient intakes with measures of fitness traits both at the individual and collective levels [18]. Our model assumes a perhaps simplistic nutritional environment (i.e. foods are not finite and do not shift spatially), as our focus is primarily on heterogeneity in individual needs, in an environment that can be experimentally replicated. Future developments of our multidimensional approach, however, could integrate spatio-temporal distributions of finite foods constituting different compositions of essential nutrients, which ultimately determine the probability of a forager locating resources [52,53]. These factors constitute perhaps the most realistic costs to foraging in complex and ecologically relevant environments. Temporal and spatial variability in food abundance will alter the value of social information, thus affecting the nutritional strategy or strategies that will be optimal, both for an individual and groups. What is more, finite food sources will intrinsically capture aspects of intra-group conflict over a limiting resource, which will further affect the cost–benefit trade-off of group living.

Previous models demonstrate that simple mechanisms of social retention can optimize nutrient balancing in groups with homogeneous nutritional requirements. Here we present the first evolutionary ABM that re-evaluates the efficacy of such mechanisms for groups with heterogeneous nutritional needs. Our model suggests that simple mechanisms of social retention can improve foraging efficiency by reducing foraging times, even in relatively heterogeneous groups. Further, counterintuitively in some nutritional environments, heterogeneity in nutritional needs may select for increased collective decision-making. However, in groups with highly bimodal distributions of nutritional requirements (e.g. where needs of the sexes differ greatly) additional mechanisms of assortative foraging must coevolve alongside mechanisms of group retention, a potential route to the evolution of sexual segregation. Finally, our model may imply an evolutionary relationship between nutritional requirements, the ecological costs associated with foraging and the evolution of sociality, and provides a powerful framework for investigating such relationships.

Authors' contributions. A.M.S., M.L. and S.J.S. conceived the study. A.M.S., M.L., J.B. and M.C. designed the model. All authors contributed to the interpretation of the findings and the preparation of the manuscript.

Competing interests. We declare we have no competing interests.

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