Paper 2

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Co-existence of learners and stayers maintains the advantage of social foraging

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ABSTRACT

Question: To what extent can learning facilitate group formation in a social forager?

Model features: An individual-based simulation model is used to explore frequency- and density-dependent interactions between mobile learners and non-selective stayers that forage in a patchy resource environment.

Key assumption: Foraging efficiency peaks at intermediate group sizes.

Conclusions: Frequency-dependent interplay between mobile learners and sedentary stayers represents a general mechanism of group formation that maintains the advantage of social foraging. When rare or at moderate frequencies, learners redistribute and aggregate in groups of optimal size. This enhances the foraging performance of both learners and stayers. When the learning strategy dominates in the population, group size dynamics become unstable, resource intake for learners drops, and stayers do best. The strategies mutually benefit from each other and may potentially co-exist.

Keywords: frequency dependence, group formation, group size, individual-based model, learning, optimal foraging theory, social foraging.

INTRODUCTION

Animals that live in groups interact with conspecifics through competition and cooperation. Social foragers experience both costs and benefits of being in a group: increased foraging rates may result from improved search and attack efficiency or sharing of information among group members, whereas vigilance or dilution effects may reduce predation risk (reviewed in Giraldeau and Caraco, 2000; Krause and Ruxton, 2002). Competition and interference will eventually reduce the benefits of increasing group size, and as a consequence resource intake rates of social foragers often peak at intermediate group sizes.

The group size that maximizes individual food intake may, however, be evolutionarily unstable (Sibly, 1983; Clark and Mangel, 1984). Solitary foragers may benefit from joining a group as long as the intake rates of group members are higher than those for solitary foragers (see Fig. 1). Group size will then increase above the optimum, and eventually reach an equilibrium size at which group foraging has no advantages. This has been referred to as the

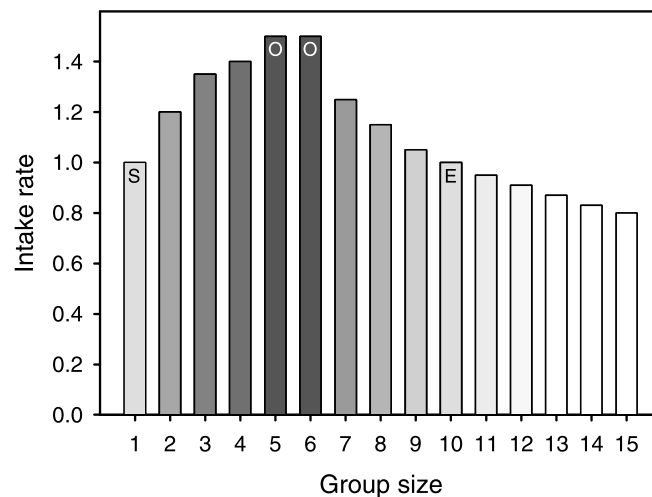---

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Fig. 1. The relationship between group size and individual resource intake per time step (adapted from Beauchamp and Fernández-Juricic, 2005). The letters denote resource intake rate of individuals foraging solitarily (S), in a group of optimal size (O), and in a group at the equilibrium size (E). The intensity of the grey shade is proportional to the intake rate of foragers in a group of that particular size; the shading corresponds to that used in Figs. 2 and 3.

paradox of social foraging, and the argument relies on the assumptions that (1) solitary foragers are free to enter a group at no cost (Giraldeau and Caraco, 2000), (2) foragers know the profitability of joining a group versus foraging alone, (3) individuals act sequentially and move solitarily between patches (Kramer, 1985), (4) group members are not genetically related (Giraldeau and Caraco, 1993; Higashi and Yamamura, 1993), and (5) resources are divided equally among group members (Hamilton, 2000). In this study, we address the first two of these assumptions.

For solitary foragers, the benefits of joining a foraging group must be outweighed by the costs of acquiring group membership. Individuals that move between groups experience reduced foraging time. Travelling may also elevate energy expenditure and increase exposure to predators. Foragers commonly experience trade-offs where high performance on one ecological function (e.g. dispersal) reduces performance on another task (e.g. foraging efficiency). Foragers may therefore differ in their mode of exploiting resource patches. Co-existence between explorative and sedentary foraging strategies has been reported in several systems, including rodents (Kotler and Brown, 1988; Benus *et al.*, 1991) and marine and freshwater snails (Wilson *et al.*, 1999; Chase *et al.*, 2001). In *Drosophila melanogaster*, 'rover' larvae travel long distances and often abandon food patches, whereas 'sitters' move to the nearest patch and feed there (Sokolowski, 1980; Sokolowski *et al.*, 1997). In the nematode *Chaenorhabditis elegans*, a similar co-existence exists between social foragers that aggregate in areas where food is most abundant and solitary feeders that distribute more randomly (de Bono and Bargmann, 1998; de Bono, 2003).

The mechanism by which an individual assesses the potential benefits of foraging in groups has seldom been considered in social foraging theory. Part of the problem concerning the 'paradox of group foraging' is the lack of a general theory explaining how groups form and split. In a recent contribution, Beauchamp and Fernández-Juricic (2005) proposed that if foragers were able to learn the quality of a patchily distributed resource, they could abandon under- and over-crowded patches and keep group sizes close to an optimal value. They argued that such a learning mechanism would solve the apparent paradox of group

foraging. However, they did not analyse the performance of their learning rule to determine whether the individual behavioural strategy was adaptive and evolutionarily stable.

The aim of this study is to establish whether learning may facilitate group formation in social foragers. Learners have to estimate environmental resources from experience and spend time travelling between foraging groups (replacing assumptions 1 and 2 above with more ecological realism). The cost of information (sampling and movements) and the benefits of using information (ending up in a better group) determine the profitability of the strategy; these are emergent properties of the interaction between forgers and the environment in our model. By studying the frequency- and density-dependent dynamics of mixed populations of mobile learners and sedentary foragers, we illustrate how co-existence between these two strategies may be evolutionarily stable. Learning is thus one mechanism that may explain group formation and thereby maintain the advantage of social foraging.

METHODS

We use an individual-based simulation model to explore group size dynamics in a population of social foragers. The environment consists of discrete identical food patches with renewable resources. Intake rate is a dome-shaped function of group size, where foragers in a group of intermediate size experience the highest intake rate [Fig. 1 (modified from Beauchamp and Fernández-Juricic, 2005)].

Foraging strategies

We distinguish between two types of foraging strategies: *stayers* are non-selective and remain within the first foraging patch they encounter; *learners*, on the other hand, may travel between foraging patches and search for groups of preferred size. These mobile foragers need to sample their environment to estimate its quality. The two strategies are analogous to the learning and non-learning foragers in Beauchamp and Fernández-Juricic (2005), with modifications in the learning algorithm, search behaviour, and the patch-leaving rule. Briefly, learning foragers know their current intake rate and use experiences from visited patches to estimate the global average intake rate in the environment. This global intake rate is then compared with their current intake rate to determine when to stay and when to leave a patch (detailed description below).

Resource intake and learning

All resources are found in patches, which are renewed every time step. Time is discretized in the model, and the duration of a time step is short compared with the period over which behaviour is studied. In each time step, the forager locates and consumes food if it is not travelling. Individual resource intake rate during time step t is denoted $i(t)$ and is determined exclusively by the numbers of foragers in the patch (Fig. 1). Average resource intake rate in patch P for a forager that enters at time step t_1 and leaves again at time t_2 is:

$$\bar{i}_P = \frac{1}{t_2 - t_1} \sum_{t=t_1}^{t_2-1} i(t)$$

Learning foragers update their expectation of the average resource intake rate in the habitat according to their experiences in patch P using a linear operator rule (Mangel, 1990):

$$E_P(i) = (1 - \alpha)\, E_{P-1}(i) + \alpha \bar{i}_P$$

The expected intake rate in the environment $E_P(i)$ is hence a weighted average of experiences from previously visited patches, $E_{P-1}(i)$, and the average intake per time step in the current patch, $\bar{i}_P$. At the beginning of the season, all learners have the same naive expectation of the average intake rate in the environment $E_0(i)$. The learning factor α represents an exponentially decaying memory, and its value determines the relative emphasis put on recent information. The model's sensitivity to learning rule parameters was tested for $E_0(i)$ in the range 0.8–2.0 and for α between 0.05 and 0.5. Foragers with high $E_0(i)$ are initially 'choosy' and may search for a long time before they settle in a patch, whereas non-selective foragers have $E_0(i)$ close to 1.0 and behave similar to stayers. The rate of learning increases with α, and a higher α is needed to trace a more rapidly changing environment. However, high learning factors also introduce more variability in the environmental estimates (see McNamara and Houston, 1987; Hirvonen *et al.*, 1999). The learning rule performed well and was relatively unaffected by changes in α between 0.1 and 0.2 as long as $E_0(i)$ remained within the range 1.1–1.4. We therefore used $\alpha = 0.1$ and $E_0(i) = 1.3$ throughout.

Patch-departure rule

We employ a patch-leaving rule inspired by the marginal value theorem (Charnov, 1976). Mobile foragers compare their expectations of future resource intake in the current patch to the expected profitability of searching for another resource location. Learners leave a patch if:

$$i(t)[T - t] < E_P(i)[T - t - t_S]$$

A forager that remains in a patch expects to receive the current resource intake rate $i(t)$ until the end of the season T. A forager that leaves a patch at time t will travel for a fixed time t_S before encountering a new patch with expected intake rate $E_P(i)$. Foragers are predicted to become increasingly reluctant to leave a patch when the end of season approaches. All foragers move solitarily between patches, and have an equal probability of ending up in any resource patch within the habitat. We present results from model scenarios with $t_S = 25$ time steps, but the model was tested for travel times ranging from 2 to 50 time steps. The cost of information acquisition increases with travel time, which thereby affects the foraging performance of learners. Dynamics of the interaction between the foraging strategies were, however, persistent to changes in travel time within this range.

Initialization and model observations

At the start of a foraging season, half the individuals in the population were randomly distributed among the 200 resource patches, while the other half were allowed to search for a patch with random travelling times ($\leq t_S$) remaining. A foraging season lasted 3000 time steps, and to prevent artificial patterns from synchronous updating (see Ward *et al.*, 2000), individuals made their patch-leaving decisions in a new random sequence every time step.

Group size distributions and intake rates were averaged over the whole foraging season and not only after reaching equilibrium distributions. In this way, we include the emergent

costs of sampling that learners accumulate during foraging periods of finite length. Forager distributions and average resource intake rates were averaged over 100 replicates, each having the same constant population size and frequency of learners. The relative frequencies of the two foraging strategies were altered from pure stayer populations, increasing the frequency of learners in steps of 2%, to monomorphic learner populations. We ran each simulation set (all learner frequencies and 100 replicates) for population densities ranging from 50 to 2000 individuals. This corresponds to an average density of 0.25 to 10 foragers per available resource patch in the environment. We present the results from the model scenarios with a constant population size of 500 individuals (population density 2.5), unless otherwise stated explicitly.

We call the frequency of learners at which the mean intake rate of stayers equals that of mobile learners the *equilibrium* frequency of the mixed strategy population. At a given population density this represents a Nash equilibrium, since the intake rate of each strategy drops as its relative proportion increases (see below).

RESULTS AND DISCUSSION

Learners move between foraging locations, alter group size distributions, and affect intake rates of other foragers within the habitat. The overall effects depend strongly on the prevalence of learners within the forager population. In the following, we (1) focus on the ecological dynamics and group size distributions as the frequency of learners changes, (2) analyse the performance of each strategy and its evolutionary implications, and (3) investigate how the performance of each strategy depends on population density.

Ecological dynamics and group size distributions

The distribution of group sizes depends on the relative frequency of movers and stayers within the population (Fig. 2). When alone, stayers distribute randomly because they settle in the first patch they encounter (left-hand side of Fig. 2a, b). When learners are introduced, they aggregate in foraging groups (from left to right in Fig. 2a, c) and consequently the number of occupied foraging patches decreases (Fig. 2a). In populations of learners only, foragers use only one-third of the available resource patches (right-hand side of Fig. 2a).

Mobile learners experience different group size distributions than stayers (Fig. 2b, c). At low densities, learners are able to explore the spatial distribution pattern produced by stayers and thereby locate more profitable patches. This increases the number of groups of preferred size (Fig. 2c), and the population quickly reaches a stable pattern of group sizes (Fig. 3a). At higher frequencies of learners, aggregation results in over-crowded groups. The fraction of learners that moves between patches increases: (1) because the number of occupied patches drops, and learners therefore need to visit several patches before they locate a foraging group; and (2) as groups grow larger than optimal, newcomers reduce the intake rate of other group members and thereby trigger patch-leaving events (Fig. 2a, c). As a consequence, it takes longer for the population to reach stable group size distributions (Fig. 3b) and learners are more often found in groups that are larger than optimal (Fig. 2c).

The perspective is slightly different from the stayers' point of view (Fig. 2b). Their resource intake is directly influenced by the rearrangement of groups caused by the movement of learners. Stayers tend to become solitary when learners abandon under-crowded patches (Fig. 2b). At the same time, stayers often function as crystallization seeds,
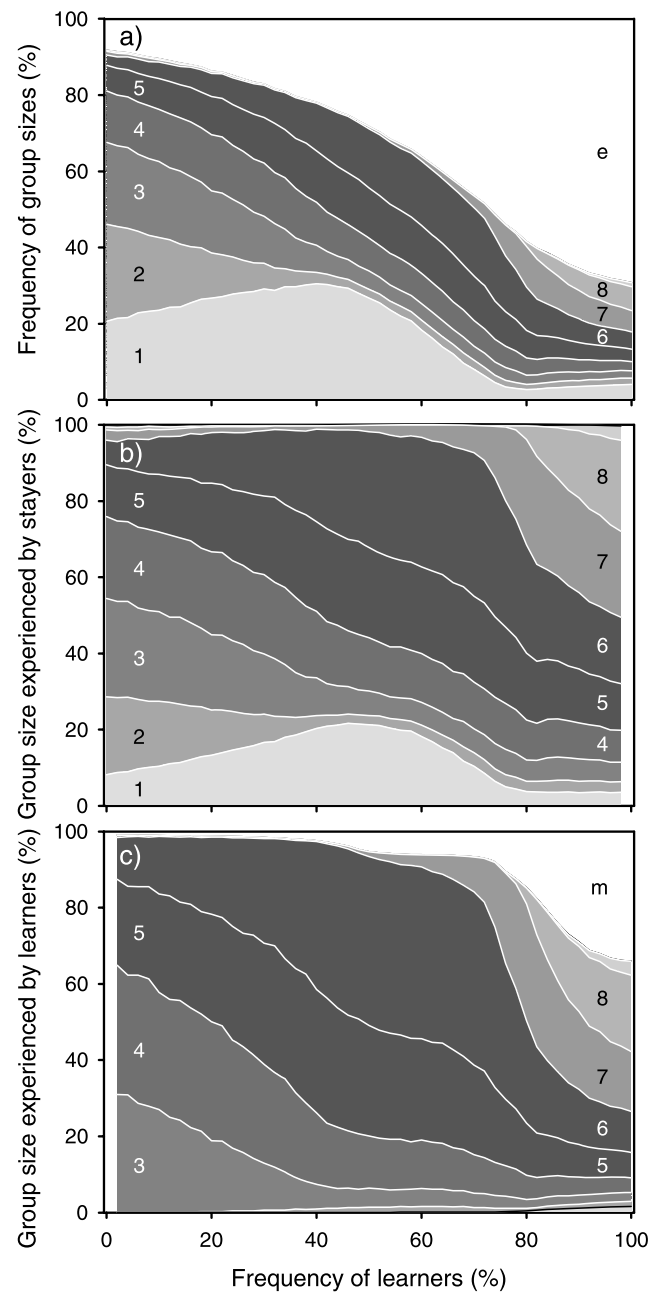
Fig. 2. The distribution of group sizes as a function of the frequency of learners in the population. (a) The frequency of *patches* with different group size. The proportion of patches that are empty is indicated by 'e'. (b) The group size experienced by *stayers*. (c) The experienced group size for mobile *learners*. Individuals on the move between patches are indicated by 'm'. The intensity of the grey shade is proportional to the intake rate of foragers. Distributions were averaged over 100 simulations for each of 50 populations varying in frequency of learners.

and stayers that reside in patches where learners aggregate benefit as learners bring group sizes closer to optimal.

Performance and evolutionary considerations

The average long-term intake rate gives a measure of each strategy's foraging performance (Fig. 4a). First, note the advantage of being rare: at low frequencies, both learners and
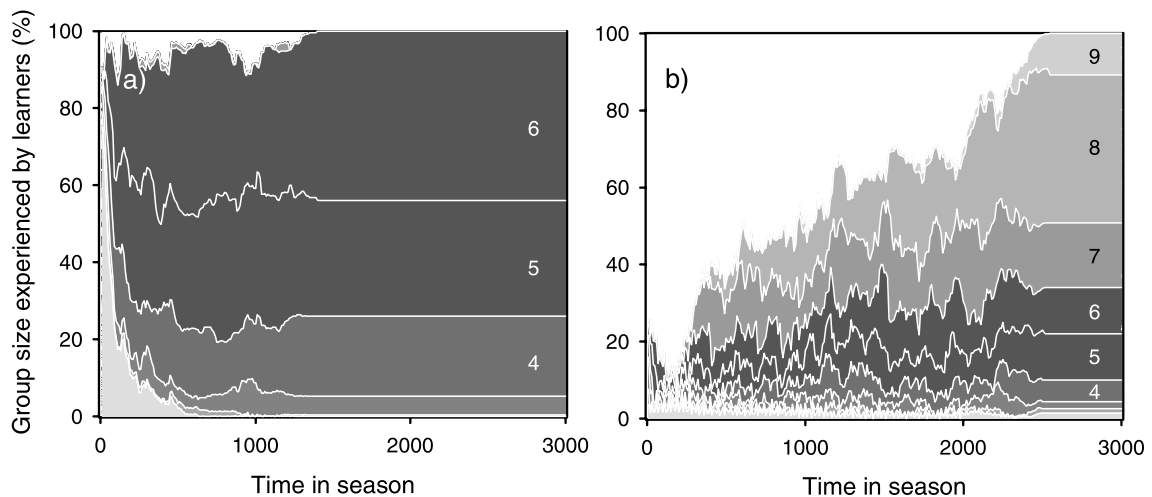
Fig. 3. The group size distributions experienced by learners in a population of (a) 40% and (b) 100% learners as a function of time in season. The intensity of the grey shade is proportional to the intake rate of foragers. The distribution of 500 individuals among 200 patches was calculated every time step.

stayers have a higher long-term intake rate than the more abundant strategy. The redistribution of learners enhances performance of both foraging strategies at low to intermediate frequencies of learners. The variation in long-term intake rate among stayers is larger, however, since learners are able to actively aggregate in groups of preferred size (Fig. 4b). The performance of learners peaks at intermediate frequencies, while stayers continue to benefit as learners become more prevalent. At the equilibrium proportion of 62% learners, the long-term intake rate of learners equals that of stayers. At high frequencies, learners experience a dramatic reduction in foraging performance (Fig. 4a).

The frequency-dependent foraging performance arises because learners and stayers alter the spatial and temporal variability in intake rates within the environment. At low frequencies, learners do well because they exploit the spatially heterogeneous but temporally stable distribution of stayers (Fig. 4c). Such populations quickly attain stable distributions of profitable group sizes (Fig. 3a). Learners aggregate in larger groups, hence the spatial variance in intake rate continues to increase until the two strategies are equally represented in the population. The spatial variation in intake rate decreases when mobile learners become even more abundant, since the number of solitary stayers declines (Fig. 4c).

Mobile learners not only influence the spatial variability, but also alter the temporal stability of groups (Fig. 4c). At high frequencies of learners, the temporal variability *within* a patch approaches the spatial variation among groups and the performance of the learning strategy declines dramatically. At this point, good patches are ephemeral. Foragers have almost the same probability of experiencing profitable group sizes by staying in the same patch as they would by searching for a new one. In such circumstances, stayers prosper because they need not pay the cost of travelling. When the learning strategy dominates, group size distributions stabilize late in the season and with relatively many groups being larger than optimal (Fig. 3b).

Effects of population density

So far, we have considered model scenarios where the number of resource patches is sufficiently high to allow foragers to choose between solitary and group foraging. We now
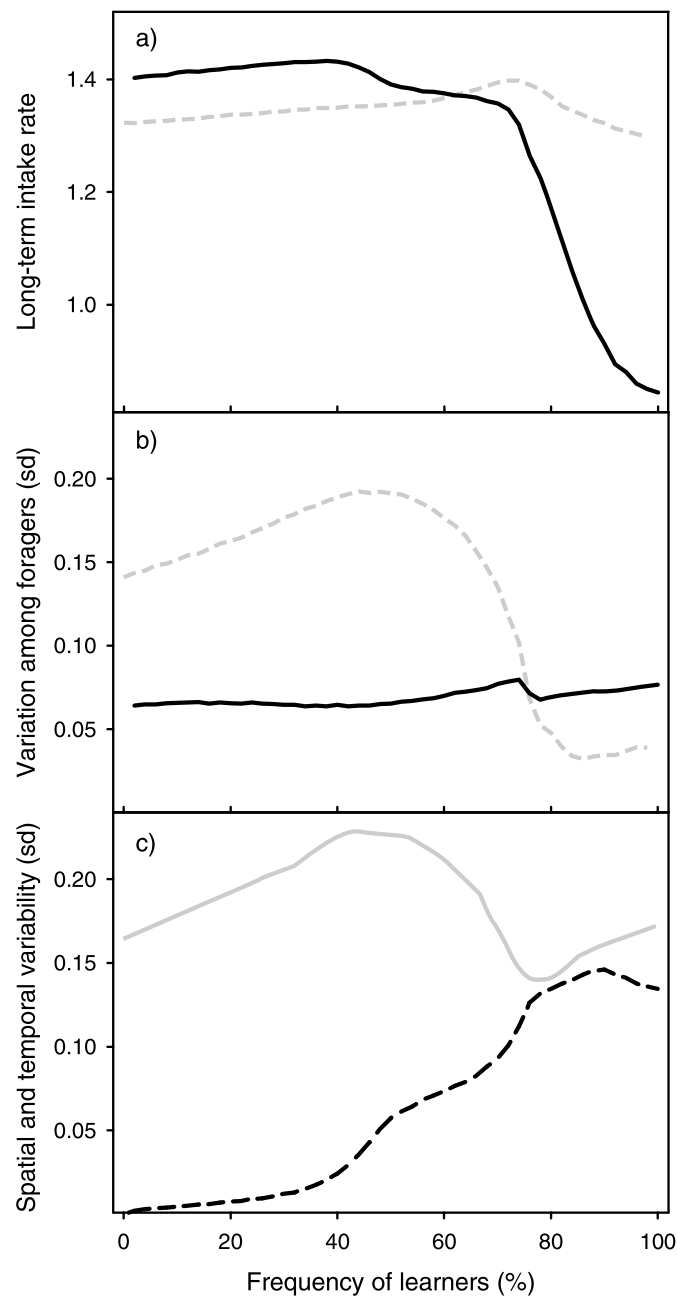
Fig. 4. Average foraging performance, individual variation, and spatial and temporal variability among groups as a function of frequency of learners in the population. (a) Average long-term intake rate of learners (black solid line) and stayers (grey dotted line), (b) variation in long-term intake rate among learners (black solid line) and stayers (grey dotted line), and (c) the temporal variability *within* each occupied patch (black dotted line) and the average spatial variation *among* occupied patches (grey solid line) (standard deviation of intake rates; sd).

consider how population density affects intake rates and the dynamics between the two strategies. Intake rates of learners are always lower than for sedentary foragers in populations consisting of one strategy only (Fig. 5a). When both foraging strategies are present at equilibrium proportions, foragers have a higher mean intake rate than they would have in pure populations of each of the two strategies. This means that there is a potential for stable co-existence between the two strategies at all population densities tested.
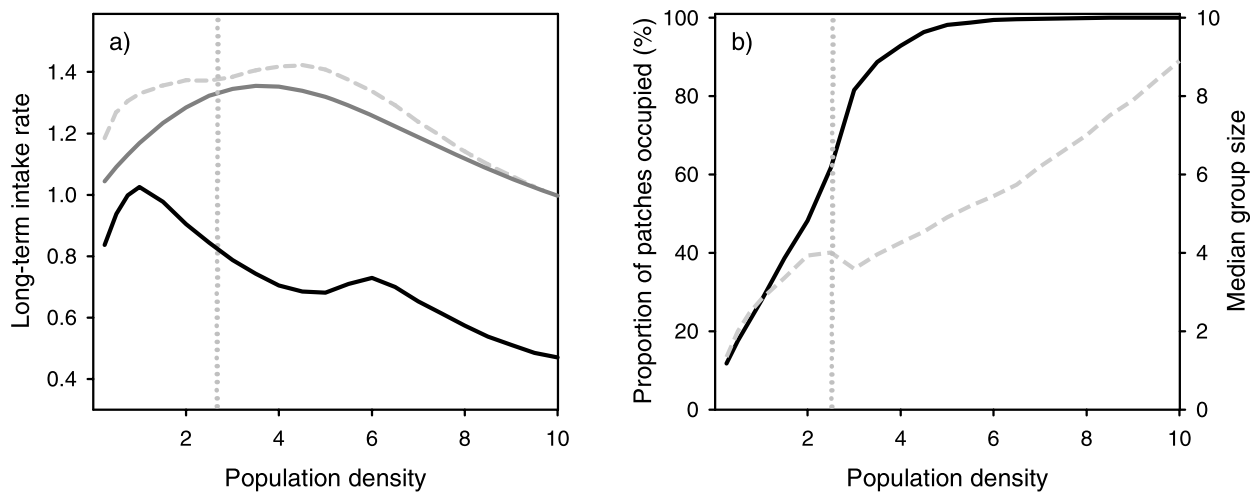
Fig. 5. (a) Average long-term intake rate of foragers as a function of population density (the x-axis gives the average number of foragers in the environment per resource patch available). The average performance of foragers in the mixed-strategy populations at the equilibrium proportion of learners (grey dotted line) is higher than for monomorphic learner populations (black solid line) and stayer populations (grey solid line). (b) The proportion of patches occupied by foragers (black solid line) and the median group size (grey dotted line) in mixed-strategy populations at the equilibrium frequency of learners. The vertical dotted line gives the population density for the model scenarios used in Figs. 2–4.

Overall, the highest intake rates are attained in a mixed population where the density of foragers is close to the optimal group size of 5–6 individuals per patch (Fig. 5a). At this point there are foraging groups distributed among all resource patches and median group size lies at the optimum (Fig. 5b). Sedentary foragers distribute randomly and are therefore better off at slightly lower population densities (Fig. 5a), since the reduction in intake rate is more severe in over-crowded than in under-crowded patches (cf. Fig. 1). In general, pure populations of learners do best at low population densities, since patches seldom become over-crowded (Fig. 5a). The intermediate peaks in long-term intake rate result in part from how parameters of the learning rule ($E_0(i)$ and α) interact with the intake rate function.

The frequency of learners in the equilibrium population also varies with population density and peaks at low to intermediate densities (Fig. 6). This population size covers the transition region between two separate challenges: in dilute populations the challenge is to locate other foragers to form groups of optimal size, while in dense populations the challenge lies in over-crowding and dealing with a limited number of resource patches. As patches become over-crowded, learners quickly suffer from frequent movements and the equilibrium frequency drops. At high densities, the distribution of foragers is Pareto optimal in the sense that individual foragers cannot increase their resource intake by joining a new group without simultaneously decreasing the intake rate of resident group members (Clark and Mangel, 1986). In such circumstances, it may be more advantageous for resident group members to defend the limiting resource and restrict the access of solitary joiners. When resources are not restricted to a limited number of patches, social foragers seek to aggregate in groups of appropriate size. In such systems, we expect the interplay between mobile and sedentary strategies to be most important.
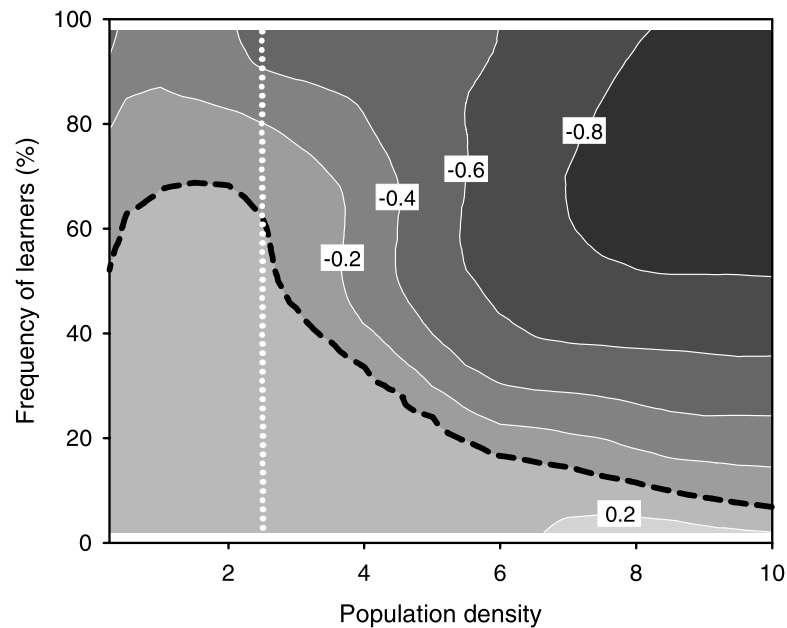
Fig. 6. Difference in average food intake of learners compared with stayers as a function of forager density and frequency of learners in the populations. Population density is given as the average number of foragers in the environment per resource patch available. The dashed line gives the equilibrium frequency of learners in the mixed populations. Below this line, average intake rate is higher for learners than for sedentary foragers. Above the line, the intensity in the grey shade gives the relative decrease in intake rate of learners compared with stayers. The vertical dotted line corresponds to the population density of the model scenario used in Figs. 2–4.

GENERAL DISCUSSION

Learners are able to aggregate in groups of more optimal size and may improve foraging performance in populations of social foragers that benefit from being in groups of inter-mediate size. The learning strategy will, however, not out-compete non-selective sedentary strategies. As learners become abundant, group size dynamics turns inherently unstable and the performance of the learning strategy drops dramatically. In this way, learners alter the environmental heterogeneity and interact with the environment in intricate ways. The frequency-dependent perspective of our analysis reveals how learners and stayers may mutually benefit from the presence of each other and thus potentially co-exist. In the following, we will (1) discuss how the profitability of mobile strategies depends on spatial heterogeneity and temporal stability, (2) investigate how frequency dependence arises from feedbacks between the strategies and the environment, (3) highlight the relevance for social foraging theory, and (4) briefly discuss some consequences for the potential co-existence of foraging strategies.

Mobile strategies require persistent cues to explore spatial heterogeneity

Habitats are seldom uniform; hence mobile foragers may exploit spatial heterogeneities by searching for better than average locations. This requires an estimate of patch quality and a measure of the general resource conditions within the environment. Environmental

information could be incorporated in behavioural rules of thumb (inherited mechanisms adapted to prevailing environmental conditions), or acquired through learning from individual experiences within a lifetime (McNamara *et al.*, 2006). Although the underlying behavioural mechanisms of learning are more complex than a fixed patch-leaving strategy, the assumptions one has to make about information flow are simpler. Foragers gather information as they search the resource habitat; hence the quality of information is an emergent property of the feeding and movement behaviour. Learning is generally favoured when there is some structure or persistence in the information stimulus and some variability within or between generations to favour flexible behavioural responses (Stephens, 1991, 1993). The ability of learners to explore the spatial heterogeneities hence relies on some temporal inertia in the group size distributions. In our model, current resource intake is a good estimate of future gain when foragers have strong site fidelity, but the persistence in this signal fades as mobile learners increase in numbers.

Feedback between learners and the environment causes frequency dependence

Foraging theory has commonly focused on how behavioural strategies are adapted to different environmental conditions (Stephens and Krebs, 1986). This perspective neglects that adaptations may also shape the environment to which they respond (Dieckmann and Ferrière, 2004; Nowak and Sigmund, 2004). Frequent movements to sample foraging options inevitably alter the surroundings, as illustrated in our model. This potentially makes the task of learning more challenging, and may reflect a fundamental property of explorative strategies.

The fitness of a strategy often depends on its prevalence within the population. Dynamics of social foragers have therefore commonly been analysed using game-theoretic approaches (reviewed in Giraldeau and Caraco, 2000). In foraging groups, behavioural strategies that actively search for resources (producers) may co-exist with individuals that exploit the foraging opportunities created by others (scroungers). Parasitic scroungers reduce the average resource intake rate in populations of producers (Vickery *et al.*, 1991; Barta *et al.*, 1997). This contrasts the mutual benefit that learners and stayers experience in our model, where mixed equilibrium populations achieve higher intake rates than monomorphic populations. It is the resource dynamics mediated by the strategies themselves that creates the potential for co-existence.

Learners benefit from the presence of other learners at low frequencies because they facilitate aggregation. An increased frequency of learners has a detrimental effect, as it causes over-crowding and unstable patch-leaving dynamics. These emergent frequency-dependent interactions illustrate how difficult it is to simply parameterize the costs and benefits of such dynamic relationships. As opposed to traditional game-theoretic approaches, individual-based models handle temporal dynamics and constantly changing competitive relationships between strategies. Our results suggest that the performance of even the simplest strategies strongly depends on the biotic environment, and that the dynamic interactions between foraging strategies and their resource environment may be more important than hitherto reflected in foraging models.

Relevance for social foraging theory

The paradox of group foraging (Sibly, 1983; Clark and Mangel, 1984), namely that solitary foragers would continue to join groups until there is no benefit of social foraging, relies on the

assumption that foragers are free to move between groups at no cost. Whenever foragers need to spend time locating a group, the benefits of joining more optimal groups must be traded off against the direct and indirect costs of moving. This has several implications for social foraging models. First, that learning foragers may keep group sizes close to the optimal value (Beauchamp and Fernández-Juricic, 2005) does not guarantee that the behavioural mechanism is advantageous or evolutionarily stable. Learners have to pay costs related to habitat exploration, hence the long-term intake rate of the strategy needs to be evaluated (Beauchamp and Ruxton, 2005). Second, the foraging efficiency of monomorphic populations may give an erroneous picture of the overall performance of a behavioural strategy. In our model, learners did quite well when rare but never performed better than stayers in pure-strategy populations. Third, in our model the benefits of mobility – that is, the increased average intake rates achieved by abandoning over- and under-crowded patches – depend on the temporal stability of the system. This emphasizes the need to consider dynamic movement patterns of all foragers in a population, and not only sequential choices made by solitary foragers.

We consider a system where resources constantly renew, which allows us to focus on the density-dependent part of the food intake function. In many natural systems, resources show only partial recovery or foragers experience diminishing returns due to reduced search or handling efficiency. In such circumstances, groups deplete patches more quickly than solitary foragers, and will spend more time travelling between patches (Beauchamp and Ruxton, 2005). This reduces the potential benefit of foraging in large groups compared with completely renewing environments (Beauchamp and Ruxton, 2005). In such situations, patch-leaving decisions are influenced both by group size and patch longevity. Foragers are thus faced with a dual problem: when to leave a patch and when to leave a group. If group members were able to synchronize their movements between patches, learners could compare their average performance within one group (both feeding and searching) to the profitability of joining differently sized groups. Foragers with strong group fidelity (analogous to stayers) and learners that select between groups could then potentially co-exist whenever group search is time-consuming or involves additional costs such as increased risk of predation. Learning and the logic of patch-leaving behaviour may thus apply to several hierarchical levels, which motivates further studies on how individual rules and mechanisms scale up to collective decisions and group cohesion (Sumpter, 2006).

Co-existence between social foraging strategies: an evolutionary outcome?

When rare, both learners and stayers performed better than the more abundant strategy. The strategies are therefore mutually invadable, meaning that they may spread from low frequencies (and thus potentially arise from single mutations). The strong frequency dependence between learners and stayers suggests two evolutionary outcomes. First, the benefit that each strategy gains from the presence of the other may facilitate stable co-existence. Alternatively, the poor performance of the learning strategy when present at high frequencies may select for more robust behavioural mechanisms. This includes foraging strategies that more actively search for foraging groups, sub-group formation with synchronized movements, and individual recognition. Learners could potentially assess group size dynamics using more environmental cues and thereby adjust to temporal instability. The problem of mobile strategies may, however, be more fundamental, as the temporal fluctuations within a patch and the reduced spatial variance among patches would

eventually decrease the efficiency of any mobile strategy. One option could be foraging strategies that switch between mobile and sedentary modes. Such strategies may be less efficient than obligate learners, however, since lower sampling frequencies introduce more uncertainty in environmental estimates. Such behavioural trade-offs in information acquisition may be interpreted in a specialist–generalist context (Dall and Cuthill, 1997).

Individuals or strategies that differ in movement behaviour will most likely differ in the way they gather information and put it to use (Sokolowski, 1998). Such strategies will not necessarily differ in overall performance, but will probably show differences in the trade-off between exploration and exploitation, or variable responsiveness to local environmental conditions. Our results highlight that information exists in an ecological context and is acquired through sampling behaviour, which in turn affects information patterns. Models including full dynamic feedback between the population, the strategies, and the environment facilitate the study of emergent costs and benefits of behavioural strategies and raise interesting questions regarding the underlying behavioural mechanisms of social organization in natural systems.

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