

# The group-size paradox: effects of learning and patch departure rules

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In many species, foraging in groups can enhance individual fitness. However, groups are often predicted to be larger than the size that maximizes individual fitness. This is because individual foragers are expected to continue joining a group until the fitness in the group falls to the level experienced by solitary foragers. If such a process were pervasive, social foraging, paradoxically, would provide little evolutionary advantages. We propose a solution to the group-size paradox by allowing foragers to learn about habitat quality and leave food patches when their current intake rate falls below that expected for the whole habitat. By using a simulation model, we show that under a wide range of population sizes, foragers using such rules abandon under- and overcrowded patches, ensuring that group size remains close to the optimal value. The results hold in habitats with varying patch quality, but we note that the lack of food renewal in patches can disrupt the process of group formation. We conclude that groups of optimal sizes can occur frequently if fitness functions are peaked and resources patchily distributed, without the need to invoke relatedness between joiners and established group members, group defense against joiners, or other mechanisms that were proposed earlier to prevent groups from becoming too large. *Key words*: learning; linear operator rule; optimal group size; simulation model; social foraging. [*Behav Ecol* 16:352–357 (2005)]

Animals that forage in groups often experience costs and benefits associated with the presence of companions. Fitness in this situation is expected to be a peaked function of group size. Increases in fitness with group size have been related to greater foraging efficiency and predation avoidance (Krause and Ruxton, 2002). Decreases in fitness, on the other hand, often result from interference among foragers in larger groups. The peak in the fitness function represents the *optimal group size* at which individuals should obtain the greatest net benefits. Earlier models of group foraging thus predicted that animals should forage preferentially in groups of optimal sizes (Pulliam and Caraco, 1984).

The optimal group size, however, has been argued to be evolutionarily unstable (Sibly, 1983). For instance, consider a solitary forager with the option of either remaining alone or joining a group containing the optimal number of foragers. Solitary foraging usually entails low fitness, and joining the group represents the best choice. The addition of one forager to the group, however, will reduce fitness for all established group members. The process of joining by other solitary foragers should eventually stop when entering the now larger group brings fewer benefits than remaining alone. This group size represents the *equilibrium group size* because no forager can increase its fitness by joining (Clark and Mangel, 1986). Ironically, at the equilibrium group size, social foraging provides little extra advantages over solitary foraging thus creating the group-size paradox (Giraldeau, 1988). Evidence that foragers often occur in groups beyond the optimal size can make sense in the equilibrium model of social foraging.

Several mechanisms have been argued to prevent groups from reaching the equilibrium group size, thus ensuring that social foraging provides evolutionary benefits. First, established group members may repel joiners to maintain group

size near the optimal value (Giraldeau, 1988). This hypothesis may not be applicable when the cost of aggression is high, and assumes that established group members can effectively control group composition (Buston, 2003; Williams et al., 2003). Second, when joiners and group members are genetically related, the equilibrium group size is predicted to be smaller and closer to the optimal value (Giraldeau and Caraco, 2000). This hypothesis requires kin recognition and applies only to populations with limited dispersal, which will increase the rate of encounters with kin.

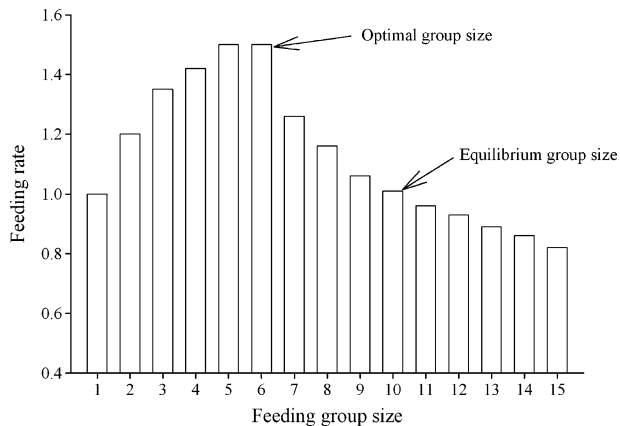
Third, if fitness in any groups larger than the optimal size is less than that of a solitary forager, optimal group size can be evolutionarily stable (Giraldeau and Gillis, 1984). This hypothesis assumes a precipitous decline in fitness in groups above the optimal size, which remains to be documented. The fourth hypothesis involves movements from one group to another by single foragers aiming to maximize their expected fitness. For instance, if foragers in too large a group have the option of joining a smaller group nearby, intergroup movement by single foragers should lead to the breakdown of the larger group. Nevertheless, after such movements, groups are still predicted to be larger than the optimal size and also, unrealistically, nearly all equal in size (Sibly, 1983). Why groups of different sizes occur initially, and how foragers can estimate relative fitness if groups are not in visual contact, is not addressed by this hypothesis.

Finally, if subgroups are allowed to break-off from groups near the equilibrium size, owing to disturbance for instance, there will be little incentive for the splintered subgroups to rejoin, and group sizes should be closer to the optimal value (Kramer, 1985). Nevertheless, nothing prevents disturbance from splitting groups near the optimal size. Consequently, the potential for small subgroups to join larger groups still exists, and this process could lead again to group size inflation.

Therefore, it appears that the above mechanisms may not propose a general solution to the group-size paradox. Here, we propose a mechanism whereby foragers learn about habitat quality as they sample food patches and choose to

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Received 31 May 2004; revised 25 August 2004; accepted 10 September 2004.



**Figure 1**  
Intake rate as a function of the number of foragers in a food patch. In this example, solitary foragers in a food patch obtain one food item per time step. The addition of foragers to the patch first increases and then decreases food intake rate. The optimal and equilibrium group sizes are shown. A similar peaked fitness function was used for patches of different quality by scaling the values up or down.

stay in a group or leave to search on their own based on their personal estimate of food intake rate in the whole habitat. In the spirit of the marginal value theorem of patch exploitation, foragers leave a group when their current intake rate falls below that expected for the habitat (Bernstein et al., 1988). We explore consequences of this mechanism for the distribution of group sizes under different habitat characteristics and population sizes.

Our approach is to model group size as the outcome of adaptive choices by individual foragers. We do not rule out the role of other factors, such as relatedness between joiners and established group members, or group defense against joiners. Instead, we suggest that more emphasis should be placed on understanding processes that lead foragers to join and leave groups.

## THE MODEL

We extend earlier models of habitat use based on interference fitness functions and learning about habitat quality (Beauchamp et al., 1997; Bernstein et al., 1988). In these models, there are no benefits to aggregate in one patch, and therefore, the optimal group size is essentially one. We incorporate a peaked fitness function in the model, which allows us to make predictions regarding optimal group sizes when there are potential benefits to aggregate.

We do not model specifically the mechanisms responsible for changes in fitness with group size. Such mechanisms are reviewed by Krause and Ruxton (2002). To provide an example, the increase in fitness with group size, inherent in a peaked fitness function, may reflect the fact that more time is available to forage owing to a reduction in vigilance. A decrease in vigilance with group size may arise, for instance, because larger groups detect predators more easily. The decrease in fitness in larger groups, on the other hand, may reflect foraging interference among individuals. Therefore, although it is not explicitly stated, the choice of foragers to join or abandon a group is motivated by the consequences of predation risk and competition on foraging.

In addition to predation risk and competition, other key ecological factors in determining group size include population density and patch renewal rate. As population density

increases, encounters between foragers are likely to increase, and this will have an influence on group size (Krause and Ruxton, 2002). When food items within patches are not renewed rapidly, fewer opportunities must exist to aggregate because the time span to exploit patches is reduced. In addition, because resources in these patches can be depleted more rapidly, foragers may be forced to spend more time traveling between patches (Chapman and Chapman, 2000), which could therefore influence their estimate of habitat quality and hence their choice to stay in a group. The model thus examines changes in group size as population density varies and in patches that can be renewed or not.

The model simulated the foraging activities of a population of  $n$  independent and identical foragers in habitats with 900 potential food locations arranged regularly on a  $30 \times 30$  grid. In each simulation, a subset of food locations actually contained a fixed number of indivisible food items. Foragers learned the quality of the habitat during the time course of the simulation and chose whether to stay in or leave encountered food patches on the basis of this estimated quality.

At the beginning of each simulation, 40 food patches, each containing the same number of food items, were distributed randomly in the habitat. Depending on habitat type, an exploited patch could become exhausted or not during the course of the simulation. Ten patches each were allocated to one of four quality classes defined by the number of food items which a solitary forager could obtain during one time step. For simplicity, patch quality was assumed to be independent of the number of food items remaining in a patch. Patches that became exhausted by foragers were replaced by full and identical patches elsewhere in the habitat so as to maintain patch density constant. Foragers were initially distributed randomly on the foraging grid.

Each simulation ran for 2000 time steps, which proved sufficient to obtain stable outcomes under all conditions tested. Foragers used the habitat following specific rules. If the location occupied by a forager contained food, the forager removed a fixed number of food items per time step. The number of food items removed by one forager during one time step (intake rate  $I$ ) varied as a function of patch quality and the number of conspecifics present at the location. In a given food patch, we assume that food intake rate first increases and then decreases with group size (Figure 1). This particular shape was used for patches of all quality classes. With this fitness function, the optimal size occurred in groups of six and the equilibrium size in groups of 10.

Foragers abandoned exhausted patches. Foragers could also leave a food patch before exhaustion if their current intake rate fell below their personal estimate of intake rate ( $H$ ) for the whole habitat. The above decision rule is based on the marginal value theorem of patch exploitation by solitary foragers (Bernstein et al., 1988). At the beginning of each simulation, all foragers started with the same estimate of habitat quality. The value of the estimate was updated at each time step as a weighted mean of past and current intake rate by using the linear operator rule (Kacelnik and Krebs, 1985):

$$H_{t+1} = I\alpha + (1 - \alpha)H_t$$

where  $H_t$  is the value of the estimate at time  $t$ , and  $\alpha$  is a memory factor ( $0 < \alpha < 1$ ). This rule is Bayesian in nature, because a prior expectation of quality is updated after the acquisition of current information to form a posterior expectation of quality (Mangel, 1990). The linear operator rule has been used in other foraging games involving frequency-dependent payoffs and has been shown to perform well relative to other rules (Beauchamp, 2000). When the rate

of food intake is equal to zero over several time steps, assessments decay to zero at a rate dependent on  $\alpha$ .

When the location occupied by a forager contained no food, individuals moved one location away in one of the four cardinal directions. On reaching grid boundaries, foragers moved one location away in the opposite direction. During such movements, foragers obtained no food, and as mentioned earlier, the value of  $H$  was decremented at each time step.

The above processes were repeated for each forager in the population at each time step. At the end of the simulation, the number of foragers in food patches was tallied and modal group size in these patches was calculated. Means and standard deviations were calculated over a set of 100 such simulations. We decided to focus on the distribution of foragers in food patches rather than on the distribution of all foragers in the habitat because individuals are forced to search for food and travel alone in the model.

We tested the model in four different types of habitats by varying the occurrence of patch renewal (present or not) and the level of variance in patch quality (present or not). In the non-renewing condition, each food patch contained 1000 items, all of which could be obtained in the course of one simulation. In the renewing condition, each food patch contained an effectively infinite number of food items. In the no-variance condition, solitary foragers in a food patch obtained one food item per time step. In the variance condition, they obtained 0.25, 0.75, 1.25, or 1.75 food items per time step, depending on the assigned patch quality, which maintained mean food patch quality constant across all habitat types. The realized food intake rate also depended on the number of foragers in the patch as mentioned earlier. Properties of the model were investigated in populations ranging in size from 50 to 500 by steps of 50.

We ran two types of simulations for all combinations of habitat type and population size. In the first type, referred to as the null model, foragers did not use the linear operator rule and therefore only left food patches after exhaustion. In the second type, referred to as the learning model, foragers used the linear operator rule to assess habitat quality leaving food patches as described above.

In the learning model, the prior estimate of habitat quality was set at two, which induced foragers to sample a number of food patches before settlement. We ran simulations with values of the memory factor ranging from 0.01 to 0.10, the usual range in the literature (Bernstein et al., 1988; Houston and Sumida, 1987), and failed to document substantial changes in the results. We thus present results with the 0.01 value. Lower values of the memory factor slow the rate of learning about habitat quality, which can only be appropriate in habitats with little expected variation in food intake rate (McNamara and Houston, 1987).

## RESULTS AND DISCUSSION

### Null model

The null model provides a baseline to predict the size of aggregations owing to chance encounters between foragers. Modal group size in food patches increased linearly with population size and reached the equilibrium group size of 10 near the population of 400 foragers (Figure 2a). In the renewing patch condition, modal group size obviously did not vary with variance in patch quality. In the non-renewing patch condition, modal group size was much reduced with and without variance in patch quality. The lack of food renewal in patches reduces the temporal window of opportunity to locate

a food patch already occupied by companions, thus providing fewer opportunities to aggregate at food patches.

The null model predicted a range of group sizes at the end of simulations (Figure 2b). The distribution of group sizes was generally flat: groups smaller than the optimal size and groups larger than the equilibrium size occurred frequently. When patches were not renewed, solitary foraging was more prevalent and large groups occurred less often.

### Learning model

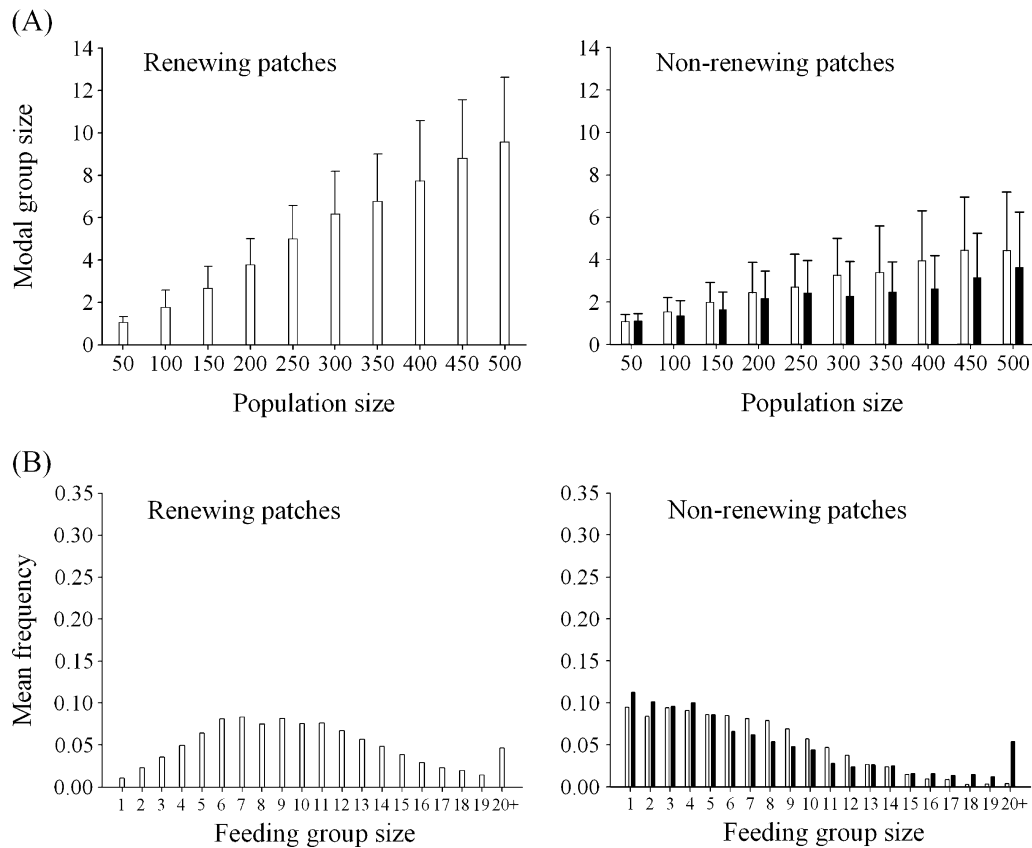
In contrast to the null model, modal group size increased more rapidly with population size but reached an asymptote at the optimal size at intermediate population sizes (Figure 3a). Modal group size in the largest populations increased anew. The same pattern was recorded with and without variance in patch quality. In the non-renewing condition, modal group size was again much reduced and increased linearly with population size without reaching an asymptote.

No groups smaller than the optimal size occurred in the habitat with no variance in patch quality (Figure 3b). Groups larger than the optimal size occurred less frequently than in the null model, but the distribution of group sizes still extended well beyond the equilibrium group size. Variation in patch quality introduced a greater range in the distribution of group sizes. Under the non-renewing patch condition, the range of group sizes was again restricted to small groups and the distribution of group sizes was flatter.

In the learning model, foragers can abandon patches with relatively low food intake rate. Low food intake rate may arise because of poor intrinsic patch quality or when too few or too many foragers settle in a patch. In particular, choices to leave depauperate patches favor the formation of larger groups in other patches, which leads to the rapid increase in modal group size with population size. The plateau phase arises because foragers in groups near the optimal size experience a decrease in intake rate after the arrival of new companions. As a consequence, foragers may choose to leave if their personal estimate of intake rate for the habitat is higher. As population size reaches higher levels, all food patches become crowded and modal group size inevitably increases beyond the optimal size. In large populations, the distribution of foragers is now dictated by interference effects occurring in these large groups.

The formation of groups above and beyond the optimal size is predicted by the learning model. Because personal estimates of habitat quality decrease when foragers fail to locate a food patch for some time, such foragers may therefore find the option of exploiting an under- or overpopulated patch more appealing (Martinez and Marschall, 1999). This process is more likely to occur when food patches vary in quality. Rich patches represent a viable choice for foragers that have abandoned patches even when these rich patches are overpopulated. The poor, underpopulated patches can also be settled by foragers with low estimates of habitat quality. Variance in patch quality is expected to produce a larger range of group sizes, and generally, the learning model predicts that patches of different quality can be settled by foragers with different estimates of habitat quality.

Depletion of food patches leads to a decrease in group size. As aggregation in food patches occurs by chance in the models, large aggregations are less likely to occur when patches fail to last very long. As foragers spend more time locating food patches in the non-renewing patch condition, lower estimates of habitat quality also favor aggregation in patches that contain fewer than the optimal number of foragers. The end result is an increased proportion of smaller



**Figure 2**

Results from the null model. (A) Modal group size in food patches is shown as a function of population size and level of patch renewal. (B) Distribution of group sizes is shown as a function of level of patch renewal in a population of 400 foragers. In each panel, simulation results are shown for habitats with no variance (open bars) or with variance in patch quality (closed bars). Each bar represents the mean of 100 simulations. Standard deviation bars are shown in panel A.

groups. In the non-renewing patch condition, the benefits of learning are less obvious and the outcome becomes closer to that expected with the null model.

### General discussion

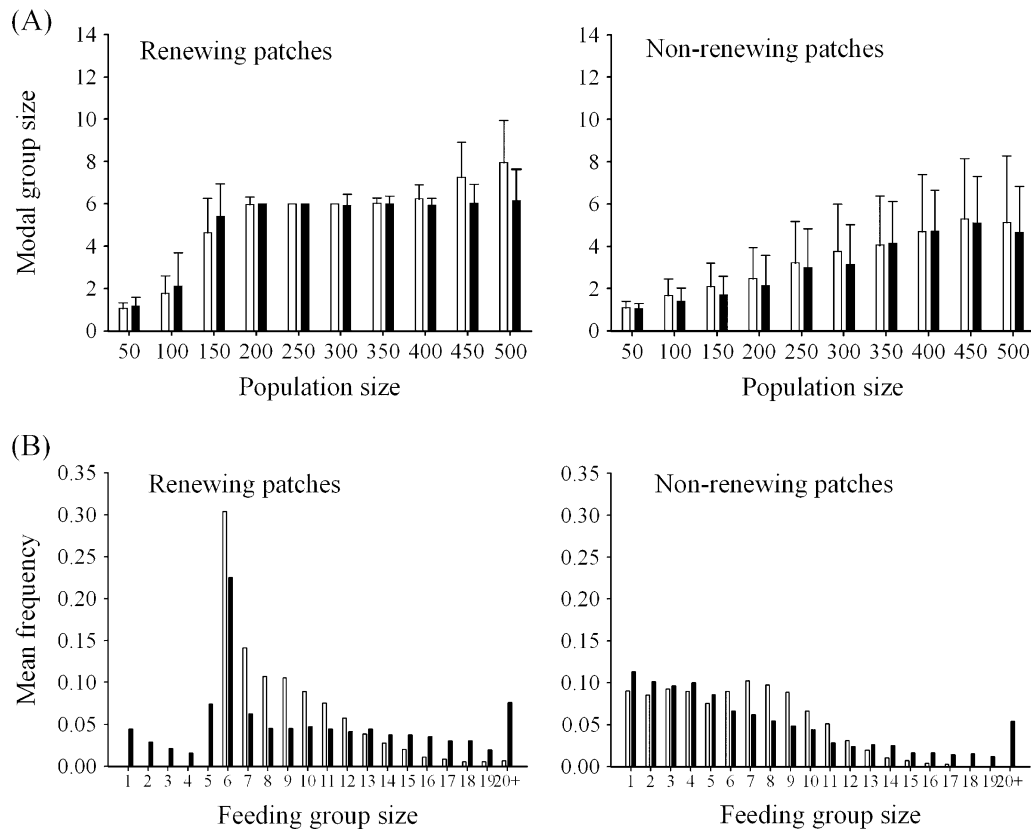
Groups are often predicted to be larger than the optimal size, as individuals are expected to continue joining until foraging in groups or alone provide the same fitness returns. Our model presents a solution to the group-size paradox by allowing foragers to learn about habitat quality and leave food patches when their current intake rate falls below that expected for the whole habitat. As a consequence, foragers tend to abandon under- and overcrowded patches, ensuring that modal group size remains close to the optimal value under a wide range of population sizes. The results hold in habitats with varying patch quality, but we note that the lack of food renewal in patches can disrupt the process of group formation. In all cases, stable outcomes include a wide range of group sizes often extending beyond the equilibrium size.

The rules that we used in the model should not be considered causal models of learning and foraging or ultimate models that prescribe optimal behavior. Nevertheless, we make a general theoretical point about the role of learning in the distribution of group sizes by incorporating biologically realistic components and by generating specific predictions that can be empirically tested. We have made a number of assumptions about learning and foraging, and these are assessed below to examine the robustness of our predictions.

In particular, the two key elements of the model are the linear operator rule, which is used to assess habitat quality, and the patch departure rule, which is used to choose whether to stay or leave food patches.

The linear operator rule weighs past and current information with a memory factor. Evidence for the use of memory in the estimation of patch quality is provided by studies showing that patch quality is devalued with time passed since the last foraging episode in the patch (Devenport and Devenport, 1994; Milinski and Regelman, 1984). More generally, models indicate that assessment of habitat quality, via the linear operator rule or other learning rules, is important to predict the spatial distribution of foragers (Beauchamp et al., 1997; Bernstein et al., 1988; Koops and Abrahams, 2003).

The patch departure rule is based on the marginal value theorem of patch exploitation by solitary foragers (Charnov, 1976). This model was derived originally for a deterministic environment with no variance in travel time and with patches of equal value. In our model, both travel time between patches and patch value could vary within habitat. Therefore, it is possible that the patch departure rule that we used performed less than optimally (Olsson and Holmgren, 1998). We showed that predictions of the model persisted with and without variance in patch quality. Recent empirical evidence also supports the robustness of our patch departure rule. In a laboratory study, nutmeg manikins (*Lonchura punctulata*) foraged in a habitat in which travel time between patches was not fixed and in which food intake in a patch increased



**Figure 3**

Results from the learning model. (A) Modal group size in food patches is shown as a function of population size and level of patch renewal. (B) Distribution of group sizes is shown as a function of level of patch renewal in a population of 400 foragers. In each panel, simulation results are shown for habitats with no variance (open bars) or with variance in patch quality (closed bars). Each bar represents the mean of 100 simulations. Standard deviation bars are shown in panel A.

linearly with time spent foraging as assumed in the model. In addition, the arrival of companions at the patch produced a decline in the rate of food intake of established group members. As predicted qualitatively by our patch departure rule, birds abandoned patches more often after the arrival of companions when overall habitat quality was high and also when the level of interference at the patch was high (Beauchamp and Giraldeau, 1997). Nevertheless, future theoretical work is needed to predict optimal patch residence time in our modeled habitat, allowing a formal comparison with the results obtained with our rule.

The model assumes that foragers only aggregate by chance at food patches. In nature, however, foragers often use the presence of companions to locate food patches (Pöysä, 1992). Conspecific attraction is not expected to alter the conclusions reached so far. As a result of cueing in on the foraging behavior of companions, one would expect aggregations to build up more rapidly, thus allowing optimal groups to form at an even lower population size than that predicted by the model. We also expect a similar effect to arise if foragers searched for food in groups rather than alone. Aggregations at food patches would increase in size more rapidly, but the dynamics of patch departure is not expected to be different in this case also.

For simplicity, we assumed that all foragers are equal and thus obtain equal shares of resources while feeding in a patch. Nevertheless, variation in intrinsic competitive ability can induce unequal success when foragers occur in groups (Livoreil and Giraldeau, 1997; Sutherland and Parker,

1985). As such, not all foragers may agree on one optimal group size. If moving to alternative patches in the face of competition is not too costly, unequal competitiveness could lead to the formation of groups assorted by competitive ability (Ranta et al., 1993). We cannot test this idea directly because our model assumed equal competitiveness. However, random encounters with food patches did create inequalities among foragers in terms of estimates of habitat quality. The large range of group sizes that we observed is probably one consequence of such inequalities among foragers. It remains to be seen whether intrinsic differences among foragers in competitive ability just add to this variance or create a new pattern of group size distribution.

In addition to the general finding that optimal group sizes should occur frequently, the model makes new predictions in the light of the above assumptions. The occurrence of foragers in groups above the optimal size is often considered evidence for the equilibrium model of group foraging. Nevertheless, as shown here, foragers are expected to occur in a wide range of group sizes. In the learning model, large groups form when individuals develop a low estimate of habitat quality and therefore settle more willingly in less suitable patches containing too many foragers. Lower estimates of habitat quality arise in the learning model when foragers fail to locate food patches after some time. The learning model thus predicts the formation of large groups; these groups should form later in a foraging episode and be composed mostly of foragers that have failed to locate patches in the recent past. A wider range of group sizes is also

predicted to occur when patches vary more in quality. A dynamic model of group-size choices in fish also predicted a wide range of group sizes when individuals encountered groups randomly (Martínez and Marschall, 1999), suggesting an important role for contingencies encountered by individual foragers.

The process of group formation was altered by food patch exhaustion. Under this condition, the time span of each patch is reduced, and therefore, aggregations are less likely to occur by chance. In nature, the rate of patch exhaustion will vary as a function of patch richness and the rate of food intake. The ability of foragers to track down habitat quality when patches deplete rapidly will be a key element to assess the predictions of the model in natural conditions.

We hope that the model will trigger more interest in the adaptive processes that lead to the formation and dissolution of groups. The model should be applicable to species in which fitness is a peaked function of group size. Peaked fitness functions have been documented across many taxa, including crustaceans (Ritz, 1998), flatworms (Cash et al., 1993), predatory fish (Eklov, 1992; Major, 1978), birds (Beauchamp, 1998), large hunting mammals such as lions (*Panthera leo*), wild dogs (*Lycan pictus*), and orcas (*Orcinus orca*; Baird and Dill, 1996; Caraco and Wolf, 1975; Fanshawe and FitzGibbon, 1993). With a peaked fitness function and patchily distributed resources, we believe that groups of optimal sizes can occur frequently without the need to invoke relatedness between joiners and established group members, group defense against joiners, the formation of subgroups, or a steep fitness function.

We thank two anonymous referees for useful comments on the manuscript. E.F.J. was supported by the College of Natural Sciences and Mathematics, California State University Long Beach.

## REFERENCES

- Baird RW, Dill LM, 1996. Ecological and social determinants of group size in transient killer whales. *Behav Ecol* 7:408–416.
- Beauchamp G, 1998. The effect of group size on mean food intake rate in birds. *Biol Rev* 73:449–472.
- Beauchamp G, 2000. Learning rules for social foragers: implications for the producer-scrounger game and ideal free distribution theory. *J Theor Biol* 207:21–35.
- Beauchamp G, Bélisle M, Giraldeau L-A, 1997. Influence of conspecific attraction on the spatial distribution of learning foragers in a patchy habitat. *J Anim Ecol* 66:671–682.
- Beauchamp G, Giraldeau L-A, 1997. Patch exploitation in a producer-scrounger system: test of a hypothesis using flocks of spice finches (*Lonchura punctulata*). *Behav Ecol* 8:54–59.
- Bernstein C, Kacelnik A, Krebs JR, 1988. Individual decisions and the distribution of predators in a patchy environment. *J Anim Ecol* 57:1007–1026.
- Buston P, 2003. Forcible eviction and prevention of recruitment in the clown anemonefish. *Behav Ecol* 14:576–582.
- Caraco T, Wolf LL, 1975. Ecological determinant of group size of foraging lions. *Am Nat* 109:343–352.
- Cash KJ, McKee MH, Wrona FJ, 1993. Short- and long-term consequences of grouping and group foraging in the free-living flatworm *Dugesia tigrina*. *J Anim Ecol* 62:529–535.
- Chapman CA, Chapman LJ, 2000. Constraints on group size in primates: the importance of travel costs. In: *On the move: how and why animals travel in groups* (Boinski S, Garber P, eds). Chicago: University of Chicago Press; 24–42.
- Charnov EL, 1976. Optimal foraging: the marginal value theorem. *Theor Popul Biol* 9:129–136.
- Clark CW, Mangel M, 1986. The evolutionary advantages of group foraging. *Theor Popul Biol* 30:45–75.
- Devenport LD, Devenport JA, 1994. Time-dependent averaging of foraging information in least chipmunks and golden-mantled ground squirrels. *Anim Behav* 47:787–802.
- Eklov P, 1992. Group foraging versus solitary foraging efficiency in piscivorous predators: the perch, *Perca fluviatilis*, and pike, *Esox lucius*, patterns. *Anim Behav* 44:313–326.
- Fanshawe J, FitzGibbon CD, 1993. Factors influencing the hunting success of an African wild dog pack. *Anim Behav* 45:479–490.
- Giraldeau L-A, 1988. The stable group and the determinants of foraging group size. In: *The ecology of social behavior* (Slobodkinoff CN, ed). New York: Academic Press; 33–53.
- Giraldeau L-A, Caraco T, 2000. *Social foraging theory*. Princeton, New Jersey: Princeton University Press.
- Giraldeau L-A, Gillis D, 1984. Optimal group size can be stable: a reply to Sibly. *Anim Behav* 33:666–667.
- Houston AI, Sumida B, 1987. Learning rules, matching and frequency dependence. *J Theor Biol* 126:289–308.
- Kacelnik A, Krebs JR, 1985. Learning to exploit patchily distributed food. In: *Behavioural ecology* (Sibly RM, Smith RH, eds). Oxford: Oxford University Press; 189–205.
- Koops MA, Abrahams MV, 2003. Integrating the roles of information and competitive ability on the spatial distribution of social foragers. *Am Nat* 161:586–600.
- Kramer DL, 1985. Are colonies supraoptimal groups? *Anim Behav* 33:1031–1032.
- Krause J, Ruxton GD, 2002. *Living in groups*. Oxford: Oxford University Press.
- Livoreil B, Giraldeau LA, 1997. Patch departure decisions by spice finches foraging singly or in groups. *Anim Behav* 54:967–977.
- Major PF, 1978. Predator-prey interactions in two schooling fishes, *Caranx ignobilis* and *Stolephorus purpureus*. *Anim Behav* 26:760–777.
- Mangel M, 1990. Dynamic information in uncertain and changing worlds. *J Theor Biol* 146:317–332.
- Martinez FA, Marschall EA, 1999. A dynamic model of group-size choice in the coral reef fish *Dascyllus albisella*. *Behav Ecol* 10:572–577.
- McNamara JM, Houston AI, 1987. Memory and the efficient use of information. *J Theor Biol* 125:385–395.
- Milinski M, Regelmann K, 1984. Fading short-term memory for patch quality in sticklebacks. *Anim Behav* 33:678–680.
- Olsson O, Holmgren NMA, 1998. The survival-rate-maximizing policy for Bayesian predators: wait for the good news! *Behav Ecol* 9:345–353.
- Pöysä H, 1992. Group foraging in patchy environments: the importance of coarse-level local enhancement. *Ornis Scand* 23:159–166.
- Pulliam HR, Caraco T, 1984. Living in groups: is there an optimal group size? In: *Behavioural ecology* (Krebs JR, Davies NB, eds). Oxford: Blackwell Scientific Publications; 122–147.
- Ranta E, Rita H, Lindstrom K, 1993. Competition versus cooperation: success of individuals foraging alone and in groups. *Am Nat* 142:42–58.
- Ritz DA, 1998. Costs and benefits as a function of group size: experiments on a swarming mysid, *Paramesopodopsis rufa* Fenton. In: *Animal groups in three dimensions* (Parrish JK, Hamner WM, eds). Cambridge: Cambridge University Press; 194–206.
- Sibly RM, 1983. Optimal group size is unstable. *Anim Behav* 31:947–948.
- Sutherland WJ, Parker GA, 1985. Distribution of unequal competitors. In: *Behavioural ecology* (Krebs JR, Davies NB, eds). Oxford: Blackwell Scientific Publications; 255–273.
- Williams CK, Lutz RS, Applegate RD, 2003. Optimal group size and northern bobwhite coveys. *Anim Behav* 66:377–387.