Geometry for a selfish foraging group: a genetic algorithm approach

ZOLTÁN BARTA, ROBYN FLYNN AND LUC-ALAIN GIRALDEAU

Department of Biology, Concordia University, Montréal, Qc, Canada H3G 1M8
(zbarta@alcor.concordia.ca, rflynn@alcor.concordia.ca, giraluc@vax2.concordia.ca)

SUMMARY

The advantages of group living are not shared equally among all group members, and these advantages may depend on the spatial position occupied by a forager within the group. For instance, it is thought that socially dominant individuals prefer the predator-safe central position of groups forcing subordinates to the periphery. Uneven spread of benefits among group members can occur when some animals (the scroungers) parasitically exploit the food findings of other foragers (the producers). Here we focus on how playing producer or scrounger affects an individual's spatial position within a group. We model the movement of foraging animals playing scrounger or producer using a spatially explicit simulation, and use a genetic algorithm to establish movement rules. We find that groups containing producers and scroungers are more compact compared to an equivalent group of producers only. Furthermore, the position occupied by strategies varies: scroungers are mainly found in central positions, with producers in the periphery, suggesting that the best position for strategies differs. Dominants, therefore, should prefer movement rules which lead to central positions because of the positional benefits provided to the scrounger strategy they use. Moreover, position within a group will introduce an asymmetry among otherwise phenotypically symmetric individuals.

1. INTRODUCTION

Living in a group is widely assumed to be advantageous for animals. Commonly, two of its major benefits have been argued to be a lower predation hazard and an increased efficiency of foraging (Hamilton 1971; Caraco & Pulliam 1984; Clark & Mangel 1986; Elgar 1989). These benefits, however, are not necessarily shared equally among all group members (Rohwer & Ewald 1981; Schneider 1984) and may depend on the spatial position occupied within the group (Krause 1994; Romey 1995). It is widely accepted, for instance, that being at the edge of a group can be more hazardous in terms of predation (Hamilton 1971) than being in the middle, and that socially dominant individuals prefer the safe central positions of a foraging group (Murton *et al.* 1971; Schneider 1984; Hegner 1985; Elgar 1989; Krause 1994). Another way in which benefits can be spread unevenly among group members is when some animals in the group parasitically exploit the food findings of others (Barnard & Sibly 1981). But, unlike for predation, the spatial consequences of this asymmetry have never been considered.

Using food discovered by others can be described as a producer–scrounger frequency-dependent game (Barnard & Sibly 1981; Caraco & Giraldeau 1991; Vickery *et al.* 1991). In the game, scroungers (parasitic individuals) do better than producers (food finders) when scroungers are rare in the group but they do worse when scroungers are common. This strong

negative frequency dependence leads to a mixed stable solution to a symmetric game where both alternatives obtain equal pay-offs (Parker 1984). The stable pay-offs, however, could differ between alternatives in an asymmetric game when the players' gains depend on some phenotypic attributes such as age, size or social status (Parker 1982; Gross 1996). Many theoretical studies have investigated the conditions of stability for mixtures of producer and scrounger (Barnard & Sibly 1981; Caraco & Giraldeau 1991; Vickery *et al.* 1991), and some evidence supports their predictions (Barnard & Sibly 1981; Hansen 1986; Giraldeau *et al.* 1994; Koops & Giraldeau 1996; Giraldeau & Livoireil 1997).

The geometry of groups of travelling animals is thought to be largely influenced by aero- or hydrodynamic forces (Hummel 1983; Weihs 1973). We, however, take a different approach and focus here on whether the geometry of foraging groups is affected by the presence of scroungers and whether the strategy (producer or scrounger) played by an individual should affect its spatial position within a group. We model the movement of foraging animals playing scrounger or producer using a spatially explicit simulation and use a genetic algorithm (Holland 1975; Sumida *et al.* 1990) to establish the movement rules that improve their net rate of energy intake. After finding the behaviour that leads to high energy intake, we address the effects of scrounger strategists on the geometry of the foraging group and then investigate the spatial positions of produc-

ers and scroungers within the group. The model was developed with small seed-eating birds in mind but applies to any situation where groups of foragers exploit hidden shareable resources.

2. THE MODEL

(a) *The foraging simulation*

The animals searched for food patches on a two-dimensional bordered surface of 2000 by 2000 units during a tournament that lasted 250 time units. The N_P food patches were randomly distributed in this area and each initially contained N_S indivisible food items. N_S was equal for all food patches. The food patch remained empty once the animals had depleted it.

The N_B individuals moved one step per time unit. The length of the steps was chosen from a normal distribution with mean L and standard deviation $L_{s.d.}$ that were kept constant throughout a tournament. The direction of the next step was chosen from another normal distribution with standard deviation $D_{s.d.}$, which was also kept constant. The mean of the distribution D was either the direction of the previous step—which means that subjects moved forward with higher probability than backward—or determined by another algorithm (see below). Upon reaching the edge of the foraging area, an animal changed its direction as if it bounced off the border.

During one time unit a subject could exclusively either be vigilant and scan for predators or perform foraging behaviour. Vigilance occurred randomly but the probability of vigilance increased with an animal's distance from other foragers (Pöysä 1994; Lima & Zollner 1996). The increased cost of vigilance with distance (i.e. less time could be spent to forage) made it profitable for individuals to stay close together; i.e. to use such movement rules which maintain group cohesion.

Foraging activities include feeding and searching for food. If the animal was already in a food patch, it continued to feed at one food item per time unit. Its energy level was increased by the amount of energy in an item (the same for all items). When no more items remained, the individual resumed searching. When the animal searched it could either: (i) look around to check the position of other subjects in the area and move one step toward them (Caraco & Bayham 1982; Bekoff 1995); or (ii) look for food. The action was randomly chosen according to the probability P_L : the likelihood that an individual looks around. The animal's checking of the spatial position of other subjects was modelled by taking the average of their direction weighted by their distances (x_i), using the weighting function $w(x_i)$ with parameter W . The function $w(x_i)$ was

$$w(x_i) = \frac{1}{\sqrt{2\pi}W} \exp(-x_i^2/2W^2).$$

W determines how far subjects are taken into account and its value was set at the beginning of each tournament. The mean direction of the next step (D) was then set to this weighted average direction.

The animal's behaviour of looking for food depended on the strategy it played. A producer individual would investigate its close vicinity for food. If no food was detected it would take a step in a random direction (here D was set to the direction of previous step as described above). If it found food, it started feeding in the next time unit. A scrounger, on the other hand, would check the area for scrounging opportunities (i.e. feeding group mates). The probability that it detects such an oppor-

Table 1. *Parameters of the simulation (a) and behavioural variables coded by the chromosomes (b)*

(The cost of a scrounging step was given by the cost rate multiplied by the length of the step. Under range, integer values mean that the variable could take only integers, while real values mean that the locus takes real values. For strategy: 0 is scrounger; 1 is producer.)

symbol	meaning	value or range
(a) parameters		
T	the length of the tournament	250
N_P	number of patch	400
C_F	cost rate of a scrounging step	0.1
S_E	energy in one food item	10
R_P	spatial radius of a food patch	10
S	parameter of probability function that a scrounger detects a forager	150
E	initial energy level of individuals	100
N_S	initial number of food items in the food patch	40
(b) behavioural variables		
St	strategy	0, 1
$D_{s.d.}$	s.d. of direction distribution	0, 1, 2, ..., 180
L	mean of step length distribution	0.0–50.0
$L_{s.d.}$	s.d. of step length distribution	0.0–25.0
P_L	probability of looking around	0.0–1.0
W	parameter of weighting function	0.0–50.0

tunity ($p(x)$) was a decreasing function of its distance x to the opportunity: $p(x) = \exp(-x^2/2S^2)$. Small values of parameter S imply that scroungers can only identify close scrounging opportunities. A scrounger that detects a feeding individual reaches it in one time unit and starts feeding in the next time unit. This fast scrounging step costs extra energy compared to other types of movement. A scrounger could only feed from a producer's finding (Vickery *et al.* 1991). If the scrounger did not detect a feeding individual, it took a step in a random direction. An individual's strategy was fixed during the whole tournament. For the value of parameters see table 1.

(b) *The genetic algorithm*

A genetic algorithm was used to find the combination of behavioural variables that yielded highest net energy intake. The algorithm has been designed to solve optimization problems by simulating the process of natural selection (Holland 1975; Sumida *et al.* 1990). It acts on a population of chromosomes that code for the input parameters. These parameters are used to evaluate the fitness of chromosomes. The chromosomes with the lowest fitness are replaced by the offspring of the fittest ones. In the process, the coded values are randomly altered,

imitating the effect of recombination and mutation, and the total number of chromosomes remains constant. By repeating these steps, genetic algorithms often reach optimal solutions (Davies 1991; Forrest 1993). Furthermore, the algorithm was already used to find solutions of evolutionary game theoretical models (Harrald 1995).

In our model the chromosomes coded for the behavioural variables (one chromosome for each individual) (table 1). The population consisted of 50 individuals divided into groups of size $N_B (= 10)$. Each of these groups was entered in a series of tournaments where the individual's fitness was determined. The individuals in the tournament behaved according to the values coded in their chromosomes. For each group of 10 individuals the tournament was repeated five times and the geometric mean of net energy gained was used as an individual's measure of fitness. The use of five repetitions and geometric means eliminates the unpredictable effects of random food patch distribution. After determining the fitness of all individuals, the 20% of individuals with the lowest fitness were excluded from the population and the rest were allowed to reproduce (including recombination and mutation). The process was repeated for 200 generations. The recombination rate, defined as the probability that some of the values of behavioural variables were swapped between two chromosomes (Davis 1991), was 0.5. A randomly selected pair of chromosomes of the same strategy was involved in recombination (Ryan 1995). The mutation rate was 0.05 and it gave the probability that the value of a locus would change to any other possible value within the given range (table 1).

We modelled two kinds of population in order to investigate the effects of scroungers' presence on group geometry: one made up of both producers and scroungers (population PS), the other consisting of producers only (population PO). The genetic algorithm was repeated 20 times for each type of populations, and at the start of each repetition the chromosomes were initialized with new random values. The ratio of producers to scroungers in the PS population could change from generation to generation according to each strategy's fitness (i.e. strategy with higher fitness spread in the population), so the algorithm could reach a solution of evolutionarily stable state (ESS, Maynard Smith 1982). At stability the fitness of the two strategies are expected to be equal since then no strategy could spread in the population at the other's expense. Moreover, the proportion of strategies should not change with increasing number of generations if the algorithm has reached the stable state (Harrald 1995). To check for stability in this way, we run another series of 20 repetitions with the same values of parameters but 500 generations.

(c) *The measuring of positions*

After determining the optimal values for behavioural variables (i.e. that coded the chromosomes of the 200th generation), a final tournament was run for each group of 10 individuals in order to describe the relative position of optimally behaving individuals within the group. We ran this final tournament with empty patches for each group in order to avoid spatial effects related to the time animals spend feeding from the same divisible patch (i.e. scroungers always eat with others by definition).

During the final tournament for each individual in each time unit, we recorded the distance from the middle of the group, the distance of the nearest neighbour, and whether the individual was on the edge of the group or not. The recording of these variables started after the first 10 time

units to eliminate the effect of beginning conditions. The middle of the group was defined as its centre of gravity: the average of coordinates of subjects in the group. Edge animals were the ones at the vertex of the smallest convex polygon enclosing all animals in the group (Krause 1994). At each time unit we also measured the mean distance among subjects (M_{DIST}), as the average of the distances between all different pairs of animals in the group. After the final tournament, the distance variables were averaged across time units, and the proportion of time spent on the edge was calculated for each individual. These averages and proportions were then averaged separately across producers and scroungers within each repetition. These averages were used as independent data points in the statistical tests (i.e. $n = 20$ for all groups in each test). Non-parametric tests were used because of their robustness. Medians (M) and interquartile ranges (IQR) are given throughout the text.

3. RESULTS

Interindividual distance (M_{DIST}) was much smaller than the total size of the foraging area, which indicates that border effects were likely negligible (figure 1a). Under the foraging conditions we used, the scrounger strategy was never eliminated by selection from a PS population and its proportion was 0.72 (IQR = 0.07). After 200 generations, the fitness of producer and scrounger strategies did not differ statistically in PS populations (for producers: $M = 238.11$, IQR = 42.39; for scroungers: $M = 256.82$, IQR = 45.63; Wilcoxon paired match test, n.s.: $p > 0.1$). Therefore, we can conclude that the genetic algorithm reached a mixed ESS. Furthermore, after 500 generations we obtained the same results (proportion of scroungers: $M = 0.72$, IQR = 0.1; fitness of producers: $M = 252.51$, IQR = 56.87; fitness of scroungers: $M = 261.36$, IQR = 74.29; none of them differs significantly from the appropriate value of 200 generations, Mann-Whitney U -test, $n = 40$), which also supports that the algorithm reached a stable solution. Individuals in the PO population experienced significantly higher net rates of energy intake than those in the PS population (for PO: $M = 500.97$, IQR = 39.76; for PS: $M = 250.68$, IQR = 50.86; Mann-Whitney U -test, $p < 0.001$).

The mean distance among individuals (M_{DIST}), was smaller in groups of producers and scroungers than in groups of producers only (figure 1a). This result implies that the presence of the scrounger strategy leads to a decrease in the area occupied by foraging groups. The nearest-neighbour distance, however, did not differ significantly between the two populations (figure 1b). The proportion of time spent on the periphery was higher for animals in PO groups (figure 1c). These results indicate that individuals in the PO groups avoided the centre, while in PS groups the periphery and centre were used more evenly (figure 1d).

In the PS groups both the distance from the middle of the group and the distance to the nearest neighbour were smaller for the scroungers than for the producers (figures 2a, b). Scroungers also spent less

Figure 1. The differences in variables of within-group position between producers only (PO) and producers–scroungers (PS) population for groups of size 10. (a) The mean distance among individuals (M_{DIST}). (b) The mean nearest-neighbour distance. (c) The proportion of time spent on the edge. Medians (columns) and interquartile ranges (vertical bars) of 20 repetitions are given. Mann–Whitney U -test: n.s. (NS), $p > 0.05$; ***, $p < 0.001$. (d) A descriptive representation of geometrical differences between groups of producers only (PO, left) and producers–scroungers (PS, right). Individuals in the PO group leave the middle of the group empty, while animals in the PS group occupy it. Drawings are based on typical patterns seen during the runs of the program.

time on the edge of the group than producers did (figure 2c). These results suggest that scroungers tended to be in the middle of the group and close to other subjects while producers did not (figure 2d).

4. DISCUSSION

In this paper, a spatially explicit social foraging model predicts that groups containing producers and scroungers should be more compact compared to an equivalent group of producers only. Moreover, the geometric structure also differs between the two kinds of groups. In groups of producers only, the individuals leave central positions empty probably because the periphery offers a higher possibility of finding new unused patches (Petit & Bildstein 1987). On the other hand, a producer–scrounger group fills the area more evenly because scroungers tend to occupy central positions, while producers occupy the periphery. Central positions may allow scroungers to maximize the probability of detecting any producer that has found food. Early detection may be important for scroungers because it may increase their share of the food patch by giving the producer less time to exploit the patch alone. Producers may continue to benefit from their peripheral location because it maximizes the chances of finding new patches (Petit & Bildstein 1987).

It is important to note that no attempt was made

Figure 2. The differences in position variables between producers (P) and scroungers (S) in mixed groups of size 10. (a) The mean distance of individuals from the middle of the group. (b) The mean nearest-neighbour distance. (c) The proportion of time spent on the edge. Medians (columns) and interquartile ranges (vertical bars) of 20 repetitions are given. Wilcoxon matched pair test: ***, $p < 0.001$. (d) The structure of a producers–scroungers group. Producers (solid birds) are on the periphery while scroungers (open birds) occupy the middle. Drawings are based on typical patterns seen during the runs of the program.

to optimize the position of individuals. The genetic algorithm simply selected individuals on the basis of their intake rate and not position. The consequence of this selection process was the difference in movement parameters between producers and scroungers that led to differences in positions.

In the model, we considered relatively small foraging groups of size that are common in free living birds (i.e. Caraco & Bayham 1982; Bekoff 1995; Lima & Zollner 1996). Additional simulations indicated that the results also hold for group sizes of five and 25, but that in larger groups the positional effects of playing a given strategy fade because of the smaller perimeter-to-area ratio of these groups.

The genetic algorithm procedure found an equilibrium solution to a complex spatial game, illustrating the usefulness of this tool. Moreover, the algorithm confirms earlier results that scrounging is evolutionarily persistent within foraging groups and causes the average intake rates within groups to decline (Clark & Mangel 1986; Caraco & Giraldeau 1991; Vickery *et al.* 1991).

Socially dominant individuals are commonly predicted to occupy predator-safe central positions within groups, thus forcing subordinates to the periphery (Murton *et al.* 1971; Schneider 1984; Hegner 1985; Elgar 1989; Krause 1994). On the other hand, agreeing with Parker's (1982) theory of phenotype-limited producer–scrounger strategies, in all dominance-driven producer–scrounger games described to date, it is the dominant individuals that

use the scrounger alternative and the subordinates that must use producer (Baker *et al.* 1981; Rohwer & Ewald 1981; Czikeli 1983; Theimer 1987). It is likely, therefore, that dominant individuals also seek central positions not only for safety but because of the positional advantages provided by the scrounger strategy they use. Hence scrounging may be an alternative factor promoting the dominants' preference for central positions.

The distinct positional advantages of each strategy suggest that an individual alternating between optimal producer and scrounger alternatives would likely incur a cost associated with a shift in spatial position within the group. This cost would reduce the value of using both alternatives and would therefore increase the likelihood that individuals specialize in one or the other alternative (Vickery *et al.* 1991).

In our model, individuals had no choice of being scrounger or producer and therefore adjusted their positions according to their fixed foraging strategy. However, when individuals choose which alternative to use, the spatial location occupied will likely influence their choice. Hence, even in otherwise phenotypically symmetric individuals, spatial position within a group can introduce an asymmetry among foragers where central individuals obtain greater benefits from using scrounger than those on the periphery. The results suggest that because of the geometry of selfish foraging groups, truly symmetric producer–scrounger games are highly unlikely (Parker 1982; Gross 1996). Moreover, spatial position, even among otherwise symmetric players, corresponds to a real, though non-phenotypic, limitation. Studies of social foraging animals should therefore pay considerably more attention to the spatial characteristics of their groups.

This study was supported by an OTKA grant (#F16818) to Z.B., an NSERC Research Grant and FCAR Equipe Grant to L.-A.G. During the study Z.B. held a NATO Science Fellowship. R.F. was supported by the NSERC Research Grant to L.-A.G. We are grateful to Dr J. Grant and two anonymous referees for comments.

REFERENCES

- Baker, M. C., Belcher, C. S., Deutsch, L. C., Sherman, G. L. & Thompson, D. B. 1981 Foraging success in junco flocks and the effects of social hierarchy. *Anim. Behav.* **29**, 137–142.
- Barnard, C. J. & Sibly, R. M. 1981 Producers and scroungers: a general model and its application to captive flocks of house sparrows. *Anim. Behav.* **29**, 543–550.
- Bekoff, M. 1995 Vigilance, flock size and flock geometry: information gathering by Western evening grosbeaks (Aves, Fringillidae). *Ethology* **99**, 150–161.
- Caraco, T. & Bayham, M. C. 1982 Some geometric aspects of house sparrow flocks. *Anim. Behav.* **30**, 990–996.
- Caraco, T. & Giraldeau, L.-A. 1991 Social foraging: producing and scrounging in a stochastic environment. *J. Theor. Biol.* **153**, 559–583.
- Caraco, T. & Pulliam, H. R. 1984 Sociality and survivorship in animals exposed to predation. In *A new ecology: novel approaches to interactive systems* (ed. P. W. Price, C. N. Slobodchikoff & W. S. Gaud), pp. 279–309. New York: Wiley-Interscience.
- Clark, C. W. & Mangel, M. 1986 The evolutionary advantages of group foraging. *Theor. Popul. Biol.* **3**, 45–75.
- Czikeli, H. 1983 Agonistic interactions within a winter flock of slate-coloured juncos (*Junco hyemalis*) evidence for the dominants' strategy. *Z. Tierpsychol.* **61**, 61–66.
- Davis, L. (ed.) 1991 *Handbook of genetic algorithms*. New York: Van Nostrand Reinhold.
- Elgar, M. A. 1989 Predator vigilance and group size in mammals and birds: a critical review of the empirical evidence. *Biol. Rev.* **64**, 13–33.
- Forrest, S. 1993 Genetic algorithms: principles of natural selection applied to computation. *Science* **261**, 872–878.
- Giraldeau, L.-A. & Livoreil, B. 1997 Game theory and social foraging: models and tests of the producer–scrounger game. In *Advances in game theory and the study of animal behavior* (ed. L. A. Dugatkin & K. Reeve). Oxford University Press. (In the press.)
- Giraldeau, L.-A., Soos, C. & Beauchamp, G. 1994 A test of the producer–scrounger foraging game in captive flocks of spice finches, *Lonchura punctulata*. *Behav. Ecol. Sociobiol.* **34**, 251–256.
- Gross, M. R. 1996 Alternative reproductive strategies and tactics: diversity within sexes. *Trends Ecol. Evol.* **11**, 92–98.
- Hamilton, W. D. 1971 Geometry of the selfish herd. *J. Theor. Biol.* **31**, 295–311.
- Hansen, A. 1986 Fighting behavior in bald eagles: a test of game theory. *Ecology* **67**, 787–797.
- Harrauld, P. 1995 Evolving behaviour in repeated 2-player games. In *Practical handbook of genetic algorithms applications* (ed. L. Chambers), pp. 57–74. Boca Raton, FL: CRC.
- Hegner, R. E. 1985 Dominance and anti-predator behaviour in blue tits (*Parus coerules*). *Anim. Behav.* **33**, 762–768.
- Holland, J. H. 1975 *Adaptation in natural and artificial systems*. Ann Arbor, MI: University of Michigan Press.
- Hummel, D. 1983 Aerodynamic aspects of formation flight in birds. *J. Theor. Biol.* **104**, 321.
- Koops, M. & Giraldeau, L.-A. 1996 Producer–scrounger foraging games in starlings: a test of mean-maximizing and risk-minimizing foraging models. *Anim. Behav.* **51**, 773–783.
- Krause, J. 1994 Differential fitness returns in relation to spatial position in groups. *Biol. Rev.* **69**, 187–206.
- Lima, S. L. & Zollner, P. A. 1996 Anti-predatory vigilance and the limits to collective detection: visual and spatial separation between foragers. *Behav. Ecol. Sociobiol.* **38**, 355–363.
- Maynard Smith, J. 1982 *Evolution and the theory of games*. Cambridge University Press.
- Murton, R. K., Isaacson, A. J. & Westwood, N. J. 1971 The significance of gregarious feeding behaviour and adrenal stress in a population of wood pigeons (*Columba palumbus*). *J. Zool. Lond.* **165**, 53–84.
- Parker, G. A. 1982 Phenotype-limited evolutionary stable strategies. In *Current problems in sociobiology* (ed. King's College Sociobiology Group), pp. 173–201. Cambridge University Press.
- Parker, G. A. 1984 The producer/scrounger model and its relevance to sexuality. In *Producers and scroungers: strategies of exploitation and parasitism* (ed. C. J. Barnard), pp. 127–153. New York: Chapman & Hall.
- Petit, D. R. & Bildstein, K. L. 1987 Effect of group size

- and location within the group on the foraging behavior of white ibises. *Condor* **89**, 602–609.
- Pöysä, H. 1994 Group foraging, distance to cover and vigilance in the teal, *Anas crecca*. *Anim. Behav.* **48**, 921–928.
- Rohwer, S. & Ewald, P. W. 1981 The cost of dominance and advantage of subordination in a badge signalling system. *Evolution* **35**, 441–454.
- Romey, W. L. 1995 Position preferences within groups: do whirligigs select positions which balance feeding opportunities with predator avoidance? *Behav. Ecol. Sociobiol.* **37**, 195–200.
- Ryan, C. 1995 Niche and species formation in genetic algorithms. In *Practical handbook of genetic algorithms applications* (ed. L. Chambers), pp. 57–74. Boca Raton, FL: CRC.
- Schneider, K. J. 1984 Dominance, predation, and optimal foraging in white-throated sparrow flocks. *Ecology* **65**, 1820–1827.
- Sumida, B. H., Houston, A. I., McNamara, J. M. & Hamilton, W. D. 1990 Genetic algorithms and evolution. *J. Theor. Biol.* **147**, 59–84.
- Theimer, T. C. 1987 The effect of seed dispersion on the foraging success of dominant and subordinate dark-eyed juncos; *Junco hyemalis*. *Anim. Behav.* **35**, 1883–1890.
- Vickery, W. L., Giraldeau, L.-A., Templeton, J. J., Kramer, D. L. & Chapman, C. A. 1991 Producers, scroungers, and group foraging. *Am. Nat.* **137**, 847–886.
- Weihs, D. 1973 Hydromechanics of fish schooling. *Nature* **241**, 290–291.

Received 26 March 1997; accepted 6 May 1997