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A test of the producer-scrounger foraging game in captive flocks of spice finches, *Lonchura punctulata*

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Abstract. Group foraging allows the co-existence of a strategy (producer) that involves searching for food, and its alternative (scrounger) exploiting the food of the producer. The use of producer and scrounger strategies has been modelled as an alternative-option scramble which assumes strong negative frequency-dependence of the scrounger's pay-offs. We tested this assumption in a flock feeding situation by manipulating the proportion of scroungers in flocks of spice finches, *Lonchura punctulata*. In a first experiment we found that: (1) the food intake of scroungers, and to a lesser extent producers, was negatively affected by an increase in the proportion of scroungers; (2) the food intake of producers and scroungers was equal when the proportion of scroungers was small, suggesting that producers, who exploited 35.4% of their patches by scrounging were opportunistically adjusting their use of the strategies until the pay-offs equalized. In a second experiment we tested whether finches could vary their use of the two strategies in response to changes in foraging conditions brought about by an increase in the cost of producing. As predicted by the game, finches reduced their use of the producer strategy and increased their use of the scrounger strategy when the cost of producing increased. These results suggest that spice finches can alter their allocation to each foraging alternative by experience and that the producer-scrounger game is a realistic model for predicting group foraging decisions.

Key words: Scrounging – Foraging – Flocking – Frequency dependence – Estrildidae

Introduction

The use of prey discovered or captured by other individuals (also termed scrounging) is possibly one of the most widespread forms of exploitation both within and between species (Barnard 1984). Forms of food scrounging have been reported in mammals (Packer and Ruttan 1988), birds (Brockmann and Barnard 1979), fish (Pitcher 1986) and invertebrates (Vollrath 1984). In avian foraging groups, scrounging has been associated with kleptoparasitism (Brockmann and Barnard 1979), in which one individual appropriates prey captured by another individual of the same or of a different species. It has also been associated with local enhancement (Thorpe 1963; Pöysä 1992), joining (Giraldeau and Lefebvre 1986; Giraldeau et al. 1990) and area copying (Barnard and Sibly 1981), all of which involve one individual moving towards and feeding in the vicinity of an individual that has already discovered or captured food. In the present study we focus on this latter form of avian food scrounging.

The producer-scrounger game is an alternative-option scramble between producers, who invest time and effort in searching for food, and scroungers, who use the food discovered by producers (Barnard and Sibly 1981; Parker 1984a, b; Caraco and Giraldeau 1991; Vickery et al. 1991). The game predicts a mixture of producers and scroungers when the pay-offs to each strategy meet the following conditions: (1) when scrounging is rare, scroungers do better than producers; and (2) when scrounging is common, the pay-offs to scroungers are lower than those to producers (Parker 1984a, b). Under these conditions, the mixture of strategies will reach an equilibrium when the pay-offs are equal (Parker 1984a). The equilibrium can be evolutionarily stable if the use of the two strategies is genetically determined and set by selection. The equilibrium can also be developmentally stable when the use of tactics is determined by experience (Dawkins 1980; Harley 1981).

Although a general producer-scrounger game has long been proposed to account for aspects of group foraging, it has only been recently formulated in terms of food intake maximization, a currency common to foraging theory (Vickery et al. 1991). The rate maximization paradigm expresses the food intake associated with producing and scrounging as a function of the proportion of each strategy within a group (Fig. 1). The model predicts

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that both the producer's and the scrounger's food intake decline with an increase in the proportion of scroungers within the group. The scrounger's food intake, however, is predicted to be more strongly affected by changes in the proportion of scroungers than the producer's. Moreover, the equilibrium proportion of scroungers depends heavily on the amount of food a producer obtains from a patch before the scroungers arrive: the producer's advantage (*a* in Fig. 1). Note that increasing the energetic cost of producing is functionally analogous to reducing the producer's advantage; increasing the producing cost increases the equilibrium proportion of scroungers in a group (Fig. 1).

Few studies have tested the predictions of the rate maximizing producer-scrounger social foraging model and fewer still have addressed the question of whether the use of producing and scrounging within individuals is fixed or altered by experience. Giraldeau et al. (1990) demonstrated that in captive foraging flocks of zebra finches (*Taenopygia guttata*) and spice finches (*Lonchura punctulata*), foragers obtained a producer's advantage. However, it was not clear whether finches could vary the use of producing and scrounging as a function of changes in local foraging conditions. A study of house sparrows (*Passer domesticus*) reported that, when the proportion of scroungers changed within flocks, pay-offs for producing and scrounging varied in the opposite direction to that predicted by the model: when scrounging was rare, scroungers and producers did equally well in terms of food intake, and, when scrounging was common, scroungers foraged at a higher rate than producers (Barnard and Sibly 1981). Individual sparrows used both producer and scrounger strategies, but failed to alter their allocation to each alternative strategy in response to changes in the proportion of scroungers within flocks, suggesting that the use of one or other of the two strategies was fixed within individuals (Barnard and Sibly 1981).

In the first experiment, we measured the food intake of producers and scroungers searching for food in flocks with different proportions of scroungers and asked whether they met the assumptions of the producer-scrounger game. In a second experiment, we used individuals that could both produce and scrounge and asked whether they could adjust their use of the two strategies in response to changes in local foraging conditions brought about by increasing the cost of producing.

Experiment 1

We developed an experimental procedure that constrained some individuals to act as pure scroungers and manipulated their proportion within foraging flocks. We used the spice finch, a common cage bird (Goodwin 1982; Immelmann 1982), as a general model species for producer-scrounger flock foraging systems because these birds form egalitarian foraging groups that readily scramble for each other's food discoveries without any effect of social dominance or sex (Giraldeau et al. 1990). We measured whether: (A) the scroungers' food intake was negatively frequency-dependent; (B) the producers enjoyed a higher food intake than scroungers when the proportion of scroungers was high; and (C) whether the scroungers' food intake exceeded that of producers when the proportion of scroungers was low.

Methods

Subjects. We used 48 adult L. *punctulata* (Estrildidae; 18 males, 21 females, 9 undetermined) purchased from a commercial supplier. They were kept on an 8:16 L:D cycle in groups of four or five in 57 × 30 × 43 cm cages and fed *ad libitum* on a commercial finch mixture of millet, and canary seed. We marked their tails with acrylic paint for easy individual identification from a distance.

We chose 24 producer finches from birds that had previously been trained to flip the covers off wells in order to obtain a seed reward (Ennis 1992) and 24 scroungers from birds that had never been so trained.

Training. Before the experiment, all subjects fed for 3 days from four wells (4 cm diameter, 1 cm deep) of a 24 × 24 cm training grid placed on the bottom of their cages. After 3 days, the cages were divided with a transparent partition and one subject was placed in each compartment and allowed to feed *ad libitum* for 24 h. Division of the cages had no other purpose than to double the number of birds that could be trained to use the grid simultaneously. After 20 h of food deprivation, the training grid was re-introduced in each of the cage's compartments. For scroungers, the lids, a cardboard plug (2.8 ± 0.06 g, $n = 15$) onto which a 5.5-cm diameter piece of black cardboard was glued, surrounded wells without covering them and each well contained ten white millet seeds. Each subject experienced five training grid presentations per day at 15-min intervals. The subjects fed *ad libitum* for 30 min following the day's trials and then were deprived of food for the next day's training. Training lasted 5 days or until the birds would consistently land and feed on the training grid upon its presentation. The same procedure was used for producer birds except that the lids were progressively moved closer to the wells until they covered them completely on consecutive presentation of the training grid. Completely covered wells were exploited by the 5th day. The birds used their bill to remove the lid by either lifting and pulling or flipping the lid to one side. After the 5th day we placed food in only two of the wells and continued training until the producers removed all the lids almost immediately upon landing on the training grid.

Flock-feeding experiment. The observer (C.S.) noted the behaviour of a scrounger and a producer subject while they foraged in a flock that contained either four other scrounger (flock S) or four other producer birds (flock P), balancing for the order in which subjects experienced the flock composition. The same four producer and scrounger subjects acted as the core of flock P and flock S respectively, but the behaviour of these individuals was not noted. Only the behaviour of the 20 producer and 20 scrounger test individuals added in pairs to the core flocks was observed.

We placed flock P in a 2.0 × 2.2 × 2.5 (height) m indoor aviary and flock S in an adjacent 1.5 × 2.2 × 2.5 (height) m aviary. We placed two test subjects, one scrounger and one producer, in each flock before the start of an experimental trial. Flock P therefore was composed of five producers and one scrounger and flock S of five scroungers and one producer. The flocks fed *ad libitum* from the grid with uncovered wells for 24 h. Following a 20-h food deprivation period, we presented each flock with a 74 × 65 cm foraging grid containing 42 equidistant wells covered by lids identical to those used during training. For each trial we randomly selected a new set of eight wells to contain ten seeds each; all other covered wells were empty. A trial started upon grid presentation and ended when all seeds were eaten, or when all birds were off the grid for more than 2 min. We exposed the birds to six trials per day. Following the 6th trial, we moved the test subjects to the other core flock and the procedure was repeated the next day for another six trials.

We defined producing as lid lifting and scrounging as feeding from patches that have been discovered by another individual. The

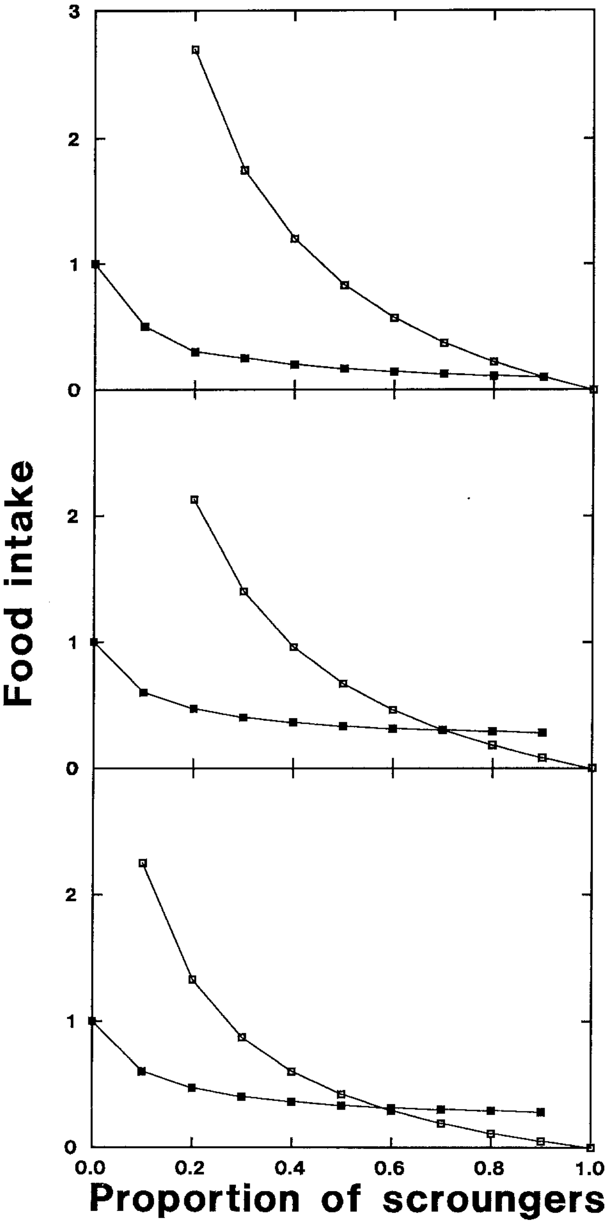

Fig. 1. The expected food intake of producers (*filled*) and scroungers (*open*) in the intake maximization model as a function of q (= 1–p) the proportion of scroungers in a group of N individuals where p is the proportion of producers. Producers search independently and encounter patches of F items at rate f. Upon encounter the producer gets a items before the scroungers arrive to share the remaining A (= F–a) items. Over a period T a producer's food intake is $I_p = fT(a + A/n)$ where $n = 1 + qN$, the producer plus all the scroungers. Scroungers encounter foraging opportunities at a rate pNf and their food intake is $I_s = pfNTA/n$. The curves are based on $N = 10$, $f = 1$, $F = 1$ and $a = 0$ (*top*), 0.2 (*middle*) and 0.5 (*bottom*)

observer used focal animal sampling and observed each subject during three of the six daily trials, balancing for observational order between days, recording producing and scrounging, the time at which the trial started and ended as well as the number of seeds eaten by each test individual on a lap-top computer programmed as an event recorder. Trials usually lasted longer than 100 s, but because the focal birds sometimes did not feed for extended periods towards the end of trials, we calculated the focal individuals' food intake as the number of seeds eaten during the first 100 s of a trial.

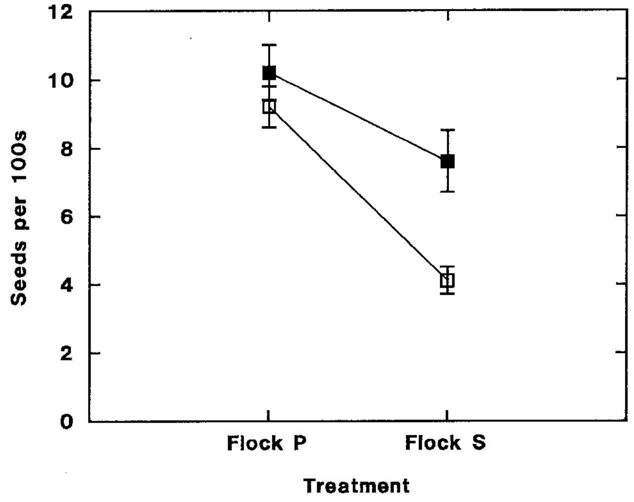

Fig. 2. Mean (±SE) food intake over a period of 100 s for producers (*filled*) and scroungers (*open*) when the proportion of scroungers in the flock was low (flock P) and high (flock S)

We analyzed our results using a two-factor repeated measures ANOVA with flock condition as a within-subject factor and strategy as a between-subject factor. We used paired-sample t-tests as *post hoc* tests to examine the effect of flock type.

Results

Producer:scrounger ratio in the flocks

All birds landed on the foraging grid soon after the onset of a trial and foraged together. The core and test scrounger birds were never observed to produce a food patch. Thus, scroungers obtained all of their food by scrounging and the test producer birds used in flock S obtained all of their food by producing. Consequently, flock S was composed of five pure-scrounger and one pure-producer strategists, leading to a producer to scrounger (P/S) ratio of 0.2.

Although we could keep scrounger birds from producing, we could not keep producer birds in flock P from scrounging. As a result, in flock P, 35.4% (SE = 27.0%) of the patches from which producer individuals obtained food were exploited by using the scrounger strategy. Flock P nonetheless provided a higher proportion of producers than flock S because it was composed of one pure scrounger (that never produced) and five individuals who allocated 65% of their foraging effort to producing and 35% to scrounging, thus leading to a P/S ratio of 1.2 [3.25/(1 + 1.75)].

Food intake

Technical problems in data transcription eliminated two focal pairs from the statistical analyses. Producers obtained a higher foraging intake than scroungers ($F_{1,34} = 8.7$, $P < 0.006$; Fig. 2). The birds in flock S obtained a lower intake than those in flock P ($F_{1,34} = 35.8$, $P < 0.0001$; Fig. 2). The flock condition-by-strategy interaction tended towards statistical significance ($F_{1,34} = 3.5$, $P = 0.07$; Fig. 2). A *post hoc* comparison indicated that the scroungers had a significantly lower foraging rate in flock S than in flock P ($t_{17} = 1.96$, $P<0.05$, one-tailed).

Discussion

The results of experiment 1 suggest that the economics of foraging decisions within foraging flocks of spice finches are consistent with assumptions of the producer-scrounger game. The food intake associated with scrounging was negatively affected by increases in the proportion of scroungers in the group, and as expected, the producer's food intake appears to have been less sensitive to changes in the proportion of scroungers. Moreover, we found that when common, scroungers experience lower food intake than producers. However, contrary to expectations, even when only one individual acted as a pure scrounger, we could find no evidence that the food intake of scroungers ever exceeded that of the producers.

We did not expect the food intake of producers and scroungers to be equal in flock P. Since the P/S ratio in that flock was skewed towards producers we expected scroungers to do better than producers. Many factors could have lowered the food intake of scroungers. For instance, the model of Vickery et al. (1991) assumes that the frequency of scrounging opportunities (*pNf*) increases linearly with the number of producers. Evidence obtained with flocks of greenfinches (*Carduelis chloris*), however, suggests that the frequency of patch production for the group likely increases more slowly than group size (Hake and Ekman 1988). The reduction in the frequency of scrounging opportunities is due to increasing overlap of the search areas covered by the producers resulting in increasing rates of revisitation of empty patches as group size increases (Hake and Ekman 1988).

It is possible that as the number of producers increases the number of simultaneously discovered patches also increases. As one scrounger can only exploit one patch at a time, scroungers can take advantage of an increased rate of encounter with patches only if these patches are encountered sequentially. If patches appeared simultaneously then scroungers could only exploit a fraction of them. A similar competitive effect could have accounted for the deviations from the producer-scrounger model's assumptions in the case of house sparrow flocks (Barnard and Sibly 1981). An increased number of producers can be obtained in two ways, by increasing the proportion of producers within a group, or, keeping the proportion constant, by increasing total group size.

The lack of difference in food intake for producers and scroungers in flock P could also be due to the producers' opportunistic use of the scrounging option. It is conceivable that had the producers never scrounged they could have done worse than pure scroungers. The fact that the producers spontaneously scrounged 35.4% of their patches suggests that they responded opportunistically to the conditions in which we forced them to forage. If this were so, then it would suggest that spice finches can vary their allocation of foraging effort to producing and scrounging as a function of changes in local foraging conditions.

If producers can adjust their use of the two strategies opportunistically, then the model predicts that when the cost of producing increases, individuals should increase the proportion of their foraging effort allocated to scrounging. We tested this hypothesis in the next experiment. We used the same foraging environment but increased the cost of producing by increasing the weight of the lids covering the wells.

Experiment 2

Methods

The foraging grids and the light lids were the same as those used in experiment 1. Heavy lids weighed 8.0 g (SE = 0.14, n = 15), and were therefore on average 2.9 times heavier than the light lids. We increased the weight of heavy lids by gluing metal coins to their underside. The birds, therefore, could only detect differences between light and heavy lids after handling them.

The subjects were 15 birds taken from the pool of producers used in experiment 1, plus three producers that had been trained to remove light lids for a different experiment (Ennis 1992). We formed two core flocks, each containing five birds, four of which were chosen from those of experiment 1. To make sure that all birds could remove lids before the onset of the experiment, they were all given training trials in their homes cages as in experiment 1, first using light lids and then heavy lids. Training was complete once birds removed lids consistently upon presentation.

Except for some minor differences, flock trials proceeded as in experiment 1. The flocks were assigned a different initial lid weight condition and one focal subject was added to each. The observer recorded the behaviour of each focal bird for six trials on a single day. The focal birds remained in the same core flock overnight. The next day the observer switched each core flock's lid weight condition and recorded the behaviour of focal subjects for another six trials. After the final trial of the 2nd day, the observer removed subjects from the flocks and replaced them by fresh subjects. Each core flock, therefore, experienced the same number of heavy and light lid conditions balancing for the order of presentation of lid conditions over the 12 subjects used. To reduce the total number of animals used in the experiment, we used four core flock members as focal subjects in the other core flock. We were interested in the focal birds' allocation to each foraging strategy. We assumed that the total number of seeds eaten by producing and scrounging and the total number of patches visited as either a producer or a scrounger over the course of a trial provide a measure of an individual's allocation.

Results

The birds foraged as in experiment 1, but there was a noticeable difference in the effort required to remove lids in the high-producing-cost condition. The subjects ate a similar number of seeds in the two conditions (71.2 seeds ±4.04, 72.2 seeds ±5.72, low- and high-cost respectively; $t_{11} = 0.175$, NS). Producing cost did not alter the division of seeds between a patch's producer and scroungers. The number of seeds eaten per patch through producing in the low (3.3±0.28) and high (4.5±0.23) cost conditions did not differ significantly ($t_{11} = 1.67$, NS). Similarly the number of seeds eaten per patch through scrounging in the low (2.1 ± 0.12) and high (2.4 ± 0.16) cost conditions did not differ significantly ($t_{11} = 0.656$, NS). Producing a patch provided a significant advantage since a bird that produced a patch obtained significantly more seeds than a bird that scrounged in both the low ($t_9 = 4.69$, $P = 0.001$) and high ($t_{11} = 8.68$, $P < 0.0005$) producing-cost conditions. However, the magnitude of the producer's advantage, obtained by subtraction, (2.07 seeds ± 0.24) in the high- and 1.79 seeds ± 0.38 in the low-cost conditions) was unaffected by the cost of producing ($t_9 = 0.94$, NS).

The cost of producing had a significant effect on the subjects' relative allocation to each strategy. The birds produced 0.34 (± 0.05) of their wells in the high-cost condition while this proportion increased significantly to 0.45 (± 0.08; $t_{11} = 1.968$, $P = 0.037$, one-tailed test) in the low-cost condition. Overall, 10 of the 12 finches increased the number of seeds obtained through scrounging by an average of 10.9% (± 6.93) when placed in the high-producing cost condition (one-tailed binomial test, $P < 0.02$). Notice that two of the 12 subjects increased the number of seeds they obtained by producing in the high producing cost treatment.

The cost of producing also had some effect on the absolute allocation to producing and scrounging strategies. For instance, individuals produced a significantly smaller number of patches in the high (7.2 ± 0.56) than in the low (9.7 ± 1.28) cost condition ($t_{11} = 1.85$, $P = 0.045$ one-tailed test). Similarly individuals ate more seeds by scrounging in the high- (41.2 ± 6.24) than in the low- (31.3 ± 6.10) cost condition ($t_{11} = 1.88$, $P = 0.043$, one-tailed test).

Discussion

The results of experiment 2 are consistent with the hypothesis that spice finches can adjust the allocation of foraging effort to producing and scrounging in response to changes in local foraging conditions. When the cost of producing was increased, most finches significantly reduced the number and proportion of patches they produced and increased the total number of seeds obtained by scrounging. Additional support for the hypothesis that finches adjusted their use of the two foraging strategies comes from comparisons of the proportion of patches produced in experiments 1 and 2. As predicted by the presence of additional producers in experiment 2, the producers in both conditions of experiment 2 exploited a smaller fraction of their patches by producing (34% in high, 47% in low cost) than the producers (65%) of flock P in experiment 1. The difference between the low-cost condition and flock P arises because only five birds could produce in flock P while all six could do so in experiment 2. Increasing the cost of producing should reduce producing even more and it did. Thus, we conclude that spice finches were adjusting the use of producing and scrounging to the local foraging conditions.

Surprisingly, despite changes in producing effort the total number of seeds eaten or patches exploited remained unaffected by producing cost. That result suggests that producing cost may not affect the frequency of producing uniformly within a group. We do not know how the core birds altered their use of producing but have noted that that two of the 12 focal birds increased their producing effort in the high producing cost condition. Producing cost, therefore, also affects the distribution of producing effort within a group; fewer individuals carrying more of the producing burden as producing costs increase. This possibility is worth investigating in future studies.

General Discussion

The producer-scrounger game has long been argued to apply to situations of flock foraging. However, to date, no study had provided evidence that the pay-offs to producers and scroungers were negatively affected by the proportion of scroungers in the group or that the pay-off functions expressed in food intake could cross for a given proportion of scroungers. Results of experiment 1 suggest that the producer-scrounger rate maximizing model can be applicable to flock feeding in spice finches. However, at the P/S ratios used in our experiment we could not provide a strong demonstration that the intake functions of each strategy cross at some proportion of scroungers. The model's predictions therefore should be tested in other group-feeding systems where a greater range of P/S ratios could be generated.

The results of experiment 1 suggest that some assumptions of the rate maximizing producer-scrounger model need to be reconsidered. For instance, the foraging model may overestimate the rise in pay-offs to scroungers associated with increases in the proportion of producers in the group. Future research should establish the extent to which the frequency of scrounging opportunities increases with increasing proportions of producers. It is likely that the rate at which scrounging opportunities are generated increases at a decreasing rate with increasing proportions of producers, possibly as a result of reduced searching efficiency. An additional factor is the possibility that as the number of producers increases, so does the frequency of simultaneous patch discoveries. If this were so, then one would expect that the rate of scrounging opportunities could start to decline at some critical proportion of producers. Such a complex scrounger pay-off curve, that first increased and then decreased, could cross the producer pay-off curve at two points, suggesting the existence of two equilibrium points rather than a single one.

A number of other studies have provided indirect evidence that avian social foragers can adjust their tendency to produce and scrounge. Theimer (1987) for instance, found that dominant dark-eyed juncos (*Junco hyemalis*) would alter their use of supplanting depending on the extent to which seeds were clumped. Similar conclusions were reached by Rohwer and Ewald (1981) for Harris' sparrows (*Zonotrichia querula*). Theoretical developments of producer and scrounger models have also suggested that behavioral plasticity in the allocation to each strategy would be more likely than fixed roles whose proportions are adjusted by selection (Caraco and Giraldeau 1991; Vickery et al. 1991). Our results thus provide the first empirical evidence that individuals can adjust the use of producing and scrounging in response to changes in local foraging conditions. Plasticity, however, may not always be the rule. Barnard and Sibly (1981) reported that house sparrows did not alter the use of producing and scrounging opportunistically. It becomes important to understand, therefore, the ecological conditions under which plastic or fixed strategies are to be expected. Our results, taken with those of earlier studies, show that group foragers can adjust the use of producing and scrounging as a function of flock composition, seed distribution and cost of producing. Future work should investigate whether foragers can also respond to factors such as the producer's advantage, patch and group size, while also addressing the issue of the game's applicability to other, possibly non-avian, group foraging systems. Intake maximizing producer-scrounger models of the type presented here as well as risk-sensitive versions of the game (Caraco and Giraldeau 1991) may pave the way for applications of foraging theory to group foraging animals.

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