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The Payoffs to Producing and Scrounging: What Happens when Patches are Divisible?

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Abstract

Although many group-foraging models assume that all individuals search for and share their food equally, most documented instances of group foraging exhibit specialized use of producer and scrounger strategies. In addition, many of the studies have focused on groups with strong individual asymmetries exploiting food that is not easily divisible. In the present study we describe individual foraging behavior of relatively nonaggressive flock foragers exploiting divisible clumps of food. Two experiments, one with flocks of spice finches and another with flocks of zebra finches, suggest that divisibility of food patches may have important consequences for social foraging behavior. Neither dominance nor the distribution and quality of food patches affect the relative advantage that producing individuals enjoy over those that scrounge. Specialized producers and scroungers are absent from flocks of both species. Systems where patches are shared may differ fundamentally from those where patches are monopolized by scroungers.

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Introduction

Group foraging is thought to provide individuals with foraging and anti-predatory advantages (BERTRAM 1978; CLARK & MANGEL 1986). In this study we focus primarily on the foraging benefits of group membership. Some of the more commonly cited foraging advantages of group membership include increased foraging rate (PULLIAM & MILLIKAN 1982; CLARK & MANGEL 1984; CARACO 1987; VICKERY et al. 1991), reduced risk of starvation (CARACO 1981, 1987) and increased ability in capturing elusive prey (KRUUK 1972; SCHALLER 1972; WARD & ENDERS 1985; PACKER 1986). These advantages follow mostly when all group

members participate in the search or hunt and all share each others' discoveries
(CLARK & MANGEL 1984; CARACO 1987; VICKERY et al. 1991). It is therefore
important to know whether all members of a foraging group invest effort in
finding prey and whether all group members are equally likely to use food
discovered by others. Surprisingly, little empirical information is available con-
cerning these aspects of group foraging.

In most instances when individuals' behavior within foraging groups has
been recorded, only some animals search for food. BARNARD & SIBLY (1981)
described the existence of specialized "searchers" and "copiers" in house sparrow
flocks where only the searchers invest time and effort in finding food. Similar role
specialization has been found within foraging flocks of Harris' sparrows (ROHWER
& EWALD 1981), dark-eyed juncos (BAKER et al. 1981), and feral pigeons (GIRAL-
DEAU & LEFEBVRE 1986, 1987). The phenomenon of asymmetric search within
foraging groups appears widespread in both mixed and single-species avian
foraging aggregations (see BROCKMANN & BARNARD 1979; BARNARD 1984 a, b;
BARNARD & THOMPSON 1985 for reviews). We follow terminology proposed by
BARNARD & SIBLY (1981) and call food finders "producers" and individuals that
forage from patches discovered by others "scroungers".

Most of the instances of producing and scrounging roles have involved
groups that harbor strong individual asymmetries. In Harris' sparrows and dark-
eyed juncos, for instance, dominant individuals displaced subordinates from food
patches (BAKER et al. 1981; ROHWER & EWALD 1981). In feral pigeons, on the other
hand, specialized scroungers were those individuals that had not yet learned the
skill required to find food (GIRALDEAU & LEFEBVRE 1987). Patch divisibility,
richness and distribution are also important. When food is indivisible, successful
scroungers do well because they obtain whole parcels of food at reduced cost
(THOMPSON 1986). Foragers use scrounging more when food patches are rich and
clumped (THEIMER 1987; BENKMAN 1988). When food is more evenly distributed,
use of scrounging is reduced (ROHWER & EWALD 1981; THEIMER 1987). Thus,
strong individual differences and indivisible food patches lead to profitable
scrounging and may even promote specialized scrounging.

Despite the common reports of asymmetries in the searching and joining
behavior of foraging group members, the most common view of group-foraging
behavior is one where individuals peacefully and equally share each other's food
discoveries. Examples of individuals sharing the same food patch without exhibit-
ing aggression cover a wide taxonomic range including some birds (RAND 1954;
NEWTON 1967), vertebrate carnivores (KRUUK 1972; SCHALLER 1972), communal
spiders (WARD & ENDERS 1985) and insects (ERLANDSSON 1988). However, there
has yet to be a systematic investigation of the payoffs to producing and scroung-
ing in avian systems when individuals share food patches. The goal of the present
study was to document the foraging decisions of avian group members with
minimal individual differences exploiting divisible food patches. Specifically, we
investigated whether all group members produce and scrounge food and
documented the payoffs that producers and scroungers obtained. We asked
whether social dominance affects an individual's propensity to produce or

scrounge as well as the share it obtains of each food source. We also asked whether resource distribution and patch quality affect an individual's tendency to scrounge and produce.

We chose to perform these experiments on two species of common grass finches (estrildidae): the spice finch *(Lonchura punctulata)* and zebra finch *(Poephila guttata)*. We chose these species because preliminary observations revealed that they forage in groups with little aggression. Thus, they appeared, at least superficially, to correspond to the ideal group forager that is often portrayed in models concerning the advantages of group foraging. The species have the following traits in common. Both are monogamous colonial breeders that forage in flocks year-round (GOODWIN 1982; IMMELMANN 1982). Foraging flock size varies from below 10 to over 300 in zebra finches, being largest in the winter (ZANN & STRAW 1984). Both species are almost exclusive granivores taking seed both on the ground and from standing grass stalks (GOODWIN 1982; IMMELMANN 1982).

The species differ in the following respects. Zebra finches have conspicuous plumage sexual dimorphism, while spice finches do not. The zebra finch originates from arid grasslands of Australia while spice finches are from the humid forests of south-east Asia. Although they are both common pet species little is known about the flock foraging behavior of either of these gregarious grass finches. The published accounts, however, suggest similar group-foraging behavior despite the differences in habitats where they evolved.

Experiment 1: Spice finches

Methods

Subjects

15 adult spice finches of unknown sex and age were purchased from a commercial supplier. Each bird was uniquely color-banded and was arbitrarily assigned to one of three flocks. Each flock was housed separately in an 83 × 83 × 106 cm high cage. The birds were maintained on a 12-h light cycle with ad libitum access to food and water.

Apparatus

The foraging area was a 2.0 × 1.2-m grid containing 198 wells 1.2 cm wide and 0.8 cm deep, distributed in equidistant rows 10 cm apart. The grid was set 1.3-m above the floor at one end of a 5.5 × 3.2 × 2.4-m high indoor aviary. Perches were not located above or near the grid to force the birds to hop on the grid to locate the food.

Procedure

A flock was introduced into the aviary in the afternoon on the day before the trials were scheduled to start. The birds were allowed to feed from a bowl of mixed millet seed placed on the grid until the lights went off at 21.00 h. From that time, food was removed until the beginning of the first trial which started the next morning when the lights came on at 09.00 h.

A trial consisted of the birds landing on the grid and foraging for the seeds placed in some of the wells. The trial began when the first bird landed on the grid and ended when the birds failed to find any food for 2 consecutive min. When a trial ended, all remaining food was removed from the grid and the birds were deprived of food until the beginning of the next trial. Five trials were performed on the same day at hourly intervals. After the last trial, the flock was returned to its holding cage and allowed

to feed ad libitum. The flock scheduled to be tested the next day was then allowed into the aviary. In all, each flock was tested on six different days.

We used focal-animal sampling, assigning a different focal animal to each of the five trials. Each flock member therefore was observed during one of the five trials that made up a daily session. The assignment of focal animals was balanced so that each individual was observed at least once in each of the five time periods in which trials were held.

Observations were made through a one-way mirror located directly in front of the grid. The observer called out behavioral events into the audio channel of a video recording of the trial. The video recording was replayed immediately after each trial and the observations were transferred to a digital event recorder. The behavioral events that were recorded were hopping on the grid surface and feeding.

The number of seeds eaten was estimated from the frequency of husking behavior. Not all pecks at a food source resulted in husking, and we assumed that husking was an accurate indication of the number of seeds consumed. It is possible, however, that some seeds went undetected if they required little or no husking or if birds could pick up and husk more than one seed per peck. Feeding was divided into the number of seeds taken from a clump in which the focal animal was the first to eat, and the number of seeds taken from a clump when the focal bird was not the first to eat. In the former case the focal animal was called a "producer" and the seeds it ate were considered seeds produced, while in the latter case the bird was called a "scrounger" and the seeds it ate were considered seeds gained from scrounging.

To calculate feeding rates we measured the time elapsed between the first and last seed eaten from the food patch and counted the total number of seeds eaten. The rates were obtained by dividing the total number of seeds by the total duration of feeding. The calculations were done for seeds produced and scrounged, but in all cases we used only those instances where individuals ate more than one seed at a patch.

All flocks had 200 white millet seeds available on each trial. Each flock was exposed to a different patchiness condition. Flock A foraged for 40 patches of 5 seeds on each trial, flock B foraged for 20 patches of 10 seeds, while flock C foraged for 10 patches of 20 seeds. The positions of the food patches on the grid were chosen randomly before each trial.

Measuring Social Status

After all the foraging trials were completed, we measured the priority of access to food following methods used by GIRALDEAU & LEFEBVRE (1986). A small commercial feeder was placed on the grid surface and arranged so that only one, rarely two, birds could simultaneously feed from it. The feeder was placed over a wire mesh box so that spillage was inaccessible to other birds. Each flock
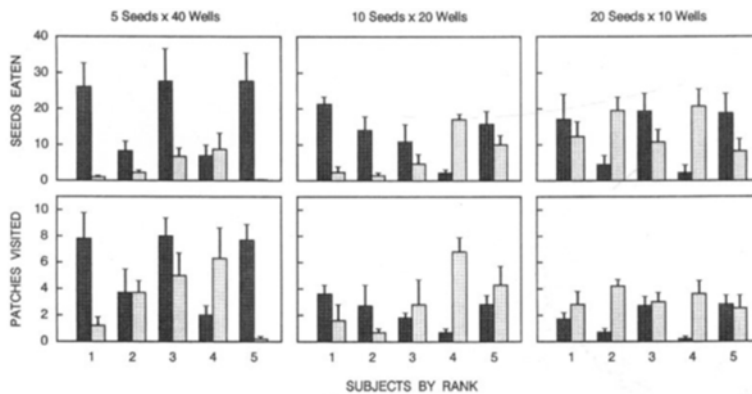

Fig. 1: Producing and scrounging profiles of spice finch individuals foraging on three different seed distributions. Individual birds are ranked in increasing order of subordinance within each flock. Top: mean total number of seeds produced (dark bars) and scrounged (light bars) per trial (n = 5); bottom: mean number of patches produced and scrounged per trial

was deprived of food for 1 h prior to start of trial. Four 30-min trials were conducted over two days. We measured, from video recordings, the latency for each member of a flock to accumulate 90 s of feeding time at the feeder. We assumed that the shorter the latency the higher an individual's priority of access to food.

Results and Discussion

Priority of Access to Food

All birds were observed to feed from the feeder and to accumulate in excess of 90 s of feeding time. The birds competed for access to the feeder since it was constantly attended by at least one individual during the first several min of each trial. The ranks recorded for each of the 5 birds on the 4 trials for each flock are consistent. The Kendall coefficient of concordance, W is 0.86, 0.66, and 0.48 for flocks A, B, and C, respectively; the respective p values are 0.01, 0.02, and 0.10. An overall rank for each bird in each flock, calculated from the sum of the ranks on the 4 trials is used in the following analyses.

Producing and Scrounging

The finches readily landed on the grid and searched for food as a group. About half the food was eaten before the criterion for the end of a trial was reached. Usually a trial ended when all the birds flew off the grid, almost simultaneously, and returned to the perches where they preened and rested. On only a few occasions did a trial end with a bird still present on the grid. Trials lasted ($\overline{X} \pm SE$) 237.6 ± 25.7 s, 140.5 ± 7.7 s, 193.5 ± 11.7 s for flocks A, B and C respectively.

The birds seldom discovered all the food patches during a trial. For all 3 flocks over the 6 days a total of 279 patches (66 %) were discovered. Flocks A, B and C discovered 164 (68 %), 64 (53 %), and 51 (85 %) of the food patches, respectively. Birds that scrounged rarely displaced birds already attending a food patch, and aggressive interactions between indidivuals feeding from the same patch were almost never seen.

A bird's rank was not related to the number of seeds produced and scrounged per trial (Fig. 1). A 5 × 2 analysis of variance confirmed this impression. Some individuals appeared to use one foraging mode more than the other. For instance, the individual ranked 4th in the 10 seed-20 well flock obtained most
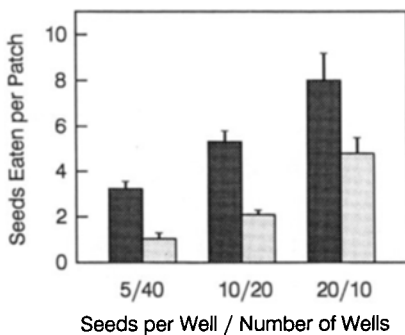

Fig. 2: Mean number of seeds eaten per patch by spice finches when producing (dark bars) and scrounging (light bars) for the three seed distributions. Vertical bars: 1 SE above mean; n = 5 birds in all cases

of its seeds by scrounging (Fig. 1). The same was true of individuals ranked 2nd and 4th in the 20 seed-10 well condition (Fig. 1). In all cases, however, the number of seeds produced and scrounged was so variable for individual birds from trial to trial that it is difficult to say that true specialist individuals occurred in these flocks. All individuals both produced and scrounged. Eleven of the 15 birds obtained most of their seeds by producing while 4 obtained most of their seeds by scrounging (Fig. 1).

The frequency with which individuals produced and scrounged sources was analyzed in the same way as the number of seeds eaten per trial. Once again there is no evidence of consistent individual specialization. Six birds ate more frequently from patches they produced while 8 ate more frequently from patches they scrounged, and one bird fed equally from both (Fig. 1). Again a 5 × 2 ANOVA confirmed that dominance rank had no effect on the frequency with which an individual scrounged or produced patches (Fig. 1).

Large and significant differences emerged in the number of seeds eaten per source between the groups for both seeds produced and scrounged. Moreover, a bird that produced a well ate more seeds than a scrounger (Fig. 2). A 3 × 2 ANOVA shows that the differences between flocks are highly significant ($F = 28.61$; df = 2,12, $p < 0.01$) as is the difference between producing and scrounging ($F = 93.61$; df = 1,12, $p < 0.01$). Dominance rank, however, had no significant effect on the number of seeds an individual obtained from a patch it had produced (see Table 1). Not surprisingly, birds ate more from larger than from smaller sources, but more importantly the increase appeared to affect the producer and scrounger equally.

Payoffs expressed in terms of feeding rate (seeds/s) at the patch were also analysed (see Table 1). A 3 × 2 ANOVA revealed a significant difference in feeding rates between flocks ($F = 4.88$, df = 2, $p < 0.05$) but no significant differences between producing and scrounging. A separate analysis confirmed that priority of access rank also had no effect on pecking rate.

In conclusion, there were no consistent producer or scrounger specialists; producing clearly yielded more seeds per source than scrounging but peck rate was not affected. Neither the social status of the individual nor the patch quality and distribution seemed to have important effects on the individuals' foraging decisions and payoffs. The major limitation of the above experiment was the lack of replication of seed distributions and the impossibility of detecting gender differences in behavior. In the next experiment we modified the design in order to replicate seed distributions and to test for gender differences.

Experiment 2: Zebra Finches

Methods

32 birds, 16 of each sex, were obtained from local pet dealers. They were housed in four unisexual flocks of 8 individuals. Each bird was individually color banded. Outside experimental periods, birds were kept on ad libitum food and water regimes.

We measured the rank of priority of access to food for all 8 birds in each flock as in experiment 1 using a criterion of 60 s of accumulated time at the feeder. This time, to see whether ranks changed

Table 1: Spice finch results. Mean per bird per trial ± SEM

	No. of seeds eaten			No. of patches		Seeds/patch		Seeds/s	
	total	produced	scrounged	produced	scrounged	produced	scrounged	produced	scrounged
Flock A	18 ± 4	15 ± 5	4 ± 2	5 ± 2	3 ± 1	3.2 ± 0.2	1.1 ± 0.2	1.34 ± 0.08	1.27 ± 0.24
Flock B	19 ± 2	12 ± 3	7 ± 3	2 ± 1	3 ± 1	5.3 ± 0.5	2.1 ± 0.2	1.95 ± 0.10	2.01 ± 0.39
Flock C	27 ± 1	12 ± 4	14 ± 3	2 ± 1	3 ± 0	8.4 ± 0.9	4.3 ± 0.4	2.12 ± 0.17	1.91 ± 0.20
Rank 1	26 ± 2	21 ± 3	5 ± 3	4 ± 2	2 ± 1	6.6 ± 2.0	2.2 ± 1.1	1.77 ± 0.16	1.26 ± 0.31
Rank 2	15 ± 5	8 ± 3	7 ± 6	2 ± 1	2 ± 1	4.8 ± 1.3	2.5 ± 1.2	2.06 ± 0.43	2.34 ± 0.73
Rank 3	19 ± 5	12 ± 4	7 ± 2	4 ± 2	4 ± 1	5.6 ± 1.1	2.2 ± 0.7	1.88 ± 0.24	1.96 ± 0.19
Rank 4	19 ± 2	4 ± 2	16 ± 4	1 ± 1	5 ± 1	5.9 ± 2.5	3.2 ± 1.3	1.66 ± 0.09	1.65 ± 0.25
Rank 5	27 ± 1	21 ± 4	6 ± 3	5 ± 2	2 ± 1	5.2 ± 0.9	2.2 ± 0.7	1.65 ± 0.32	1.44 ± 0.08

during the course of the experiment, priority of access was measured four times before the grid experiment started and four times after it had ended.

The foraging grid was the same as in experiment 1, but it was now enclosed in a flight cage. A flock was introduced into the flight cage in the afternoon preceding the day of the experiment. When the lights went on the next morning at 09.00 h, food was removed. Trials started at 13.00 h. Four trials were run each day at hourly intervals. After the last trial the flock was returned to its holding cage and allowed to feed ad libitum.

As in experiment 1, we used focal-animal sampling. Four focal animals were chosen on the basis of their priority of access to food rank; these were the two most dominant and the two most subordinate individuals in each flock of 8 birds. A different animal was observed on each trial. Each flock was tested 16 times, once every fourth day. All observations were made from a blind, and records were entered directly into a digital event recorder. The observer recorded hops, flights, producing and scrounging of a food source and number of seeds obtained from produced and scrounged patches.

Only two levels of patch quality were used in this experiment. In both conditions, 10 wells contained food. In the rich-patch condition, wells contained 40 white millet seeds, while in the poor-patch condition each well contained 10 seeds. Thus, unlike experiment 1, the total number of seeds available varied but the number of patches did not. The positions of the food patches on the grid were chosen randomly before each trial.

To replicate feeding conditions each flock was given 8 trials at one patch quality and then switched to the other. A flock of each sex started the trials in the rich-patch condition, while the two other flocks started in the poor-patch condition.

Results and Discussion

Priority of Access to Food

Kendall coefficients of concordance were calculated for each flock for the four sessions before the foraging trials and for the four sessions after. Pearson's correlation coefficients calculated on the ranks were then calculated for each flock between the overall ranks for each flock before and after the foraging trials. Coefficients of concordance are significantly positive for three of the four flocks for the sessions before the grid experiments and for three of the four flocks after (Table 2) suggesting that reliable differences in priority of access to food are characteristic of zebra finch flocks. The correlation coefficients between the ranks of flock members before and after the grid experiments are also positive, but only one is significant ($p \leq 0.05$). These results suggest that rank differences among

Table 2: Kendall coefficients of concordance (W) between priority of access ranks of zebra finches measured in four trials before and four trials after the grid experiment, as well as Pearson's correlation coefficient (r) between ranks obtained before and after grid experiments

Flock	W before	W after	r
Male 1	0.72**	0.61**	0.71*
Male 2	0.76**	0.40 ns	0.40 ns
Female 1	0.56*	0.52*	0.56 ns
Female 2	0.44 ns	0.60*	0.28 ns

* = $p \leq 0.05$, ** = $p \leq 0.01$.

Table 3:   Zebra finch results. Mean per bird per trial ± SEM

| Habitat | Dominance | No. of seeds | | | No. of patches | |
		total	produced	scrounged	produced	scrounged
Poor	high	13 ± 1	9 ± 2	5 ± 2	1.9 ± 0.3	2.5 ± 0.7
	low	8 ± 1	3 ± 1	6 ± 1	1.1 ± 0.3	2.9 ± 0.6
Rich	high	32 ± 4	16 ± 4	16 ± 4	2.5 ± 0.5	3.0 ± 0.8
	low	23 ± 3	11 ± 2	12 ± 3	1.6 ± 0.2	2.4 ± 0.5

flock members are stable over short but not over long time intervals. Since the birds had been housed together for several months prior to the experiment these changes could not be attributed to the presence of new members disrupting the hierarchy. We do not know whether these slowly changing hierarchies are characteristic of estrildid flocks generally. To the best of our knowledge no other avian social foraging study measured dominance both before and after trials. Our results suggest, therefore, that this procedure should be followed.

Producing and Scrounging

The zebra finches readily foraged on the grid, but on the first day there was visibly more aggression than in spice finches. The aggression was not specifically centered around food patches however. During the first day, individuals sometimes kept others from landing altogether. In the male flocks especially, some individuals were involved in long chases around the grid. Nonetheless, the level of overt aggression did not remain high, and did not prevent several individuals from feeding simultaneously from the same food source. Unlike experiment 1, all food patches were almost always found before the end of a trial, presumably because flocks were larger than in experiment 1 and the patches fewer.
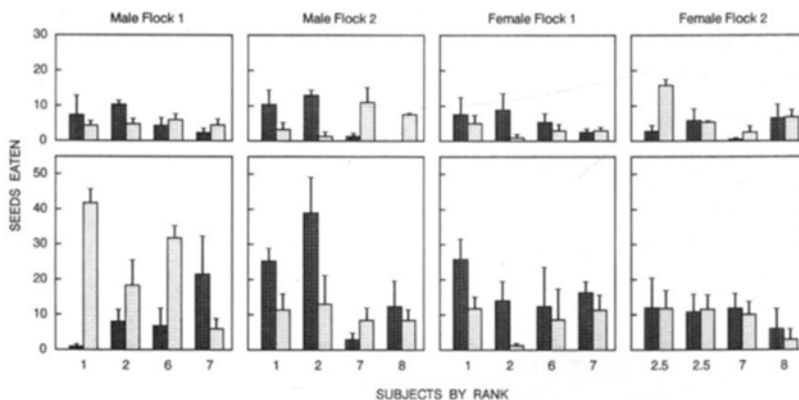

Fig. 3:   Producing and scrounging profiles of individuals in four flocks of zebra finches expressed as mean number of seeds produced (dark) and scrounged (light) per trial when foraging in habitats with all poor (top) or all rich (bottom) patches. Individuals are ranked in increasing order of subordinance

The same measures of feeding behavior were calculated for the zebra finch flocks as were calculated for the spice finches in experiment 1. Preliminary analysis of the data for number of seeds eaten and number of patches visited showed that males ate more than females (for males = 21.8 seeds per session; for females $\overline{X}$ = 16.2 seeds per session) and visited more patches than females (for males $\overline{X}$ = 5.3 patches; for females = 3.8 patches) and these differences are significant (2 × 2 × 2 × 2 ANOVA). However, these kinds of differences between the sexes were not of special interest in this study, and because the sex variable did not interact with any of the other variables, the variable of sex was not included in the final analysis. Further, because the experiment had been designed with rank as an independent variable, the data were analyzed using 2 × 2 × 2 ANOVAs with rank as a between-subjects variable and with density and role (produced versus scrounged) as within-subjects variables.

Birds tested in the poor-patch condition ate about 10 seeds per trial, while in the rich-patch condition they ate about 28 seeds per trial (Table 3; F = 32.7; df = 1,14; p < 0.01). This difference was expected because four times as many seeds were available in the rich-patch condition. Unlike the spice finch experiment, however, higher ranking individuals ate about 50 % more then lower ranking individuals (Table 3; F = 7.12; df = 1,14; p < 0.05). The differences are not significant between the total number of seeds eaten from produced and scrounged patches.

As was true of spice finches, the producing and scrounging profiles of the zebra finches suggest that some individuals tended to obtain their food by favoring one of the two foraging modes (e. g. individuals ranked 1 and 2 in male flock 2 and individuals 1, 2 and 6 in male flock 1 in the rich-patch condition [Fig. 3]). As with spice finches, the tendency to use one or the other foraging mode was not related to social status (Fig. 3). Moreover, changing patch quality did not have a consistent effect. In female flock 2, for instance, one individual
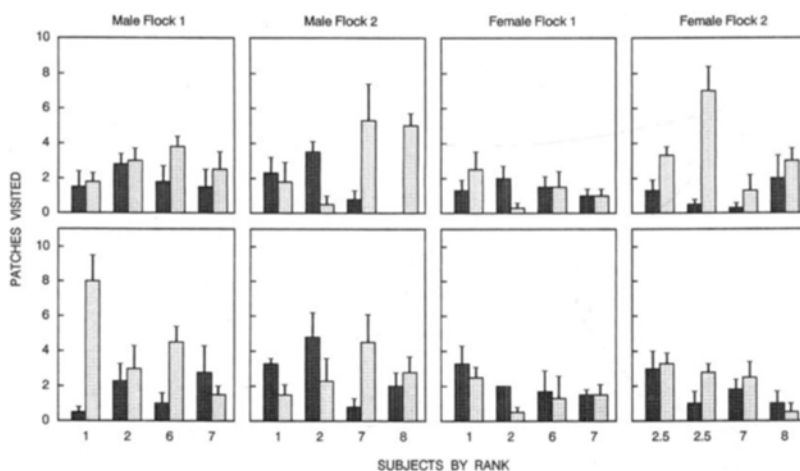

Fig. 4: Producing and scrounging profiles of zebra finches of Fig. 3 expressed as mean number of patches produced and scrounged per trial
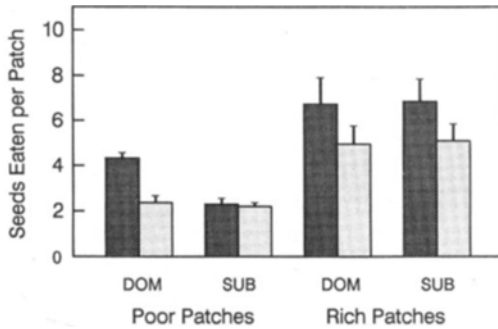
Fig. 5: Mean number of seeds eaten per patch by zebra finches that produced (dark) and scrounged (light) when foraging on rich and poor patches. The two most dominant individuals of each flock were lumped together as were the most subordinate. Vertical bars: 1 SE above mean

went from almost pure scrounging to an equal mixture of producing and scrounging when patch quality went from poor to rich (Fig. 3). On the other hand, individuals ranked 1 and 2 in male flock 1 went from slight preference for producing to favoring scrounging when patch quality was changed from poor to rich (Fig. 3). Overall, consistent individual specialization is absent and neither dominance nor patch quality affected the use of the alternative foraging modes. The same conclusions hold when considering the number of patches of each type visited by the birds (Fig. 4).

Birds ate about twice as many seeds per patch in the rich-patch condition as in the poor-patch condition (Fig. 5; $F = 47.57$; $df = 1,14$ $p < 0.01$). Zebra finches, as with spice finches, ate more seeds when they produced a source than when they scrounged (Fig. 5; $F = 11.58$; $df = 1,14$; $p < 0.01$), and like spice finches rank had no significant effect on this variable ($F = 0.79$). In conclusion, zebra finch flocks do not harbor consistent, specialized producers and scroungers. As was observed in spice finches, scrounging in zebra finches yields fewer seeds per patch than producing, and neither dominance nor patch richness appear to have important effects on the use of the alternatives and their relative payoffs.

General Discussion

Our study suggests that grass finch foraging flocks differ in three important ways from species in which animals supplant each other to gain exclusive access to food patches. 1) Neither dominance nor patch distribution and quality affect the relative payoff of scroungers; 2) flocks lack consistent specialized scroungers; and 3) the food patch is not shared equally between its producer and the scroungers but rather producers have a consistent advantage.

No Effect of Dominance or Patch Quality

Unlike many other avian systems, priority of access to food has no strong effect on foraging success. In particular, dominance neither constrained an individual's use of scrounging nor did it influence the payoffs obtained per source (though in zebra finches in the poor-patch condition subordinates did not appear

to gain a producer's advantage). Total seeds eaten was not affected by dominance in spice finches but in zebra finches dominants ate more per trial than did subordinates.

Modifications of patch quality and distribution did not have a strong effect on the use of scrounging nor did they affect the existence of a producer's advantage, except possibly for subordinate zebra finches. Changes in food patchiness do affect the use of scrounging in more aggressive species such as Harris' sparrows and dark-eyed juncos (ROHWER & EWALD 1981; BAKER et al. 1981; THEIMER 1987). Whether the difference is due to the divisibility of food patches or to intrinsic characteristics of grass finches, however, remains to be shown.

Lack of Specialized Producer and Scrounger Roles

As far as we know, this is the first quantitative description of an avian system where all group members appear to search for and share food patches without any consistent bias for one alternative foraging mode or the other. The lack of specialized scroungers may result from scrounging providing fewer seeds per patch than producing. A specialized scrounger, therefore, could do worse than a specialized producer. In many instances where specialized scroungers occur there is reason to believe that they obtain a larger share of a food patch than the producer. This is especially obvious when the resource is not divisible and the scroungers can supplant producers (ROHWER & EWALD 1981; HANSEN 1986). Thus, the extent to which resources can be shared may determine the degree to which specialized scroungers are expected. This would need to be tested experimentally. In this respect, however, estrildid foraging flocks conform more closely to the assumptions of equal search effort and equal food sharing that characterize many social foraging models (CLARK & MANGEL 1984; CARACO 1987) than most of the avian systems described to date (BAKER et al. 1981; BARNARD & SIBLY 1981; ROHWER & EWALD 1981; GIRALDEAU & LEFEBVRE 1986, 1987).

That a producer obtains more food per source than do scroungers raises the question of why individuals do not specialize exclusively in producing instead of persisting in scrounging. If the objective of the finches' behavior is to maximize the number of seeds obtained per source then we expect scrounging to wane during successive foraging sessions as more and more individuals overlook scrounging opportunities in order to find their own food patch. A trend of this sort was observed in pigeons foraging for three patches of food (LEFEBVRE 1983). That we did not observe this progressive reduction of scrounging suggests that the birds do not behave in a way that is consistent with maximizing the number of seeds eaten per food source encountered.

Grass finches appear to play a conservative foraging game, never overlooking an opportunity to forage, not even one that provides fewer seeds. Such a strategy would provide increased probability of eating at least some seeds before all other birds leave the foraging area. The behavior of the birds, therefore, would be consistent with risk-averse foraging strategies (CARACO 1981; REAL & CARACO 1986; CARACO 1987). Such risk-averse behavior is expected from animals that are on positive energy budgets (REAL & CARACO 1986). Although we food-deprived

our birds before trials it is possible that they were still on positive energy budgets. We know that an individual's energy budget affects its propensity to join foraging groups (CARACO 1981) but we do not know whether it also affects its use of scrounging.

The Producer's Advantage

As far as we know, this is the first time that avian producers have been found to obtain larger shares of food than the scroungers. A similar producer's advantage has been documented in communal spiders and follows possibly from a positional advantage of the first individual to bite a prey (WARD & ENDERS 1985; WARD 1986). Similarly, it is possible that the social carnivore that first captures a prey gets a choice of the best feeding location (KRUUK 1972). It is becoming increasingly clear that models of group-foraging behavior that include the producer's advantage, especially in situations where food patches are divisible, will be more realistic (MANGEL 1990; VICKERY et al. 1991).

In conclusion, systems in which food patches are shared appear to be fundamentally different from those where patches can be monopolized by scroungers. Producing in a patch-sharing system provides a consistently larger share of each patch. A producer's advantage exists as was anticipated by VICKERY et al. (1991). This advantage possibly prevents some individuals from specializing as scroungers. Dominance neither affects scrounging frequency nor the share of a patch that is obtained. It is not clear whether this lack of effect of dominance can be attributed to patch sharing or to characteristics of grass finches. Future work, therefore, should focus on establishing whether these differences are common to other species that share their food patches. Grass finch scroungers do not behave in a way that maximizes the number of seeds eaten per patch. Their behavior was consistent, however, with either rate maximization or foraging-risk minimization. It would be necessary for future research to design predictive models of optimal scrounging strategies, much like those of conventional foraging theory (STEPHENS & KREBS 1986) that would allow us to determine the design feature of scrounging behavior in patch sharing-systems.

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