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The frequency of scrounging by foraging spice finches affects flock geometry

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ABSTRACT

The frequency of scrounging by foraging spice finches affects flock geometry

Robyn E. Flynn

When foraging in a group, animals can either search for their food (produce) or wait until others find food and join their discoveries (scrounge). In this study, I investigate the geometric consequences of changes in the frequency of scrounging in flocks of ground-feeding granivorous spice finches, Lonchura punctulata. Individuals using the producer tactic may be more successful if they avoid others who may be scrounging. Conversely, scrounging individuals may be more successful if they are near potential producers. If this is so, flocks with high proportions of scrounging should be more compact than equivalent flocks with lower scrounging proportions, and, in addition, scroungers should be closer to the center of the group than producers. I tested these predictions by observing flocks of six spice finches as they foraged for hidden clumps of food on an aviary floor. I altered the proportions of scrounging effort in a flock and compared flocks in which I expected low proportions of scrounging to those in which I expected high proportions. As predicted, flocks were significantly more compact when the proportion of scrounging was higher. In addition, producers tended to be farther from the center of the flock than scroungers. This first empirical evidence shows that producer-scrounger tactics can influence the geometry of a group as well as interact with other factors, such as dominance and vigilance, to

determine the spatial positions of individuals within a group.

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INTRODUCTION

Group foraging and spatial positioning

Living with others can provide benefits and costs that solitary-living individuals do not experience. Benefits of group living include greater foraging success (Krebs et al 1972; Benkman 1988), enhanced predator detection (Powell 1974; Cresswell 1994), and reduced chance of being selected by a predator (predator-dilution effect, Hamilton 1971; Krause 1994a) or the one that is parasitized (Mooring & Hart 1990). Alternately, costs of group living include increased aggression (Barnard 1980), competition for resources (Krebs & Davies 1978, Praw 1998), and increased conspicuousness (Andersson & Wicklund 1978). The advantages and disadvantages of living with others are not always shared equally among group members, and the actual fitness level experienced by an individual may be due to a combination of its phenotypic attributes such as sex, age, social status, energy reserves, etc. However, an individual's spatial position relative to other group members can also affect its fitness (Romey 1995; Krause 1994b).

Different spatial positions within a group have different cost-benefit ratios associated with them. For instance, individuals on the edge of a group often have a higher food intake rate than those in the center (Okamura 1986; Black et al 1992; Keys & Dugatkin 1990). Also, in colonial nesting birds (black-headed gulls *Larus ridibundus*, Patterson 1965), fish (bluegill sunfish *Lepomis macrochirus*, Gross & MacMillan 1981), and insects (tropical polistine wasp *Ropalidia plebeiana*, Ito et al 1988), central nests often produce more young than edge nests, for a variety of reasons. In the great snipe (*Gallinago media*), a lekking species, males near the center of the lek achieve a

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disproportionate number of matings compared to more peripheral males (Hoglund & Lundberg 1987). An animal on the edge of a group is usually more vulnerable to predation than one in the center (Fitzgibbon 1990; Rayor & Uetz 1990), according to Hamilton's (1971) selfish herd theory. Also, in the case of groups in motion, different positions are associated with different hydro- or aerodynamic properties. For instance, Canada geese *Branta canadensis*, flying in formation require less individual energy expenditure than those flying in a mass or alone (Hainsworth 1987; Hummel 1983). Fish swimming behind a companion consume less energy than those swimming alone (Weihs 1973; Bushnell 1991). Similar observations were found in mallard ducklings (*Anas platyrhynchos*, Fish 1995). Also, lobsters that form a queue when migrating conserve energy compared to solitaries (Bill & Herrnkind 1976). The costs and benefits of a group member, then, may depend on its spatial position in the group.

Since there is an asymmetry in terms of fitness expenditures and returns between spatial positions, an individual may choose its position according to its current physiological state. Hungry whirligig beetles (Coleoptera: Gyrinidae), for example, tend to be found on the edge of a swarm where their prey capture rate is highest, despite the higher predation hazard they experience there (Romey 1995). Likewise, hungry roach (*Rutilus rutilus*) and chub (*Leuciscus cephalus*) show preferences for the leading edge of a group where food is first encountered (Krause 1994a). In these situations, the tendency of an individual to gravitate to the edge of a group to feed may be opposed by the tendency to seek the center to avoid predation. Hence, the overall configuration of a group may be the outcome of its constituents' choice of spatial positions in order to maximize their food

intake while minimizing their energy expenditure and predation risk.

An individual's spatial position may also be correlated with its choice of foraging tactic. White ibis (*Eudocimus albus*) hunting for fiddler crabs *(Uca* spp.) on the edge of a group tend to hunt visually, chasing crabs on the surface and capturing them before they retreat into burrows, whereas those hunting in the center tend to probe the prey's burrows and find them by tactile means (Petit & Bildstein 1987). The authors hypothesized that the positional difference in tactic was due to the disturbance created by hunting ibis: in the center of the flock where many birds are milling around, crustaceans tend to hide in their burrows, whereas on the edge of the flock, prey are still on the surface of the sand because they have not yet been disturbed. They also noticed that the focal birds tended to change foraging tactic when they changed position within the group. However, the direction of the causality remains unknown here: whether the foraging tactic is chosen on the basis of an individual's current spatial position or the reverse. Possibly group members choose their foraging tactic based on the nature of the food or the characteristics of the social group, and then choose their spatial position on the basis of their foraging tactic. Other factors such as social status may affect individuals' choice of tactic or position (Robinson 1981, Czikeli 1983, Hall & Fedigan 1997), which in turn affects factors such as the time they spend vigilant for predators.

The ability of a group to detect predators increases with increasing group size (Pulliam 1973, Elgar & Catterall 1981). However, not all group members share the burden of vigilance equally. Often, individuals on the edge of a group are more vigilant than those in the center (starlings *Sturnus vulgaris*, Jennings & Evans 1980, Keys &

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Dugatkin 1990; Brent geese *Branta bernicla bernicla*, Inglis & Lazarus 1981; white ibis *E. albus*, Petit & Bildstein 1987). Since the spatial position of individuals determines how vigilant for predators they must be, and the spatial position is associated with the foraging tactic chosen, then the tactic choice of individuals may affect their vigilance level. This difference in time allotted to vigilance may in turn affect individuals' intake rates, possibly giving a fitness advantage to those individuals using the tactic that requires less vigilance.

Dominant individuals can out-compete subordinates for access to resources, including choice spatial positions. In groups exposed to predation, dominants may defend locations in the center of the group when cover is unavailable (Robinson 1981; Janson 1990a & b; Ron et al 1996; Hall & Fedigan 1997), or closest to cover when it is available (Ekman & Askenmo 1984; Schneider 1984; Ekman 1987; Desrochers 1989; Suhonen et al 1993; Slotow & Rothstein 1995). In groups of barnacle geese (*B. leucopsis*), to which predation is less important perhaps than to smaller species, dominants defend locations on the edge of the group, which for them are the best foraging sites (Black & Owen 1989); however, in species that use different foraging tactics to procure food, the best foraging sites may depend on the tactic chosen by the individual. Dominant individuals can use their rank to appropriate subordinates' food discoveries (Baker et al 1981, Rohwer & Ewald 1981, Czikeli 1983, Theimer 1987). If a given spatial position in a group gives a foraging advantage to individuals who usurp others' food discoveries, then we expect that dominants will defend these positions.

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The Producer-Scrounger game

The decision to usurp the food discoveries of group mates or to forage independently has been modeled as a producer-scrounger (p-s) game (Barnard & Sibly 1981); in this game, producer and scrounger are two mutually exclusive foraging tactics. An individual playing producer looks for food regardless of what others in the group are doing, and one playing scrounger waits for others to find food and then feeds from the discovery. Individuals are free to choose a tactic and can change tactics at any time during a foraging bout to improve their payoff (Caraco & Giraldeau 1991). Producers are first at a patch and so can feed without competition until joined by scroungers. Producers are limited, however, by their patch-encounter rate. Scroungers by definition have to share patches with others, and always get less of each patch than producers, but their patch-encounter rate is equal to the producers' rate multiplied by the number of producers in the group. The pay-offs to producer and scrounger tactics depend on the proportion of others in the group that are using each tactic. Scroungers do well compared to producers when they are rare in the group but poorly when they are common, and vice versa (Barnard & Sibly 1981). This negatively frequency-dependent relationship between payoffs to producer and scrounger permits a stable mixed-tactic solution in which pay-offs to the two alternatives are equal. The symmetric game assumes that all individuals have equal ability and propensity to play both tactics and that the only factor for an animal to consider when deciding on a tactic is the number of others using the same one. The same is true if the dominance status of foragers leads to only weak differences in the extent to which food can be monopolized (Barta & Giraldeau 1998).

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When individuals exhibit phenotypic differences, the game can become asymmetric, although its solution is still stable (Parker 1982; Gross 1996, Barta & Giraldeau 1998). An asymmetry between players may occur when some individuals derive more benefit from playing a particular tactic than others; such an asymmetry may be due to higher social status, as mentioned above, or to their spatial position within the group. Strong asymmetries predict that dominants should specialize in using the scrounger tactic and subordinates in using producer (Barta & Giraldeau 1998).

Barta *et al* (1997) modeled the spatial characteristics of foraging groups of producers and scroungers using a genetic algorithm that optimized their movement in terms of food intake. For each obligate producer or scrounger, several genes coded for movement rules that were fixed for that individual, such as the length of the step, the extent to which the positions of others were weighed when determining direction, the probability of looking around, &c. The algorithm selected the combination of genes that yielded the highest intake rates (Sumida et al 1990) over 200 generations. In addition to these specific movement parameters, individuals' foraging behavior also depended on the strategy they used. Producers tended to search their immediate area for food, and when food was not found, to move in a random direction; scroungers, conversely, checked the area for feeding flock mates and then fed from a discovered patch if one was available. If not, they moved in a direction weighed by the positions of all other group members. When individuals' movement rules were optimized, Barta's model compared the geometry of flocks of producers only to that of flocks of both producers and scroungers to determine the effect that the presence of scroungers has on the spatial distribution of

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individuals within a foraging flock. Although they did not attempt to optimize positions of foragers (reproductive fitness was based on food intake generated from movement rules and foraging strategy), they found that in the flocks containing evolutionarily stable combinations of both types of foragers, producers spent significantly more time on the perimeter than did scroungers. The average distance between individuals was larger in flocks of only optimal producers; producers, in the presence of scroungers, spent more time on the periphery of the flock than scroungers did. The results suggest that the two foraging tactics, producer and scrounger, have different optimal individual spacing rules associated with them. Producers do better when they are farther from others and from the center of the group than scroungers.

Evidence that individuals adjust their spatial positions in a producer-scrounger context comes mainly from instances of inter-specific kleptoparasitism. Barnard & Thompson (1985), for instance, report that tactic-specific spacing behavior occurs in black-headed gulls *(L. ridibundus)* that kleptoparasitize the food discoveries of plovers *(Pluvialis apricaria)* and lapwings *(Vanellus vanellus)*. Gulls, as scroungers, tend to disperse themselves widely throughout the colony of producers, avoiding each other and defending territories of producing plovers and lapwings (Barnard & Thompson 1985). Barta's model predicts that in order for the producers to minimize the probability of a gull detecting its discovery, a lapwing or plover should move away from a landing gull. Indeed, Barnard & Thompson (1985, p 228) found that 5-8 min after a gull landed in their vicinity, lapwings and plovers had moved an average of 2.4 m and 2.0 m away from it respectively. Scrounging gulls, conversely, tend to attack preferentially producers that are

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near them, because the probability of a lapwing or plover detecting, and hence avoiding, an approaching gull increases with the distance the gull must travel in order to attack (Barnard & Thompson 1985). This preference for closer producers by gulls and avoidance of gulls by plovers and lapwings is consistent with the idea that producer individuals can maximize their food intake by staying relatively far from scroungers, and that scroungers can maximize theirs by staying close to producers. Although gulls and plovers constitute an inter-specific instance of different p-s spacing rules, the same idea should apply to intra-specific p-s interactions, in which it may not be so easy for individuals to know which tactic other group members are playing. For this reason, in an intra-specific context, producers may prefer to be far from all others, because all others are potential scroungers, and vice versa for scroungers.

Approach and objectives of this study

The goal of this study is to test the hypothesis that, in an intra-specific context, the producer and scrounger foraging tactics have different spacing rules associated with them. I predict, following Barta's model, that groups with high proportions of producing will be more spread out than groups with high proportions of scrounging, and that producing individuals will be farther from the center of the group, on average, than scroungers. I used flocks of spice finches, *Lonchura punctulata* to test these predictions.

Spice finches are small (13.2 ± 2.2 g), social, sexually monomorphic estrildids originating in Southeast Asia (Goodwin 1982). They are highly social, even in the breeding season, and can be found in flocks of a few to a few hundred birds; their habitat

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ranges from open or semi-open areas with trees and scrub brush to town parks and gardens. Flocks feed on grass seeds, either from growing plants or directly from the ground with the occasional live insect; also, in Australia, individuals have been documented feeding from road kills (Immelman 1962, cited in Goodwin 1982). Flocks develop dominance hierarchies, however an individual's social status does not affect its access to food (Giraldeau et al 1990). They have been found to forage socially in the laboratory (Giraldeau et al 1990, Beauchamp et al 1997) and studies have found their behavior to be consistent with predictions of a producer-scrounger game (Giraldeau et al 1994, Giraldeau & Livoreil 1998, Mottley MS, Coolen et al MS).

In the first experiment, to alter individuals' investment in each tactic I trained a number of birds to perform a food-producing task. Using these birds in combination with untrained birds, I created low-scrounging and high-scrounging flocks. In the second experiment, all birds could produce; I manipulated the stable frequency of scrounging by altering the seed distribution, following Giraldeau & Livoreil (1998). In both experiments, I compared three parameters of flock geometry: flock area, perimeter, and average inter-individual distance, between the two scrounging conditions.

METHODS

Subjects

Spice finches were obtained from a commercial supplier and housed indoors in a 2.13 x 0.91 x 0.61 m cage on a 12h light cycle. Water and seed mixture, containing white, red, golden, and Siberian millet in addition to niger, poppy, flax, and canary seed, were available *ad libitum*. Spray millet, mashed hard-boiled egg, and sprouted seeds were given on occasion. Birds used in the study were marked with colored acrylic paint on the head or tail to facilitate identification from a distance and wore colored leg bands for permanent identification.

Training

Birds were trained to push lids away from wells to obtain a food reward following Beauchamp & Giraldeau (1997). Animals were food-deprived overnight and trained in late morning, after a total of about 16 h deprivation. Wells contained 14.5 seeds ± 1.8 during training. Training cages were 59 x 32 x 46cm and divided into equal-sized compartments by a wire panel, allowing two birds to be trained per cage. The 24cm^2 training grids had four wells, either all large (4cm diameter) wells; all small (1 cm diameter) wells; or mixed with two wells of each size. Each well was covered by a lid: a square piece of white foam (6.9cm^2 ± 0.6 for small wells, 24.0cm^2 ± 2.3 for large) board topped by a slightly larger (3.3mm ± 1.3 on each side) piece of black cardboard. A small weight (2.7g ± 0.3) was glued to the underside of small lids for ballast, to prevent them from blowing away when the birds flew near. At the start of training, lids were placed adjacent to wells, and were then moved gradually to cover an increasing portion of the

wells on successive trials. As birds learned to push lids aside with their bills, the lids in successive trials eventually covered the entire well. When a bird consistently pushed lids from wells on large-well grids or mixed-well grids, it was then presented with the grid containing only small wells. A bird was considered trained when it pushed lids immediately upon being presented with the small-well training grid three times in succession.

Flock formation

Two types of flock were formed using combinations of trained and untrained birds. Untrained birds were obligate scroungers in that they could obtain food only by scrounging; trained birds were potential (not obligate) producers. Six labile flocks each contained six trained birds. Six fixed flocks each contained one trained bird (taken from a labile flock; only one bird per labile flock was selected to be in a fixed flock) and five untrained birds. In fixed flocks, trained individuals were marked with white acrylic paint on the tail, and one randomly chosen untrained individual per flock was marked on the head. In total, I tested 12 flocks containing 66 randomly chosen birds.

Testing

Flocks were tested in a 2.5 x 2.4 x 2.4m aviary containing a large tree branch perch suspended horizontally 0.5m from the ceiling and a 2.0 x 1.2m wooden testing grid containing 198 small wells (1 cm in diameter) placed on the floor away from the perch. A vertical black plastic screen was hung between the perch and grid, to prevent scroungers from monitoring producers while remaining on the perch. Two 32 x 17cm access holes in either end of the screen 25cm above the perch allowed birds to fly from the perch to the

grid.   Flocks were videotaped using an 8mm video camera equipped with a wide-angle

converter lens (0.7x) suspended in the ceiling of the aviary 2.38m directly above the center

of the grid and wired to a VCR and TV outside the testing aviary. Trials began when at

least five birds were on the grid, and lasted 20 min or until more than one bird left the grid

for more than 3 min, whichever came first. Each flock was given two days to habituate to

the aviary and underwent two trials per day for two days. Fifteen randomly chosen wells

containing 15 seeds each were assigned to each trial number, so all flocks on the first trial

experienced the same distribution, and so on for subsequent trials. Each flock, however,

experienced each distribution only once.

Image capture and measurement

Individual video frames were captured at 10s intervals using the "Videoblaster SE100"

capture board and *Digital Video Producer* software. Frames containing feeding events,

defined as three or more birds in a radial formation with their heads at the vertex, and

those containing fewer than five birds on the grid were excluded from the analysis. Birds

in flight in the image (determined by blurry wing-shapes on either side of the bird or by a

bird appearing several times larger than its conspecifics) were omitted from the

measurements.

I measured, in pixels, the area and perimeter of the smallest polygon that enclosed

all individuals (Krause 1994a), the average distance between individuals in the flock, and,

for fixed flocks only, the distances from the marked producer and scrounger to the center

of gravity of the flock (average of all birds' X and Y coordinates) using custom-written

software. Numerical output was converted from pixel measurements to cm using the

conversion factor 42px = 30cm, determined by UTHSC's *Image Tool* shareware. I also

measured the duration of each trial.

Data manipulation and statistical analyses

In case birds follow an unknown landing rule that governed the spatial positions they

choose when landing upon the grid, which may bias spatial measurements, I divided the

trials arbitrarily into an early portion, the first two minutes of a trial, and a late portion, the

remainder of the trial. This procedure should separate the effect of a hypothetical landing

rule from geometric effects due to the proportion of scrounging. I compared the area of

the flock, the perimeter, and the average inter-individual distance between fixed and labile

flocks in the two trial portions separately using one-tailed independent-samples t-tests. I

then compared the three geometric parameters between trial portions within flock types

using paired t-tests. The effect of flock type on the distances from the center to the

marked individuals was evaluated with a paired t-test. To describe the approximate shape

of the flock, I determined the minimum area for a given perimeter (that of a circle) and

divided the area associated with that perimeter by this minimum to give an "index of

longness." The lower the index of longness (closer to 1), the more circular the group

becomes; the higher the index, the more linear.

RESULTS

Between trials, the birds tended to perch on the wire connecting the camera to

the VCR housed outside the aviary. At the start of a trial, the birds landed on the grid

within a few seconds of each other. Image capture in about half the trials (21/43) began

with five birds on the grid; the other half started with six birds present. Producers quickly began pushing lids upon landing on the grid. Gaps in the records of foraging trials occurred when all birds left the grid but returned within 3.5 min; trials had on average 3.1 ± 3.1 gaps, lasting 25 ± 19 sec. Trials lasted a mean of 10min 25 sec ± 4 min 21 sec, in which an average of 11.8 ± 3.7 patches (79%) were discovered. The number of images captured for each trial varied from 17-100, and the current analysis is based on a total of 2149 images (251 frames of 2400 were rejected, either because they depicted feeding events or because fewer than 5 birds were on the grid). Twice, both times in a flock's first trial, an untrained bird started to push lids. One of these birds was replaced using a subject from the colony and the first trial was rerun. In the other case the subject pushed lids so insistently and consistently that it was marked as a producer. The previously marked producer, which was never observed to push lids once the untrained bird began to do so, was unmarked and treated as an untrained bird.

The mean area (0.438 m^2) covered by the flocks as they foraged on the grid was, on average, 18% (range 13-29%) of the total area (2.4 m^2) of the grid itself. Producers were found to forage an average of 4.8 cm farther from the geometric center of the flock than scroungers (49.8 ± 3.7 cm vs. 45.0 ± 3.1 cm; t_5=2.678, p=0.022). Labile flocks were not significantly more or less elongated than fixed flocks (1.32 ± 0.02 vs. 1.31 ± 0.03, p=0.491). Labile flocks were larger in all three geometric parameters later in the trials compared to earlier, but fixed flocks were not different early compared to late in the trials (Table 1). Labile flocks were also significantly larger than fixed flocks later in the trials, but not in earlier (Table 1), although differences were always in the predicted direction.

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Although the variances of all three geometric parameters were larger in the labile flocks compared to the fixed, these differences were not significant.

DISCUSSION

My results support both predictions of Barta's geometric model of social foraging. First, groups in which producing is common are more spread out than groups in which scrounging is common. Second, producers are farther from the group's center, on average, than scroungers. In fixed flocks, the producer was consistently farther from the center of the flock than a randomly chosen scrounger. This result also indicates that scroungers did not gather around the producer while it was foraging, but that the producer was always farther from the scroungers than they were from each other. It is possible that the more compact nature of the flock was simply due to the five scroungers following one producer around the grid; however, if this were the case, the index of longness would show more elongated flocks in the fixed condition. I found no significant difference between the longness of the flocks between the conditions, so scroungers were not simply queueing behind the producer. The different location of the producer relative to the marked scrounger supports the idea that the use of the producing and scrounging foraging tactics are associated with different spacing rules.

My results differ from those of the simulation in that the geometric effects are more pronounced later in the trial compared to earlier. Three factors present in my experiments which were absent in the simulation are changing hunger levels and the ability of foragers to alternate tactics.

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Birds were relatively close to each other in the early portions of the trials. As time passed, the birds in the labile flocks spread out more, but those in the fixed flocks did not as much. The initial aggregated nature of the flock could be due to two equally plausible factors, either operating separately or together. First, birds may have a specific behavioral rule that governs the spatial position they choose when landing, either alone or joining others already present on the substrate. Antipredatory selective pressures may favor birds that land either in the middle of an open area if no others are present, or close to others if they are. Second, birds in the labile flocks may increase their proportional use of the producer tactic as time passes, possibly due to increasing energetic requirements if their needs are not met by the food they find. Birds in fixed flocks, although they may also have been experiencing increasing energetic requirements, could not switch foraging tactics because they were constrained by their training or lack thereof. Both these explanations can account for the flocks being more compact at the start of a trial; however, if only the landing rule were in effect, then both labile and fixed flocks would spread out over time. The landing rule may govern birds' starting positions on the grid, but is unlikely to affect their geometry throughout the trial. Only the latter explanation can account for the difference in geometry between labile and fixed flocks that was seen toward the end of the trial. Possibly both are occurring: the landing rule affects where birds locate themselves upon arriving on the grid, and then the proportions of producing and scrounging become the major predictor of flock geometry.

The model also assumes a constant patch number throughout foraging bouts (Barta et al 1997). This is not feasible experimentally, because patches become scarcer as

they are found and depleted. The effect of declining patch numbers on the birds' use of

producer and scrounger is unclear. Rate maximizing models predict no effect of patch

encounter rate on tactic use (Vickery et al 1991, Giraldeau & Livoreil 1998). As

individuals' expectations of the numbers of patches remaining drops, risk-sensitive models

predict that they will tend to favor scrounging (Caraco & Giraldeau 1991, Koops &

Giraldeau 1991). According to such a model, as the birds find and deplete patches, they

should increase their scrounging effort. In fact, I observed that labile flocks, capable of

switching tactics, spread out over the course of the trial, an observation that is consistent

with increased producing effort, not increased scrounging.

The simulation compared flocks of all producers to flocks in which both producers

and scroungers were present. I could not constrain trained spice finches to play only

producer. Instead, I compared flocks containing six trained birds, in which we expected

low levels of scrounging, to flocks containing one trained and five untrained birds, in

which high scrounging levels were expected.

Trained producers were able to push lids to find food, but they were not forced to

do so since they could switch to scrounging at any time. Individuals in the labile flocks

were therefore free to play either producer or scrounger and could alternate between

tactics at any time. Hence, the potential number of producers varied between treatments

from one in the fixed flocks to six in the labile flocks. I would expect to observe the

maximum difference in geometry between labile and fixed flocks when labile flocks

averaged a producer-to-scrounger (p:s) ratio of 6:0. On the other hand, if labile flocks

happened to forage at an average p:s ratio of 1:5, no difference in geometry would have

been expected between the flocks since they would have a similar p:s ratio. The actual p:s ratio in the labile flocks is unknown. However, because a difference in geometry was detected between the flock types, I predict on the basis of Barta's model that the labile flocks must have been foraging at an average p:s ratio greater than 1:5. If birds could have been restricted to playing only producer, as they were in Barta et al's simulation, then the difference in geometry between the conditions would likely have been larger than what I found here.

Hypothetically, if both types of flock were foraging at the same 1:5 p:s ratio, then a difference detected in geometry between them must be due to some inherent property of the flocks that differs between treatments. The experiment compares flocks of individuals that can change their foraging tactic to flocks of individuals that cannot. Although the results of my experiments support the predictions of Barta et al's model, it is possible that the difference in geometry that I attribute to a difference in producing and scrounging activity between the flock types is in actuality simply due to the difference in tactic lability between them. To determine a more direct relationship between scrounging activity and geometry, it is necessary to compare the geometry of flocks that differ in their producing and scrounging tendencies but are identical in their ability to alternate foraging tactics: this is the object of the next experiment.

The effect of labile producer-scrounger roles on flock geometry

For this experiment, I changed the flocks' investment in producing and scrounging by altering food distributions. An earlier study with spice finches showed that an individual's allocation to one tactic or the other can be modulated by changing the patchiness conditions of the food (Giraldeau & Livoreil 1998). They found that as food became more patchy (fewer patches, more seeds per patch), birds increased their proportional use of scrounger. Their study used three patchiness conditions: low, medium, and high. In this experiment, I used low and high patchiness conditions, identical to Giraldeau & Livoreil's conditions, to change birds' investment in the scrounger tactic.

In contrast to the first experiment, here individuals were symmetric in terms of their ability to choose either foraging tactic. I again measured flock geometry, but for this experiment I also measured the actual proportions of producing and scrounging occurring in the flocks, to make a direct link between flock geometry and scrounging activity. In addition, to determine an individual's investment in each foraging tactic, I measure both their attempts to and their successes in procuring food using a given tactic. This is in contrast to some previous studies (Barnard & Sibly 1981, Koops 1993, Giraldeau & Livoreil 1998) that measured only the proportion of food obtained using a given tactic, a measure that can be affected by the food distribution provided. By including attempts, I have a more complete picture of their allotment to each tactic.

METHODS

Food distribution and flock training

Two patchiness conditions were provided: dispersed (5 seeds in each of 40 randomly chosen wells), and clumped (20 seeds in each of 10 randomly located wells). All wells were filled with rat bedding (Heat-treated Beta Chip Laboratory Bedding, Northeastern Products Corp, Warrensburg NY); if they also contained food, the seeds were hidden under the bedding. Flocks were trained to expect a given patchiness condition by exposing them to that seed distribution for three consecutive days at a rate of 3-4 trials per day. Half the flocks were first trained to expect the dispersed condition, the other half to expect the clumped condition.

Flock formation and testing

Thirty-six birds were randomly assigned to six flocks of six each. Trained flocks were moved to the test aviary and their foraging observed for three consecutive days at a rate of seven trials per day. Unbeknownst to the birds, one of these trials had no food present on the grid; this trial was videotaped and could be any of the second to sixth trials. It began when the sixth bird landed on the grid and ended when fewer than five birds were on the grid for more than 60s. At the start of a trial, I encouraged birds that did not immediately (within 20-30s) join conspecifics on the grid by either waving a notebook (21.5 x 28.0cm) at them from a distance of about a meter, or by moving their perch about gently. Images were captured from the videotape at 5s intervals. Because the grid contained no food during these videotaped trials, the birds quickly lost interest and either sat motionless on the grid or flew to the perch, so that only the first 2min of the trial were used, providing a

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total of 24 video frames per trial.

For the other six trials, a focal animal was observed from a 72 x 135 x 56cm hide constructed of wood, black plastic sheeting, and cloth. The side of the hide facing the grid was a transparent fiberglass sheet covered with mirrored auto-glass tint. A different focal bird was observed in each trial. Focal trials began when the focal bird and at least three other birds were on the grid, and lasted 7min. The timer was stopped when the focal bird left the grid for more than 5s.

Each occurrence of the following events was recorded:

- producing event-a bird is the first to peck at a well and eats (evidenced by mandibulation). A peck is defined as a rapid downward movement of the head toward the well, resulting in beak contact with the bedding and usually its displacement;

- scrounging event-a bird is not the first to peck at a well and eats at least one seed;

- producing attempt- as producing event, but no eating is observed;

- scrounging attempt- as scrounging event, but no eating is observed.

A producing or scrounging event pertained to pecks at a single well. Pecks directed at different wells were noted as distinct events. If the bird then pecked at the previous well, it was again considered a new event. In this way, a bird could actually scrounge part of its own discovery. In cases where it was questionable whether the focal bird pecked first or not (i.e. simultaneous pecks), nothing was recorded. In cases where it was questionable whether the bird was eating seed or mandibulating beta chips, nothing was recorded.

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Data manipulation and statistical analysis

The total numbers of attempts at and events of producing and scrounging were calculated for each bird and then the numbers for each bird were averaged to give means for each flock. Producing and scrounging "effort" was calculated as the sum of events and attempts for producing and scrounging, and was considered a measure of investment in each tactic. I converted the total attempts, events, and effort into proportions by dividing the number of scrounging records of one type by the total number of producing and scrounging records of that type. I normalized the distribution of proportions using the arcsine-root transformation and performed two-tailed paired t-tests on the transformed data. The activity levels of individual birds were compared between days using repeated-measures ANOVA and between conditions using a paired t-test on 3-day averages. Because the hypothesis makes directional predictions, one-tailed paired t-tests were used to compare the geometric parameters.

RESULTS

Technical problems caused the first experimental flock to be tested three times under the same condition. After this flock had been tested under one condition, I added producing and scrounging attempts to the recording protocol, and so retested the flock under the same condition with the new behavioral recording protocol. Following that second test, a bird died; I replaced it, retrained the flock, and retested it under that same condition. One more bird died after the first condition; it too was replaced, but this time the flock was tested on the next condition. The geometry of this flock and its behavior did

not show any significant differences from other flocks so it was included in the analysis.

At the beginning of a trial, four to six birds landed on the grid shortly after being encouraged to do so, in contrast to the previous experiment in which no encouragement was necessary. Some individuals stopped searching after 2-5 min and stood stationary on the grid, mandibulating pieces of the beta chips. This happened in 11 of 216 trials, predominantly in the dispersed condition (9 of these 11 trials). Several times (20/216 trials) birds left the grid before the 7-min trial was finished, and could not be encouraged to return. These trials were included in the analysis because the amount of time the birds spent on the grid was close to 7 min (average 5 min 45 s ± 52 s).

A total of 864 images are included in the geometric analysis. The mean area (0.359 m^2) covered by the flocks as they foraged on the grid was, on average, 15% (range 10-19%) of the total area of the grid itself. Producing effort was considerably greater than scrounging effort in both conditions; however, the food distribution significantly affected the producing and scrounging effort of the birds. When food was dispersed, proportional scrounging effort, scrounging events and scrounging attempts were lower (Table 2), than when food was clumped. When food was dispersed, an average of 0.47 of 6 birds were scrounging, whereas when food was clumped, the average was 1.50 of 6. Flocks did not differ in their levels of activity from day to day (F=1.178, p_2=0.356) or between conditions, (paired t_5=1.085, p=0.328), nor were they more elongated in one condition than the other (t=1.127, p=0.311). When scrounging effort is plotted against the values of geometric parameters for each flock, four of the six flocks exhibited a decrease in the geometric parameters as their scrounging effort increased (Fig 1). One flock (flock 6, Fig

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1) showed only a weak response, while another (flock 3, Fig 1) actually experienced the reverse response, increasing in size with higher proportions of scrounging effort. As a whole, flocks showed a significant decrease in geometric parameters from dispersed to clumped food distributions (Table 3).

DISCUSSION

The goal of this second experiment was to measure flock geometry while varying the flocks' ratio of producers to scroungers, using flocks in which individuals had equal opportunity to alternate between foraging tactics. I changed the p:s ratio between treatments by using different food distributions. The proportion of producing was in fact higher when food was dispersed, as was found by Giraldeau & Livoreil (1998), so the flocks should have been more spread out in the dispersed seed condition compared to the clumped. Such a difference indicates that flocks do indeed spread out when individuals produce more, and shrink when individuals scrounge more, confirming the geometric prediction of Barta et al's simulation model. Producers could not determine simply by looking whether wells contained food or not, and thus had to probe the well. Similarly, scroungers were unlikely to be able to tell whether producers were pecking at seeds or bedding. The presence of bedding therefore likely increased the number of unsuccessful attempts at both producing and scrounging as well as lengthening the time necessary to find seed-containing patches, thus encouraging the birds to higher levels of total activity than would be present in a condition with no bedding. The activity levels of individual birds varied over the three-day testing period and between food distributions, making the

total numbers of producing records or scrounging records between conditions incomparable. Instead, I compared the proportions of attempts, events, and effort devoted to each tactic.

It is important to note that the significant differences in flock geometry reported here were measured over only the two minutes of observation following the birds' arrival on the grid. During the same time span, no geometric effect could be detected in the first experiment. Hence, the geometric effects measured here are likely conservative estimates of the effects that would have been observed had the flocks searched the grid for longer than two minutes.

GENERAL DISCUSSION

The values of all the geometric parameters of the second experiment are smaller than those in the early portions of the first experiment's trials. This could be due to a variety of factors that promote less dispersed foragers in the second experiment. In the second experiment, I observed producing and scrounging activity from a blind adjacent to the foraging grid. Although I was not in the hut at the time of the videotaping, birds could have become accustomed to avoiding the hut when they were searching. This would have reduced the size of the birds' effective foraging area, thus causing them to become more aggregated on the portion of the grid they used. Also, the birds had to contend with 198 cardboard well covers in the first experiment which were absent in the second. If for any reason the birds avoided standing on unstable well covers, then restricting themselves to the space between covers may have caused them to spread out more, since the foraging surface was more cluttered than in the second experiment. Finally, the shorter but more numerous daily trials necessary to sample focal animals in the second experiment may have had an unexplained effect on the geometry of the flocks. In essence, the differences in geometric parameters are absolutely comparable within experiments; however, a comparison of geometry between experiments may not be valid due to the many differences between the methods used in the experiments.

The results of the current study confirm a relationship between the frequency of scrounging occurring in a group and the group's geometry. Flocks are more spread out when individuals are producing more, and they become more compact as the frequency of scrounging increases. Producers tend to forage on the periphery of the group, avoiding

others, while scroungers prefer the center, where they can minimize the time required to reach producers. These results demonstrate that the producing and scrounging tactics are associated with specific rules governing an individual's spatial position relative to others. This association has ramifications for the likelihood of a symmetric producer-scrounger game, the effect of dominance on within-group positioning, and vigilance within groups. Each of these issues will be addressed in turn.

The symmetric producer-scrounger game assumes that players have equal phenotypes, so that in any given condition, a tactic will provide the same costs and benefits to all individuals adopting it. Hence, in the symmetric game, for a given food distribution, an individual's choice of tactic is dependent only on the proportion of others using the same tactic. My results show an association between individuals' tactic choice and their spatial position; however, the direction of the causality relationship between them is unknown. Possibly, an individual will note its position and choose its foraging tactic accordingly; if it finds itself on the periphery, it plays producer, and vice versa. This would mean that the tactic used by an individual is conditional, governed by a simple behavioral rule: when on the periphery, play producer; when in the center, play scrounger. Alternately, an individual may choose to play a given tactic and then relocate to a position that maximizes the returns for that tactic; if it chooses producer, it then moves to the periphery, and vice versa. The results are consistent with both of these explanations.

If the spatial position of individuals determines their foraging tactic, then spatial position becomes an asymmetry in what could otherwise appear to be a symmetric producer-scrounger game. A spatially explicit asymmetric model, similar to Barta &

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Giraldeau's (1998) phenotype-limited producer-scrounger model, would likely have more predictive power and possibly greater generality in this case.

If individuals indeed change positions when they switch foraging tactics, then tactic alteration may present a cost in terms of foraging time lost while changing positions. Vickery et al (1991) predict that when individuals experience a cost of changing foraging tactics, they should switch less frequently, and hence specialize in one tactic or the other. This could be done by either not changing tactics at all, and using one exclusively, or by changing tactics less frequently and hence using longer bouts of each tactic before switching. In experiment 2, where individuals' producing and scrounging tendencies were measured, there was no evidence of specialization, i.e. all individuals changed their allocation to each tactic when the food distribution changed. Since I did not record a sequence of behavioral events, it is unknown whether individuals used longer bouts of each tactic. More work is needed to determine the direction of the causality relationship between the frequency of scrounging in a group and the group's geometry.

Dominant individuals have been shown to scrounge from subordinates' discoveries (Baker et al 1991, Rohwer & Ewald 1981, Czikeli 1983, Theimer 1987). Dominants have also been shown to prefer the center of foraging groups (Hall & Fedigan 1997, Janson 1990a & b, Robinson 1981). This preference has been attributed to the relative safety from predation of the center of a group (Hamilton 1971). Barta et al concluded that scroungers do best when occupying central positions within groups. My results confirm that scroungers tend to be more centrally located, suggesting that the center might give dominants foraging advantages, in addition to the safety the position confers. In

circumstances where the center of a group is not the safest position, (e.g. when greatest safety is provided by cover located outside the group) then dominants tend either to occupy the most predator-safe positions, regardless of their foraging payoffs (Schneider 1984, Ekman & Askenmo 1984, Ekman 1987, Desrochers 1989, Slotow & Rothstein 1995), or to oscillate between predator-safe locations and those with high foraging payoffs (Romey 1990, Suhonen et al 1993). When predation is not a factor, dominants should position themselves so as to maximize foraging returns (Black & Owen 1989) and my results suggest that if they scrounge this will be the central positions within the group.

If scroungers require vigilance to detect scrounging opportunities, as suggested by Ranta et al. (1998) and Giraldeau et al (MS), then scroungers being centrally located should imply more vigilance activity in the center than in the periphery of groups. Vigilance will be higher in the center of the group than on the edge, because center individuals will be vigilant both to search for scrounging opportunities and to scan for predators, and so consequently have no reason to look down. Conversely, peripheral individuals will be vigilant only for predators, and hence alternate between head-up scanning and head-down searching (Giraldeau et al MS). Most studies to date have found that group foraging individuals located on the edge are more vigilant than those located in the center (Jennings & Evans 1980, Inglis & Lazarus 1981, Keys & Dugatkin 1987, Petit & Bildstein 1990). It is worth noting that none of these studies report any scrounging in the group. In that case center-edge differences in vigilance may be expected from the asymmetry in predation hazards associated with an individual's position within the group. It is possible that studies of vigilance in foraging groups in which scrounging is common

will find that center-edge differences in vigilance either disappear or are reversed.

The frequency of scrounging in a foraging group does indeed affect the geometry of the group, supporting the predictions of Barta et al's simulation model, that flocks in which scrounging is common are more compact than flocks in which producing is common, and that producers are, on average, further from the center of the group than scroungers. Consideration of the spatial position of individuals can affect studies of group foraging in three ways: it can introduce an asymmetry into the otherwise symmetric producer-scrounger game; it can attract to the center of the group socially dominant individuals that scrounge from subordinates' discoveries, and it can change the expected amounts of vigilance between the center and the edge of the group. I suggest that future studies of social foraging should look further into the spatial characteristics of groups and of the individual animals that comprise them.

EVIDENCE OF ADJUSTABLE PRODUCER-SCROUNGER INVESTMENT

A number of previous studies have explored the extent to which the producing and scrounging tactic investments are flexible within individuals (Barnard & Sibly 1981; Giraldeau et al 1990, 1994; Koops & Giraldeau 1996; Beauchamp et al 1997; Giraldeau & Livoreil 1998). The usual method used to determine investment is to measure the relative proportion of successful producing and scrounging events for a given food distribution (Barnard & Sibly 1981, Koops & Giraldeau 1996, Beauchamp et al 1997, Giraldeau & Livoreil 1998). To date, only Barnard & Sibly (1981) report a fixed p-s investment; all other studies, all in spice finches, suggest the ability to alter investment in each tactic. The method of measuring investment, however, does not always fully account for either individuals' unsuccessful attempts or any variation in the animal's total activity levels. The proportion of successful events can be an accurate measure of an individual's investment only when a reward is procured each time a given tactic is used. This will happen under two conditions: (1) the number of patches is very large or functionally infinite, so that individuals will not find all the available patches within an experimental period. If all patches have been found, but foragers are still searching, then the investment in the tactic is still there but the payoff is not, and so the group's investment in either tactic is much larger than is indicated by its success; (2) the number of food items available to scroungers (total food items in a patch less the finder's share, Vickery et al 1991) is larger or equal to the number of scroungers in the group. When the scroungers' share is less than the number of individuals that attempt to scrounge, then some individuals will not be recorded to have scrounged, and the proportional investment in the scrounger tactic will be

underestimated. Both these conditions are dependent on the food distribution available, and so at least part of the earlier-noted ability to alter investment in producer and scrounger tactics may have been an unavoidable by-product of changing the food distribution, and not necessarily a change in the animals' behavior. Effort (the sum of attempts and successes for each tactic) is a more useful measure of an individual's investment in a given tactic, because it is independent of the food distribution. It takes changes in both events and attempts into account to calculate an individual's total investment, successful or not, in a given foraging tactic. The conclusions of Barnard & Sibly (1981), Giraldeau et al 1994, and Koops & Giraldeau (1996) are not affected by this problem, because they satisfy the above conditions or have modified individuals' scrounging frequencies while keeping a constant food distribution. Giraldeau & Livoreil (1998), however, determine investment for three different food distributions as the number of producing and scrounging events for five-bird flocks. Their measure of scrounging investment in the low clumpiness distribution (5 seeds in each of 40 wells) may be too low. They report an average producer's proportion of 0.30 of each patch, or about 1.5 seeds. This leaves 3.5 seeds on average for up to four scroungers, so if all flock members excluding the producer of that patch try to scrounge from it (four birds), at least one will get no food. Because of this, I believe scrounging effort may have been underestimated in this condition.

Given that past experiments that have used food distribution to control individuals' investment in producing and scrounging may have been affected by this distribution artifact in an unquantified way, I suggest that my results provide the first experimental

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evidence that flock-foraging birds can alter their investment in producing and scrounging tactics in response to changes in food distribution. Future studies should utilize effort rather than success alone to avoid the confounding effects of distribution.

In conclusion, the current study provides experimental evidence that individuals' choice of foraging tactic exerts an influence on the geometry of a group of foragers. While the evidence so far is limited to ground-feeding birds, which adopt an essentially two-dimensional group structure, future studies should document whether such geometric foraging rules also apply to other animals, especially those such as schools of fish or flocks of swallows that adopt a more three-dimensional foraging group.

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Table 1. The area, perimeter, and average inter-individual distance of flocks of spice finches (*L. Punctulata*). Fixed flocks contain one trained producer and five untrained scroungers. Labile flocks contain six trained producers that can also scrounge. Comparisons are between early and late portions of the trials using two-tailed paired t-tests and between labile and fixed flocks using one-tailed independent-samples t-tests.

AREA (cm^2)

	Early	Late	Significance between trial portions
Labile	4292.0 ± 1097.0	5908.3 ± 1406.8	t=6.581 p=0.001
Fixed	3505.1 ± 576.6	4285.6 ± 590.2	t=2.303 p=0.070
Significance between flock types	t=1.555 p=0.076	t=2.605 p=0.013	

PERIMETER (cm)

	Early	Late	Significance between trial portions
Labile	299.6 ± 36.6	363.3 ± 38.7	t=8.743
			p=0.0003
Fixed	274.6 ± 29.0	305.5 ± 22.5	t=2.444
			p=0.058
Significance between flock	t=1.312 p=0.110	t=3.167 p=0.005	

AVERAGE DISTANCE BETWEEN INDIVIDUALS (cm)

	Early	Late	Significance between trial portions
Labile	70.8 ± 10.4	86.0 ± 9.6	t=7.384
			p=0.001
Fixed	63.1 ± 8.0	70.5 ± 5.8	t=2.282
			p=0.071
Significance between flock types	t=1.444 p=0.090	t=3.407 p=0.004	

Table 2. Three measures of the mean (± SD) proportions of scrounging by six captive flocks of six spice finches (*L. punctulata*) each foraging on dispersed and clumped food distributions. The significance of the difference in the proportions of scrounging between food distributions is based on two-tailed paired t-tests performed on the arcsine-square-root transformations of the proportions. The power of the test=1.0 in all cases.

	Dispersed	Clumped	Significance
Events	0.16 ± 0.06	0.73 ± 0.05	t_5=13.734; p<0.0001
Attempts	0.06 ± 0.02	0.13 ± 0.03	t_5=9.172; p<0.0003
Effort	0.07 ± 0.01	0.20 ± 0.05	t_5=10.893; p<0.0002

Table 3. The means (± SD) of the area of the flock, the perimeter (peri), and the average inter-individual distance (avgdist) for six flocks of spice finches (*Lonchura punctulata*) foraging in dispersed and clumped food distributions. Paired t-tests are one-tailed.

	Dispersed	Clumped	Significance	Power of test
Area (cm^2)	3947.0 ± 523.5	3236.2 ± 762.1	$t_5=2.535$	0.70
			$p=0.026$	
Peri(cm)	243.2 ± 24.1	224.7 ± 29.9	$t_5=2.051$	0.55
			$p=0.048$	
Avgdist (cm)	54.9 ± 5.3	50.3 ± 7.1	$t_5=2.390$	0.66
			$p=0.031$	

Fig 1. Relationships between the perimeter of the flock (cm), its area (cm^2), and the average inter-individual distance (cm) and the proportion of scrounging in flocks foraging in two food distributions. Points on the left ends of the lines represent the dispersed distribution; those on the right ends represent the clumped. Numbers are the designations of the flocks.