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Experimental evidence that group foragers can converge on predicted  
producer-scrounger equilibria

Kieron Mottley

A Thesis

In

The Department

of

Biology

Presented in Partial Fulfilment of the Requirements  
for the Degree of Master of Science at  
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## ABSTRACT

### Experimental evidence that group foragers can converge on predicted producer-scrounger equilibria

Kieron Mottley

When foraging together, animals are often observed to feed from food discoveries of others. The producer-scrounger game predicts how frequently this phenomenon of food parasitism should occur. The game has two major requirements: (i) all individuals must either produce, meaning they invest time and/or energy getting resources, or scrounge, meaning they try to get resources from producers, and (ii) the payoffs received from the scrounger tactic must be highly negatively frequency-dependent such that they do better than producers when rare, but worse when common. This study provides the first experimental support for the use of the producer-scrounger game in group foraging contexts. A total of five flocks of spice finches (*Lonchura punctulata*) were used on two experiments. Payoffs were measured by feeding rate (seeds/s) in two feeding conditions. In all cases, payoffs to scroungers were found to be highly negatively frequency-dependent on the frequency of scrounging. All functions were linear ( $p < .05$ ). In the second part of experiment 2, birds adopted the predicted producer or scrounger foraging tactics over a series of trials lasting 16 days (eight consecutive per feeding condition). In both experiments, individuals in the flocks also demonstrated plasticity in tactic used. Future studies should look at testing the performance of different learning rules using a similar experimental design.

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## INTRODUCTION

### **Parasitic Foraging**

Whenever animals forage in groups there are usually individuals within these groups that parasitically exploit food items others have obtained. This behavior usually results in a number of costs and benefits (see Barnard and Thompson 1985 for a review; also Pitcher 1986, Lott 1991). According to Barnard (1984), these types of parasitic interactions (previously termed *local enhancement* [Thorpe 1956], *area copying* [Krebs et al. 1972], *social facilitation* [Curio 1976], *joining* [Lefebvre 1986; Giraldeau and Lefebvre 1986], *robbing* [Kushlan 1978; Ens et al. 1990], *piracy* [Hatch 1973, Vollrath 1984], etc., but in this study referred to as *scrounging*) are widespread forms of exploitation both within and between species, and have been reported in mammals (Packer and Ruttan 1988; Kruuk 1972), birds (see Brockmann and Barnard 1979 for a review), fish (Pitcher 1986), invertebrates (Vollrath 1984), and humans (Smith 1981). However, despite the prevalent nature of these interactions, behavioral ecologists have not been able to demonstrate that the economics of parasitic foraging can be applied in a group foraging context. This study will be the first attempt to accomplish this by testing whether the major requirements of the producer-scrounger (PS) game can be met in foraging flocks of birds.

### **The Producer-Scrounger (PS) Game**

The PS game was formalised by Barnard and Sibly in 1981 from game theory. In this theoretical approach, individuals play games against each other for the purpose of winning a reward (see Maynard Smith 1982). There are several types of games, usually broadly

characterised into two groups: contests and scrambles. Contests are games between only two individuals. Scrambles (also called  $n$ -player games) are games between three or more individuals. Within these two categories, the games can be further subdivided according to the number of strategic options open to each individual. Alternate-option games occur when there are only two available options than can be played. Following this terminology, PS games are classified as alternative-option scrambles (Parker 1984). Game theory assumes that the payoff an individual receives from performing a behaviour is dependent on the frequency of individuals performing that behaviour (such cases are termed *frequency-dependent* [Parker 1984]).

The PS game has been applied in non-foraging systems (e.g. to account for kleptogamist male red deer [*Cervus elaphus*] [Clutton-Brock et al. 1979]). However, the game has since been developed into frequency-dependent foraging models (Vickery et al. 1991; Ranta et al. 1996). The currency of fitness used by these models is the long-term net rate of food intake (commonly used by rate-maximizing foraging models [e.g. Charnov 1976; Cuthill et al. 1990; Kacelnik 1984; Vickery et al. 1991]), but at least one stochastic version of the game uses survival probability as a currency of fitness (Caraco and Giraldeau 1991).

Studies have used the PS game to explain parasitic foraging behavior in house sparrows (*Passer domesticus*, Barnard and Sibly 1981), bald eagles (*Haliaeetus leucocephalus*, Hansen 1986), pigeons (*Columba livia*, Giraldeau and Lefebvre 1986), zebra finches (*Poephila guttata*, Giraldeau et al. 1990), and spice finches (*Lonchura punctulata*, Giraldeau et al. 1994; Giraldeau and Livoreil 1998; see also Giraldeau and Beauchamp 1998 for a review).

Two major requirements must be met whenever frequency-dependent models of this game are applied. First, all individuals must either *produce*, meaning they invest time

and/or energy getting resources, or *scrounge*, meaning they try to get resources from producers. This assumed inability of individuals to simultaneously produce and scrounge is termed *complete incompatibility* (West-Eberhard 1989; Field 1989; Ens et al. 1990; see Vickery et al. 1991 for a full description of possible types of compatibility). Secondly, the payoffs received from the scrounger behaviour must be highly negatively frequency-dependent on the frequency of individuals playing scrounger in the group such that when the frequency of scroungers is high, scroungers tend to receive a lower payoff than producers but, when the frequency is low, scroungers tend to receive a higher payoff than producers. This frequency-dependence should result in some stable equilibrium frequency (SEF) of scrounging where both alternatives obtain the same payoff (Fig. 1). The SEF is stable because, while a rare scrounger alternative will spread in a group, at some frequency of scroungers the fitness of both alternatives will be equal (Parker 1984). It is usually assumed that the scrounger would benefit from reduced energy expenditures by not having to search for feeding opportunities. In the game, no assumptions are made about the relationship of the producers' payoffs to their frequency in a group, although Giraldeau et al. (1994) showed the producers' payoffs were less affected by scrounger frequency than the scroungers' payoffs.

### **Producer-Scrounger Strategies**

PS games assume that individuals use foraging *strategies*, which are genetically based programs that express specific behavioral phenotypes (Gross 1996). *Producing* and *scrounging* are *tactics* comprising these phenotypes. Strategies become stable in a group when they cannot be replaced by rare alternatives (Parker 1984). The group reaches this stability either

through natural selection (e.g. Brockmann et al. 1979, Hori 1993, Sinervo and Lively 1996) or learning (Dawkins 1980). There are three types of strategies: pure, mixed and conditional. Pure strategies result in individuals performing unique tactics (i.e. “*Do producing*” or “*Do scrounging*”). Mixed strategies result in individuals performing many tactics at varying randomly chosen probabilities (i.e. “*Do producing with probability  $P(A)$ , do scrounging with probability  $P(B)$* ”). When an individual’s constraints (e.g. size, ability to perform a behavior, strength, etc.) have an effect on the probability of a tactic being performed, then the individual uses a conditional strategy (e.g. “*If small then do producing with probability  $P(A)$ , if large then do scrounging with probability  $P(B)$* ”).

### **Group Foraging as a PS Game**

Hansen (1986) claimed his study on the foraging behaviour of bald eagles (*Haliaeetus leucocephalus*) was the first to test and, therefore, meet the major requirements of the PS game. He noted that these eagles often engaged in contests with each other over chum salmon (*Oncorhynchus keta*) carcasses, and applied the PS game to 467 such parasitic interactions. However, his results were only based on pairwise interactions between these birds making it unclear whether the PS game was the best method to use. Hawk-Dove contests, a two-player alternative to the PS game, may have been a better choice. Such confusion over the application of game theory illustrates the importance of knowing the number of individuals affecting the payoff an individual obtains from a given tactic. Also, the degree of compatibility between the producer tactic (*pursue live prey or carrion that is unclaimed by a conspecific*) and the scrounger tactics (e.g. *fly towards feeder and descend upon it with feet and talons outstretched*) in his study is uncertain.

Despite the fact that the producer-scrounger game has long been argued to apply to situations of flock foraging, there is little evidence that the frequency-dependence of the scroungers' payoffs exists or that groups of foragers can reach the SEF. Giraldeau et al. (1994) used flocks of spice finches to explore this frequency-dependence assumption. They showed that the scroungers' payoffs were affected by their frequency in a group in a manner similar to that of the PS game. They trained 24 spice finches to remove covers off wells in order to obtain the seeds contained therein. Another 24 finches were kept naive. Only the trained lid-lifting birds could produce so the other 24 naive birds had to scrounge in order to obtain seeds.

The birds foraged in flocks of 6 of which 4 were referred to as the core birds (i.e. the same individuals were used throughout). The behavior of individuals in the core flock was not noted; it was only the behavior of the 5th and 6th individuals (the test birds- a producer and a scrounger) that was recorded. The test birds were placed in two core flock types, flock P (4 core producers) and flock S (4 core scroungers). In all, the behavior of 20 producer and 20 scrounger test birds added in pairs to the core P and S flocks were observed. Four major results were obtained: (i) producers obtained a higher food intake rate than scroungers in both flock types with scroungers lowering the intake rate of the producers throughout, (ii) scroungers had a significantly lower foraging rate in flock S than in flock P so their payoff appeared to be negatively frequency dependent, (iii) the producer's food intake was less sensitive than scroungers' intake rate to changes in the proportion of scroungers, and (iv) the food intake of scroungers was not greater than the producers in flock P. The final result was unexpected since the PS game requires that when scroungers are rare they should do better than producers. One reason given for this inconsistency was that simultaneous



discoveries of food patches by producers, when they were common, reduced the scroungers' ability to exploit the resources discovered as effectively. More likely, however, is the possibility that the producers refused to accept lower payoffs from specializing as producers and spontaneously increased their amount of scrounging (producers spontaneously scrounged 35.4% of their patches). Thus, the experimenters never observed producers with lower payoffs than scroungers (Fig. 2). Because no way has since been found to prevent producers from opportunistically playing scrounger, it has not been possible to test the game using foraging flocks of these birds.

### **Objectives of Study**

In this thesis I test whether the major requirements of the PS game can be met in a group foraging context. This is made feasible by the development of an experimental apparatus that successfully prevents a bird from performing more than one tactic during a trial. A result of this partitioning of tactic use should be the creation of a situation of complete incompatibility between producer and scrounger alternatives. In this situation, I have complete control over the birds' use of tactics. Using the apparatus I obtained the payoffs of producers and scroungers for all possible scrounger frequencies for a given flock size. At low frequencies of scroungers, producers should do worse than scroungers, while at high frequencies producers should do better than scroungers. This relative difference in payoffs resulting from tactic use should be due to the high negative frequency-dependence of the scroungers' payoff on their frequency in the flock. There should also be some frequency of scroungers at which both producers and scroungers obtain the same payoff (i.e. the SEF).

In Experiments 1 & 2, *Measuring the frequency-dependence of producer and scrounger payoffs*, I

generated producer and scrounger payoff functions for flocks of six birds over an entire range of scrounger frequencies, demonstrated the effect scrounger frequency has on these functions, and estimated the SEF values for each flock. This was done in two environmental conditions. For experiment 2, each condition led to a different SEF value for each flock. In Experiments 1& 2, *Equilibrium under free choice*, I remove the constraint on tactic use and observe the proportion of scrounging individuals at the stable equilibrium. For experiment 2, I also test the flocks to see whether they would adjust their scrounger frequency to reach the previously determined SEF values specific to each flock and condition. Evidence of this adjustment both within and between conditions would suggest that some form of learning may be taking place by individuals in the flocks.

## GENERAL METHODS

### Subjects

Spice finches (*Lonchura punctulata*) are native to India, China, and the south-eastern corridor of Asia. They are small (14g), sexually monomorphic, social, granivorous birds that naturally forage in flocks without noticeable aggression (Immelmann 1982). Natural habitats include various types of open or semi-open country containing bushes, trees, shrubs, or secondary forests containing grassy patches. In these habitats, they feed largely on grass seeds that are taken from the ground or from growing plants (Goodwin 1982). Spice finches are ideal animals with which to conduct these experiments. They are rarely aggressive and do not exhibit a stable feeding dominance hierarchy, thus reducing the differences in access to food among individuals (Giraldeau et al. 1990). They can also be taught producing behaviour such as pulling on string-like objects in order to obtain a seed reward (Ennis 1992). The birds

used were purchased as juveniles from a commercial supplier, and were over 1 year old at the time of the experiment, and of undetermined sex. When not used in trials they were housed in flocks of 6 in common 59(length) x 32(width) x 46cm(height) cages made of galvanised wire mesh and kept on a 12:12 L:D cycle at 27 degrees Celsius ( $\pm 2$  degrees). They were fed *ad libitum* on a mixture of white and red millet seeds and offered *ad libitum* water. Each bird was marked with a unique combination of two coloured leg bands. In addition, the tail and neck feathers of each individual were coloured with acrylic paint to allow individual identification from a distance.

### **Apparatus**

The purpose of the experimental apparatus is to constrain subjects to act as either producers or scroungers in order to manipulate the frequency of each tactic within any given foraging flock. The apparatus consisted of a 273(length) x 102(width) x 104cm(height) indoor cage with a producer and a scrounger compartment divided by a series of 22 patches of which every second one was a food patch (i.e. contained seeds) (Fig. 3).

Each patch consisted of a seed container with an attached string that prevented the seeds from falling out (Fig. 4). Once the string was pulled, the seeds fell into a 2 x 2cm square collecting dish located just below the container where they remained available until eaten. Since the strings were available only from the producer compartment, each food patch could only be produced by a bird within it. Birds in the scrounger compartment had access only to the collecting dish and hence could only scrounge within it. Scrounging in the producer compartment was prevented by forcing birds to sit on narrow perches that could seat only one bird at a time, in order to have access to the string and collecting dish. When a

perch was occupied, no other bird could feed from that patch. When measuring the frequency-dependence of scrounger payoffs an opaque barrier prevented birds from moving between the producer and scrounger compartment. When testing for the SEF the barrier was removed to allow birds to move from one compartment to the other.

### **Training**

Spice finches were first trained to feed from the patches before experimentation began. They were placed in individual 29.5(length) x 32(width) x 46cm(height) cages, and were taught to recognise experimental patches and pull the string to obtain a seed reward by a series of shaping trials. This was done by first gluing seeds to the string, enticing the birds to peck at it, and ultimately resulting in the string falling out, releasing the seeds from the seed container. Eventually, birds were presented with strings without attached seeds. Training lasted until each bird consistently approached the experimental patch, pulled the string, and ate the seed reward within 30 s of presentation of the food patch, 10 consecutive times. To familiarise the birds with the experimental apparatus, a pair was placed in the producer compartment and a pair in the scrounger compartment and allowed to search for food 6 times per day in both compartments for a period of five days. Each pair was placed in the producer compartment for three trials then in the scrounger compartment for the other three. Scrounging behaviour appears spontaneously in these birds (Giraldeau et al. 1990, 1994) and consists of simply watching for another to find food, then going over and eating from the discovered patch. All together, patch recognition, string pulling and apparatus familiarisation took 21 to 28 days per bird.

## EXPERIMENT 1

This experiment is divided into two parts. In the first, the frequency-dependence of producer and scrounger payoffs was measured for a complete range of scrounger frequencies in flocks of six individuals. In the second, individuals in the same flocks were tested to see what proportion of scrounging they adopt at the SEF estimated from the payoff functions measured in the same foraging condition. Both parts of the experiment were run under two food conditions: high and low patch qualities. In the high patch quality condition, every other food container had 10-20 seeds while in the low patch quality condition, food containers had only one to five seeds.

### **Measuring the frequency dependence of producer and scrounger payoffs**

Twelve adults were haphazardly selected from a group of 30 birds, divided into two flocks of six, and trained as described above. Subjects were deprived of food for 18-20 h (six to eight hours + overnight) in order to ensure they would actively search for food once released into the apparatus. Because these birds store food in their crops, long deprivation periods are required. Experiments were conducted 6 h before darkness and the birds allowed to feed *ad libitum* for the last 2 h before darkness. The experiments were timed in order to take advantage of the observed main feeding bout that occurred at the end of their photoperiod. Both flocks had 2 h of trials per day in the apparatus with between 3 to 6 trials performed per hour. Birds were placed in a holding cage before being released into the apparatus. The flocks were tested alternately each hour. A barrier between the producer and scrounger compartments prevented movement between compartments.

The producing tactic for these experiments was defined as searching (hopping from

patch to patch with the head moving from side to side) for patches with strings and the scrounging tactic as searching for discovered patches. Preliminary trials showed that the birds quickly depleted the patches and that the time spent searching for food decreased with the total number of seeds available at each patch. A trial ended 60 s after a producer landed on a perch in the low quality patch condition, and after 100 s in the high quality patch condition. I used focal animal sampling and a different focal individual was followed on each trial. The order of focal sampling was haphazardly selected each day based on the initial distribution of birds upon entering the apparatus. This was done by simply allowing birds to fly spontaneously from the holding cage into one of the compartments. Since not all birds leave the cage at once it is possible to move the cage into the other compartment so that the birds remaining in the cage fly into the other compartment. A random order of sampling was not used to minimise the amount of handling of the birds. At the end of a trial, the birds were guided back into their holding cage until the next trial, which occurred 15-20 min later. I recorded the total number of seeds eaten by the focal bird during the trial through a one-way mirror located at one end of the apparatus. A seed was counted as eaten when a bird, having pecked at the collecting dish, mandibulated and dropped a seed husk. Trials in which the focal bird sang, preened or slept were discarded.

All possible scrounger frequencies for a flock of 6 were tested and the feeding rate for each individual for every frequency was calculated in separate trials. For each trial, a different frequency of birds in each compartment was used yielding 7 distinct scrounger frequencies per flock that was tested (6P:0S, 1P:5S, 2P:4S, 3P:3S, 4P:2S, 5P:1S). 0P:6S was used as a control for the effectiveness of the experimental apparatus to partition the tactics. Each bird was tested in both compartments at every scrounger frequency resulting in a total of

132 trials for the two flocks. The experiment lasted 14 days with each flock tested independently.

The total number of seeds eaten during a trial divided by the duration of the trial gave individual food intake rates. The average food intake rates of the six flock members were used to calculate the mean rate of seed intake per scrounger frequency per tactic. The effects of scrounger frequency, tactic of focal bird, and patch quality on rate of seed intake were analysed using linear regression to determine the extent of payoff frequency-dependence and the SEF if one existed.

### **Equilibrium under free choice**

Flocks were tested in the apparatus much as described above. In this case, however, the barrier preventing birds from moving from one compartment to the other was removed so that the birds could freely move between compartments. During each trial I recorded a focal bird's rate of seed intake as well as the compartment from which it was foraging at five second intervals. I also noted the flock's distribution between compartments at five second intervals using scan sampling. Six trials/flock/day were conducted. All individuals began three trials in the scrounger compartment, and three trials in the producer compartment. By alternating between compartments in this way, individuals in the flocks were set at a default scrounging frequency of 50% (when averaged over two consecutive days). Every bird in the flock was tested once each day. In the low patch quality condition, the trials lasted 60 s starting from the time the focal bird took its first seed or 60 s after the birds had been released into the apparatus, whichever came first. The same procedure was used for 100s trials in the high patch quality condition. An individual's rate of seed intake, use of foraging

tactic, and the flock's use of foraging tactics were calculated using this trial duration. Trials were conducted for six consecutive days in the high patch quality condition. In the low patch quality condition, the flocks were tested over ten days in which the first two allowed birds to adjust to the possibility of moving between compartments. Pure strategists are defined as individuals adopting either 100% or 0% scrounging at the end of these test periods.

## RESULTS

### **Measuring the frequency-dependence of producer and scrounger payoffs**

A total of 12 spice finches in two flocks were observed in a total of 264 trials. All birds released into the experimental apparatus were observed to start searching for food immediately at the onset of each trial. Birds released in the scrounger compartment never produced a patch, so scroungers obtained their food exclusively by scrounging. Similarly, producers obtained all their food by producing and no displacements from discovered patches were observed among these individuals. The birds actively searched for food in the apparatus for the whole trial, before usually becoming stationary within it after the end of the trial period. Trials in which the focal bird sang, preened or slept occurred only rarely.

Tests of nonlinearity for all payoff functions generated p values not less than 0.3. Thus all functions are assumed linear with no curvilinear model providing a significantly better fit. For both flocks and both patch qualities the results of linear regressions were consistent. In all instances, increasing the scrounger frequency resulted in a significantly decreased feeding rate of scroungers (all scrounger payoff functions' slopes' significantly non-zero,  $p < .01$ ,



Table 1) but had no significant effect on the feeding rate of individuals playing producer (all producer payoff functions not significantly different from zero,  $p > .05$ , Table 1) (Fig. 5). When the frequency of scroungers was low, scroungers had higher feeding rates than producers, especially in the high quality patches. As would be expected, individuals on average had higher feeding rates in the high patch quality than the low patch quality.

SEF ranges for the two flocks in both conditions were calculated by taking the mean of the intersection points for the producing and scrounging functions of each individual bird. The subsequent 95% confidence interval generated for these means became the SEF ranges (Table 2). Paired-sample t-tests for Flock A ( $t = -0.185$ ,  $df = 5$ ,  $p = .860$ ) and Flock B ( $t = -0.197$ ,  $df = 5$ ,  $p = .852$ ) indicated that SEF values between conditions for both flocks are not significantly different from each other. All SEF ranges contain the default scrounger frequency of 50% scrounging.

### **Equilibrium under free choice**

A total of 12 spice finches in two flocks were observed in a total of 192 trials. Birds searched for food either in the producer or scrounger compartments during a trial. Switching between compartments was rare, occurred largely at the start of each trial, and involved flying from one compartment to the next. The time spent flying across the apparatus was negligible ( $< 1$  s) compared to the trial length (60 or 100 s).

Values of individual tactic use over the test period of days are shown in Figs. 6 & 7. These data are based on the average of each individual's use of scrounging over two consecutive days in which each bird began trials once as a producer and once as a scrounger. Eleven out of a possible 24 adjustment periods ended with individuals adopting a

pure strategy (i.e. 100% scrounging or 0% scrounging).

The standard error of the mean scrounging frequency of a flock within a day declined over the days of the trial for both flocks in the high quality patch condition (both slopes significantly negative,  $p$  values  $<.05$  for test of slope  $\neq 0$ , Fig. 8). However, no such decline was observed for the flocks in the low quality patch condition (Flock A has a slight positive slope [ $p=.037$  for the same test] and Flock B has a slope not different from zero [ $p=.79$ ] Fig. 8).

## DISCUSSION

The results of the experiment clearly reveal a strong negative frequency-dependence of scrounger payoff on scrounger frequency. However, the producer payoffs were consistently less affected by the scrounger frequency than the scrounger's payoffs, providing support for Giraldeau et al.'s (1994) observation. Also, changing patch quality did not affect the SEF values obtained, providing support for Hansen's (1986) observation. This finding is contrary to Vickery et al.'s (1991) model, which predicts different SEFs when patch quality changes. In cases where patch quality is poor, producers may obtain a disproportionately larger number of food items from each than scroungers, resulting in scroungers receiving lower payoffs for the entire range of possible scrounger frequencies in the group. This should result in a SEF value containing fewer scroungers than in conditions where patch quality is good. In this experiment, both tactics overall received lower payoffs in the low patch quality condition, but the producer's payoffs appeared to be as equally affected as the scroungers. This may be due to the scrounger's ability to reach produced patches quickly

and successfully defend these patches by blocking the producer's (and any other scroungers') access to the food items. Also, the model assumes an environment of unlimited patches with larger search times than patch exploitation times. My apparatus is a patch-limiting environment with variation between patch search and exploitation times. The depletion of patches during a trial should not affect the predicted result, but variation between search and exploitation times could act as a confounding factor.

A cost/benefit analysis in great egrets (*Casmerodius albus*) revealed that scrounging offered less reward than other foraging tactics when food was abundant (Kushlan 1978). Both Kushlan (1978) and Stalmaster and Gessaman (1984) concluded that scrounging may be adaptive when food is scarce but is suboptimal at other times. Their definition of abundance, though, may be based on the number of patches available rather than the number of food items contained within each patch. In cases where there are many producing opportunities but few food items at each one, it may be more profitable for individuals to produce rather than obtain a minimal number of food items at discovered patches.

By looking at the variance in flock use of tactics (and therefore scrounger frequency) over days, it seems that while the variance decreases in the high quality patches, the low patches show no significant change. This may be due to the fact that variance in the low quality patch condition was already minimal to begin with. A possible cause of this low initial variance might be the preliminary two days allotted for individual adjustment to the possibility of moving between the compartments. The birds may have used this time period to cue in on the SEF resulting in a lowering of the variance in their use of tactic on days three and four.

Although the apparatus clearly generated the frequency-dependent payoffs expected of a producer-scrounger game, it still remained unclear whether individuals in the flocks could reach SEF values when given the freedom to choose tactics. This experiment was unable to test this because all SEF ranges already contain the default scrounger frequency of three scroungers set by the experimental design. In order to test the ability of individuals in a flock to reach the SEF, two distinct SEF values were required in order to eliminate the possibility that adjustments were being made by chance or by confounding factors specific to the apparatus (e.g. flock bias towards one compartment). Thus, the experiment was repeated, this time including a different method for generating and testing these SEFs.

## EXPERIMENT 2

Methods were as above except for the following. Instead of low and high patch qualities the two conditions in this experiment were: *uncovered* and *covered* patches. In the uncovered patches the collecting dish was left unchanged allowing equal access to the seeds by both producers and scroungers. In the covered patches, the collecting dish was partially covered by gluing half of another dish on the top of it at the scrounger end, thus restricting access to the dish by the scroungers without affecting the producer's access in any way. Each food container contained five to ten seeds.

### **Measuring the frequency-dependence of producer and scrounger payoffs**

Three flocks of six birds were formed from a new set of 32 birds that were haphazardly chosen from a main group of 78 birds. From these, only the 18 best string pullers were selected for the experiment. The food deprivation regimen was altered in order to reduce the amount of time birds went without food between daily experimental sessions.

Experimental subjects were food-deprived overnight then allowed to feed *ad libitum* for 80-100 min after the lights came on in the morning. Tests started five hours before darkness and the birds were allowed to feed *ad libitum* for the last two hours before darkness.

Between three to six trials in the apparatus per hour were conducted during the three hours of daily experimentation. Each trial lasted for 60 s starting when a bird first landed on the producing perch and corresponded to the time the birds spent actively searching for food in the apparatus.

During measurement of payoff functions each bird was tested in both compartments for each possible scrounger frequency resulting in a total of 198 trials for the three flocks. This experiment took 21 days and the three flocks were tested over the same time period but on different days.

### **Equilibrium under free choice**

The objectives and methods were the same as above except for the following. During each trial I recorded a focal bird's rate of seed intake as well as the compartment from which it was foraging at 10 s intervals. I also noted the flock's distribution between compartments at 10 s intervals using scan sampling. Six trials/flock/day were conducted balancing for the compartment into which the birds were released. Every bird in the flock was tested once

each day. The trials lasted 60 s starting from the time the focal bird took its first seed or 60 s after the birds have been released into the apparatus, whichever came first. An individual's rate of seed intake, use of foraging tactic, and the flock's use of foraging tactics were calculated using this trial duration. Trials were conducted for 18 consecutive days in which the first two days allowed birds to adjust to the possibility of moving between compartments. The next 16 days had the birds experience the covered-patch condition (eight days), followed by the uncovered-patch condition (the last eight days). Pure strategists are defined as individuals adopting either 100% or 0% scrounging at the end of these adjustment periods.

## RESULTS

### **Measuring the frequency-dependence of producer and scrounger payoffs**

Eighteen spice finches in three flocks were observed for a total of 396 trials. All birds released into the experimental apparatus behaved as in experiment 1.

Tests of nonlinearity for all payoff functions had  $p$  values not less than 0.3. Thus all functions are assumed linear with no curvilinear model providing a significantly better fit. For all flocks and both conditions the results of linear regression were consistent. In all instances, increasing the scrounger frequency resulted in a decreased feeding rate of scrounging individuals (all scrounger payoff functions' slopes significantly non-zero,  $p < .01$ , Table 3) but had little significant effect on the feeding rate of producing individuals (producer payoff functions not significantly different from zero, except Flock 2: Uncovered ( $p = .02$ ) and Flock 1: Covered ( $p = .03$ ) at  $p < .05$ , Table 3) (Fig. 9). Producers had a higher

feeding rate than scroungers when the frequency of scroungers was high.

SEF ranges were calculated as in experiment 1 (Table 4). Paired-sample t-tests for Flock 1 ( $t=-7.019$ ,  $df=5$ ,  $p=.001$ ), Flock 2 ( $t=-3.596$ ,  $df=5$ ,  $p=.016$ ), and Flock 3 ( $t=-3.134$ ,  $df=5$ ,  $p=.026$ ) indicate that the SEF values differ significantly between conditions for all.

### **Equilibrium under free choice**

Eighteen spice finches in three flocks were observed for a total of 324 trials. Birds searched for food as either producer or scrounger during a trial. Switching tactics within a trial was rare, observed to occur largely at the start of each trial, and was accomplished by flying from one side of the apparatus to the other. The time spent flying across the apparatus was negligible (<1s) compared to the trial length (60 s).

Values of individual tactic use over days of the adjustment period are shown in Fig. 10. These data are based on the average individual use of scrounging over two consecutive days in which the bird began trials once as a producer and once as a scrounger. Twenty-one out of a possible 36 adjustment periods ended with individuals adopting a pure strategy (i.e. 100% scrounging or 0% scrounging).

All three flocks adjusted their frequency of scrounging towards the expected SEF values (Fig. 11) (all flocks' frequency functions' [covered condition functions ranging from days one to eight; uncovered condition functions ranging from days nine to 16] slopes significantly non-zero,  $p<.05$ ; except Flock 1: Uncovered, Table 5). In all cases, flocks' frequency of scrounging was not significantly different from the corresponding SEF range at the end of the eight day adjustment period for both conditions (Table 6). The 95% confidence intervals calculated for all flocks on days eight and 16, indicated that all flocks'

frequencies on day eight were different from the default frequency of 50% scrounging. None of the flocks' frequencies, however, were different from the default frequency on day 16. The standard error of the mean scrounger frequency of a flock within a day declined over the course of the experiment for Flocks 2 and 3, but not Flock 1 (all slopes for Flocks 2 & 3 significantly negative while Flock 1 had p values of .52 and .62 for the uncovered and covered conditions respectively on the test slope  $\neq 0$ , Fig. 12).

## DISCUSSION

The results of this experiment confirm the strong negative frequency-dependence of scrounger payoff on scrounger frequency noted in experiment 1. Once again, the producer's payoffs were consistently less affected by the scrounger frequency than the scrounger's payoffs. Individuals within a flock seem to be able to adjust their use of the tactics such that the flock as a whole reaches the expected SEF values; a view strengthened by the fact that the flocks were able to discriminate between two significantly different SEF values. The flocks' ability to reach these two different SEF values indicates that use of producer and scrounger alternatives are not genetically fixed in these individuals.

Other than adjustment, flock scrounger frequencies during the 16-day test period can be attributed to two factors: random movements by individuals and flock bias towards one compartment. Observed flock frequencies over the first eight days rule out random movements, as all frequencies on day eight are different from the expected random default of 50% scrounging. Observed flock frequencies over the last eight days rule out the bias factor, as all frequencies on day 16 are not different from the expected random default.



From Fig. 12 we see that only in Flocks 2 & 3 do the birds appear to be cueing in on a specific scrounger frequency. The fact that the variance in these two flocks decreases over days nine to 16 of the adjustment period is further evidence that observed flock frequencies for this period are due to individual choice and not random movements. One reason why Flock 1 may not show a decrease in variance of scrounger frequency could be due to its already low variance at the start of the experiment.

## GENERAL DISCUSSION

This is the first study in which all major requirements of the PS game are explicitly met in a group foraging context. When the complete incompatibility constraint is approximated in these contexts, *(i)* a high negative frequency-dependence of the scrounger's payoff on the frequency of scrounging occurs, *(ii)* scroungers when rare do better than producers, but do worse when common, and *(iii)* a frequency of scrounging exists where both producers and scroungers receive equal payoffs (the SEF). Barnard and Sibly's (1981) experiment with house sparrows showed fixed use of tactics with individuals not responding opportunistically to flock composition by switching between searching (producing) and interacting (scrounging) for food. Giraldeau et al. (1994) found opportunistic behaviour in spice finches but could not demonstrate the high negative frequency dependence of scrounger payoff on the number of individuals playing scrounger in their flocks. The current study demonstrates the high negative frequency dependence required for the PS game with experiment 2 also supporting the ability of individuals in a flock to adjust tactic

use in response to different SEF values. These adjustments indicate plasticity in these spice finches' use of tactic in the direction predicted by the PS game.

### **Producers' payoff function**

Although the game makes no prediction about the shape or effect of scrounger frequency on the producer's payoff curve, results indicate that this relationship in these flocks is linear with little or no significant effect. This *no effect* result provides support for Giraldeau et al.'s (1994) observation. When there are many producers, each patch discovered is shared with few scroungers. However, in the limiting environment of the apparatus there will be fewer patches available to be produced. On the other hand, with few producers and many producible patches, the increased patch sharing incurred by the numerous scroungers would also limit the producers' feeding rate. These two effects may have counterbalanced themselves across the entire scrounger frequency range, giving rise to the *no effect* result for the producer payoff. In no cases do the producer's payoff curve increase with increasing flock scrounging, indicating all observed PS relationships were parasitic in the current study.

### **Complete incompatibility assumption**

When applied as a frequency-dependent model, a basic requirement of the PS game is the assumption of complete incompatibility (West-Eberhard 1989; Field 1989; Ens et al. 1990). Studies that apply the PS game should at least demonstrate that this requirement is approximated (e.g. producing opportunities are rarely found when the scrounger tactic is used; see Vickery et al. 1991 for complete description of types of compatibility). To date, other studies using behaviour patterns identified as producer and scrounger tactics have

been complicated due to uncertainty about the degree of compatibility between the alternatives (e.g. Lavoie unpublished; Hansen 1986; Giraldeau et al. 1994; Giraldeau and Livoreil 1998).

Considerable evidence exists that there is at least some degree of incompatibility between foraging behaviours. The different techniques required to maximise efficiency on different foraging tasks (e.g. Persson [1985] where perch [*Percia fluviatilis*] could not capture two types of prey [a crustacean zooplankton {*Daphnia magna*} and the phantom midge {*Chaoborus obscuripus*}] equally well because opposing actions were required), combined with the costs of switching between tasks (Murdoch 1969), would probably result in decreased foraging efficiency if these techniques were used at the same time.

Incompatible tactic definitions based on spatial location such as the ones resulting from the producer and scrounger compartments used in this study are not new to game theory. Zooplankton were observed to migrate vertically to different depths in a water column in order to escape predation with *upper* and *lower* corresponding to different tactics (Gabriel and Thomas 1988). Vickery et al. 1991 also gave two examples of situations in which the physical displacement of individuals from areas where producing is likely to areas where scrounging is likely. In the first, birds flying at high altitudes would optimise their ability to scrounge, while they must fly lower if they wanted to produce. Similarly, an animal foraging in dense undergrowth may need to move to higher places to scan for scrounging opportunities effectively.

By basing tactic definition on spatial location either side of a central division, my apparatus' set-up may look like an environmental situation that would be used to test the Ideal Free Distribution (IFD). The IFD is another  $n$ -person alternative option game in

which foraging decisions are based on the distribution of  $n$  consumers over two alternatives (Parker 1984). PS games, however, are based on a different type of frequency-dependence (termed *compound* frequency-dependence [Giraldeau & Livoreil 1998]) in which, as scroungers replace producers, the payoff to scrounging is negatively affected in two ways. First, there are not as many producers discovering food patches, resulting in fewer exploitable food items at any given time. Second, there are more scrounger competitors with which to share each parasitised food patch. My apparatus demonstrates the type of frequency-dependence specific to PS games with the highly negative frequency-dependent result showing that the payoffs received from the scrounger tactic clearly depend not only on the number of individuals playing that tactic, but also on the number of individuals playing the producer tactic. For example, when there are no producers in the flock the scroungers' payoff is zero, and as individuals enter the scrounger compartment they effectively decrease the number of possible food items available to all individuals in that compartment. These are cases of compound frequency dependence, which differ from IFD games.

### **Individual use of strategy**

Giraldeau et al. (1990) showed that the dominance hierarchy of spice finches has no effect on the frequency of producing and scrounging performed by each individual. Hence, it is usually assumed that SEFs of spice finches are due to unconditional strategies with individuals receiving the same payoff regardless of the tactic used. Since the feeding rate of only one bird was measured per trial over all adjustment periods, this study is unable to determine whether conditional or unconditional strategies were in fact being used by the

spice finches. Follow-up trials could be done in which the feeding rate of every bird in the flock is measured six times per day of the adjustment period, resulting in 36 trials per flock per day. This will ensure an appropriate number of observations per bird per day.

Crawford (1989) indicated that dynamics between individuals in a group learning to adjust to the SEF are such that mixed-strategy equilibria are highly unstable. He states that pure-strategy configurations are the only possible stable outcomes of learning dynamics. In both experiments, analysis of individual tactic use indicates that only 52% of all individual scrounger frequencies after the adjustment periods can be attributed to pure strategies. However, 83% of birds in experiment 1 and 78% of birds in experiment 2 would adopt pure strategies after the adjustment periods in at least one condition if the pure strategist definition was relaxed to include individuals adopting  $>90\%$  scrounging or  $<10\%$  scrounging. It is interesting to note that in experiment 2, SEM values decreased significantly only in flocks and conditions that resulted in a high number of pure strategists ( $>70\%$  pure strategy adoption). This suggests an association between flock stability and choice of strategy. While it is not unexpected for SEM values to decrease as the flocks' mean scrounging frequency approaches zero (Figs. 11-12. Flocks 2 & 3: Covered Condition), the fact that SEM values also decrease when the flocks' mean scrounging frequency moves away from zero (Fig. 12. Flocks 2 & 3: Uncovered Condition) is a good indication that flock stability is a factor in the reduction of these values in my experiments. Follow-up trials may be needed using longer adjustment periods in order to be confident that flocks not only reach but also stabilise at the SEF. Until then, whether or not all the birds will adopt pure strategies in both conditions is unknown, and the pure strategy requirement of Crawford (1989) remains untested.

Experiment 2 indicated that individuals in a flock could adjust their proportion of tactic used to approximate that of different environmentally determined optima. This leads to the conclusion that all observed SEF values are due to learned strategies. In variable and unpredictable environmental contexts like my apparatus, where the SEF can change without notice, there is a clear advantage for individuals to adopt strategies through learning rather than receive them genetically. My findings support the concept that a group comprising individuals with a fixed proportion of tactic types could be invaded by individuals that change probabilities of using a tactic on the basis of environmental constraints (Davies 1982; Gardner et al. 1987). Giraldeau and Livoreil 1998 showed similar adjustments by individual spice finches towards SEF values predicted by Vickery et al.'s (1991) model. Milinski (1984) used the IFD to study the foraging behaviour of three-spined sticklebacks (*Gasterosteus aculeatus*) at two patches in a 48 (length) x 58.5 (width) x 19.5cm (height) aquarium, and found that increasing the speed at which his test subjects were switching between tactics decreased the likelihood of a early resolution to the SEF. This, he reasoned, was due to a reduction in the opportunities an individual would have of experiencing the SEF by chance and thus identifying it as the optimum. Since the spice finches switched very rarely in experiment 2 one might expect a quick arrival at the SEF. The eight days allotted in the experiment appears to have been a reasonable amount of time for this adjustment, compared to analogous IFD experiments like Milinski (1984) where animals reach the equilibrium distribution within minutes if not seconds. Whether or not eight days was sufficient time for stability in a PS game with spice finches remains unclear.

## **Future Studies**

Recent studies show that flock geometry is an important factor in the success of the scrounging tactic (Barta et al 1997; Flynn 1998). Scroungers will tend to occupy positions in the flock that would maximise their ability to find and quickly reach producing opportunities. This would increase their share of discovered food patches and allow them to occupy feeding positions with the best access to food items (in cases where there can be defendable patches). In my apparatus, however, the scroungers were unable to do this as an opaque division between the two sides prevented individuals from seeing what was occurring in the adjacent compartment. Similarly, producers were unable to determine which patches were furthest away from the scroungers. If a transparent division were used in follow-up experiments, it would be possible to test the effect the factors leading to observed flock geometry have on PS dynamics in this game.

The mechanism by which a group reaches the appropriate SEF resulting from learned strategies, is termed a *learning rule*. These rules are under selection pressure, so Evolutionarily Stable (ES) learning rules are ones that can bring a group to the SEF in a single generation (Harley 1981). The Relative Payoff Sum (RPS) learning rule was determined by Milinski (1984) to be the ES learning rule used by his fish. The fact that the birds in experiment 2 showed adjustment to appropriate SEF values is evidence they also have an ES learning rule. Which ones are the most likely candidates to approximate the one used by spice finches? Further studies would have to be done using my apparatus in environmental conditions where more switching occurs during trials. As well, all birds will have to be followed for each trial in order to measure every individual's sampling effort and scrounging frequency for each day of the adjustment period. Recent studies have shown

that the position of the head relative to the horizontal may give a good indication of the feeding tactic in use by a spice finch (Lavoie unpublished). One could imagine that if the requirement for switching were made as easy in my apparatus, individuals might be more ready to sample between the tactics. Other systems should also be tested to see if the results presented here are comparable to different conditions and species.

## CONCLUSION

I have shown that the major requirements of the PS game can be met in a group foraging context. Other studies have tried to test the PS game by attempting to meet these requirements but none have been successful. I have shown that there is a high negative frequency-dependence on the payoff obtained by the scroungers on the frequency of scrounging occurring in the flocks, while the producers' payoff can be much less affected. Also, if given the opportunity, individuals in a flock will converge towards the SEF. The speed at which they do this may depend on the amount of switching occurring in the flock and the ability of all individuals to make the appropriate adjustments. These results indicate that the rate of foraging is an appropriate currency of fitness, and that PS games, as well as parasitic foraging theory as a whole, can be a useful method to analyse decisions made within groups of animals that exploit sharable food. In any event, even when the frequency-dependence of payoffs is as complex as assumed by PS games, small granivorous birds appear capable of converging on the SEF. Whether other animals are capable of this remains to be shown.



## REFERENCES

- Barnard, C.J. 1984. *Producer and Scroungers: Strategies of Exploitation and Parasitism*, (C.J. Barnard ed.), New York, Chapman & Hall.
- Barnard, C.J. & Sibly, R.M. 1981. Producers and scroungers: a general model and its application to captive flocks of house sparrows. *Anim. Behav.* 29: 543-555.
- Barnard, C.J. and D. B. A. Thompson. 1985. *Gulls and Plovers: The Ecology and Behavior of Mixed-species Feeding Groups*. Croom Helm, London.
- Barta, Z., Flynn, R. & Giraldeau, L.-A. 1997. Geometry for a selfish foraging group: a genetic algorithm approach. *Proc. R. Soc. Lond. B.* 264: 1233-1238.
- Brockmann, J.H. and Bernard, C.J. 1979. Kleptoparasitism in birds. *Anim. Behav.* 27: 487-514.
- Brockmann, J.H., Grafen, A., and Dawkins, R. 1979. Evolutionarily stable nesting strategy in a digger wasp. *J. Theor. Biol.* 77, 473-496.
- Caraco, T. and Giraldeau, L.-A. 1991. Social foraging: Producing and scrounging in a stochastic environment. *J. Theor. Biol.* 153: 559-5
- Charnov, E.L., Orians, G.H. & Hyatt, K. 1976. The ecological implications of resource depression. *Am. Nat.* 110: 247-259.
- Clutton-Brock, T.H., Albon, S.D., Gibson, R.M. & Guinness, F.E. 1979. The logical stag: adaptive aspects of fighting in red deer (*Cervus elaphus* L.). *Anim. Behav.* 27: 211-225.
- Crawford, V.P. 1989. Learning and mixed-strategy equilibria in evolutionary games. *Jour. Theor. Biol.* 140: 537-550.
- Curio, E. 1976. *The Ethology of Predation*. New York, Springer-Verlag
- Cuthill, I.C., Kacelnik, A., Krebs, J.R., Haccou, P. & Iwasa, Y. 1990. Starlings exploiting

- patches: the effect of recent experience on foraging decisions. *Anim. Behav.* 40: 625-640.
- Davies, N.B. 1982. Behavior and competition for scarce resources. In: *Current problems in Sociobiology*, King's College Sociobiology Group, ed., pp. 363-380. New York: Cambridge University Press.
- Dawkins, R. 1980. Good strategy or evolutionarily stable strategy? Pages 331-367 In: (G. W. Barlow and S. Silverberg eds.) *Sociobiology: beyond nature/nature?* Boulder, Colorado, Westview Press.
- Ens, B.J., Esselink, P., and L. Zwarts. 1990. Kleptoparasitism as a problem of prey choice: a study of mudflat-feeding curlews, *Numenius arquata*. *Anim. Behav.* 39: 219-230.
- Ennis, N. 1992. Do flocks of specialists forage more efficiently than flocks of generalists: a test of the skill pool hypothesis using flocks of spice finches, *Lonchura punctulata*. Unpublished MSc thesis, Concordia University, Montreal.
- Field, J. 1989. Intraspecific parasitism and nesting success in the solitary wasp *Ammophila sabulosa*. *Behavior* 110: 23-46.
- Flynn, R. 1998. The frequency of scrounging by foraging spice finches affects their flock geometry. Unpublished MSc. Thesis, Concordia University, Montreal.
- Gabriel, W. & Thomas, B. 1998. Vertical migration of zooplankton as an evolutionarily stable strategy. *Am. Nat.* 132, 2:199-216.
- Gardner, R., Morris, M.R. & Nelson, C.E. 1987. Conditional evolutionarily stable strategies. *Anim. Behav.* 35: 507-517.
- Giraldeau, L.-A. & Beauchamp, G. 1998. Group foraging as a producer-scrounger game. *T.R.E.E.* in press.

- Giraldeau, L.-A., Hogan, J.A., Clinchy, M.J. 1990. The payoffs to producing and scrounging: what happens when patches are divisible? *Ethology* 85: 132-146.
- Giraldeau, L.-A. and Lefebvre, L. 1986. Exchangeable producer and scrounger roles in a captive flock of feral pigeons: a case of the skill pool effect. *Anim. Behav.* 34: 797-83
- Giraldeau, L.-A. & Livoreil, B. 1998. Game theory and social foraging. In: *Advances in game theory and the study of animal behavior*. Dugatkin and Reeve, eds. Oxford University Press.
- Giraldeau, L.-A., Soos, C., and Beauchamp, G. 1994. A test of the producer-scrounger foraging game in captive flocks of spice finches, *Lonchura punctulata*. *Behav. Ecol. Sociobiol.* 34: 251-256.
- Goodwin, D. 1982. *Estridid finches of the world*. Oxford University Press, Oxford.
- Gross, M.R. 1996. Alternative reproductive strategies and tactics: diversity within the sexes. *T.R.E.E.* 11: 92-97.
- Hansen, A. 1986. Fighting behavior in bald eagles: A test of game theory. *Ecology* 67: 787-797.
- Harley, C.B. 1981. Learning the evolutionarily stable strategy. *Jour. Theor. Biol.* 89: 611-633.
- Hatch, J.J. 1973. Predation and privacy by gulls at a ternery in Maine. *Auk* 87:244-254
- Hori, M. 1993. Frequency-dependent natural selection in the handedness of scale-eating cichlid fish. *Science* 260: 216-219.
- Immelmann, K. 1982. *Australian finches in bush and aviary*, 3rd. Angus and Robertson, London.
- Kacelnik, A. 1984. Central place foraging in starlings (*Sturnus vulgaris*). I. Patch residence

- time. *Jour. Anim. Ecol.* 53: 283-300.
- Krebs, J.R., MachRoberts, M.H. and J.M. Cullen. 1972. Flock and feeding in the great tit *Parus major*—an experimental study. *Ibis* 114: 507-530.
- Kruuk, H. 1972. *The spotted Hyena: a study of predation and social behaviour*. Chicago University Press, Chicago.
- Kushlan, J.A. 1978. Nonrigorous foraging by robbing egrets. *Ecology* 59: 649-653.
- Lavoie, M. Head orientation indicates the use of producer and scrounger tactics among seed-eating birds. unpublished
- Lefebvre, L. 1986. Cultural diffusion of a novel food-finding behavior in urban pigeons: an experimental field test. *Ethology* 71: 295-334.
- Lott, D.F. 1991. *Intraspecific variation in the social systems of wild vertebrates*. Cambridge: Cambridge University Press.
- Maynard Smith, J. 1982. *Evolution and the Theory of Games*. Cambridge University Press, Cambridge.
- Milinski, M. 1984. Competitive Resource Sharing: an experimental test of a learning rule for ESSs. *Anim. Behav.* 32: 233-242.
- Murdoch, W.W. 1969. Switching in general predators: experiments on predator specificity and stability of prey populations. *Ecol. Mono.* 39: 335-354.
- Packer, C. and Ruttan, L. 1988. The evolution of cooperative hunting. *Am. Nat.* 132: 159-198.
- Parker, G.A. 1984. Evolutionarily stable strategies. In: Krebs J.R., Davies N.B. (eds) *Behavioural ecology: an evolutionary approach*, 2nd edn. Sinauer, Sunderland, pp 30-61.

- Persson, L. 1985. Optimal foraging: the difficulty of exploiting different feeding strategies simultaneously. *Oecologia* 67:339-341.
- Pitcher, T.J. 1986. Functions of schooling behavior in teleost. Pages 294- 337, In: (T.J. Pitcher ed.), *The behavior of Teleost Fishes*. London, Croom Helm.
- Ranta, E., Peukhuri, N., Laurila, A., Rita, H. & Metcalfe, N.B. 1996. Producers, scroungers and foraging group structure. *Anim. Behav.* 51: 171-75.
- Sinervo, B. & Lively, C.M. 1996. The rock-paper-scissors game and the evolution of alternative male strategies. *Nature* 380: 240-243.
- Smith, E.A. 1981. The application of optimal foraging theory to the analysis of hunter-gatherer group size. In: *Hunter-gatherer foraging strategies* (Winterhalder, B. and Smith, E.A., eds.), pp36-65, Chicago University Press.
- Stalmaster, M.V. & Gessaman, J.A. 1984. Ecological energetics and foraging behavior of overwintering Bald Eagles. *Ecol. Mono.* 54: 407-428.
- Thorpe, B. 1956. *Learning and Instinct in Animals*. London, Methuen.
- Vickery, W.L., Giraldeau, L-A., Templeton, J.J., Kramer, D.L., and Chapman, C.A. 1991. Producers, scroungers, and group foraging. *Am. Nat.* 137: 847-863.
- Vollrath, F. 1984. Kleptobiotic interactions in invertebrates. Pages 61-94. In: (C.J. Barnard ed.), *Producers and Scroungers: Strategies of Exploitation and Parasitism*. New York, Chapman and Hall.
- West-Eberhard, M.J. 1989. Phenotypic plasticity and the origins of diversity. *Ann. Rev. of Ecol. Systematics* 20: 249-278.

**Table 1.** Slopes of producer and scrounger payoff functions for experiment 1 and their corresponding p values for the test, slope  $\neq 0$ .

	<u>Tactic</u>	<u>Condition</u>	<u>Slope</u>	<u>p value</u>
<b>Flock A</b>	Producer	High Patch Quality	-0.0121	0.0711
	Scrounger	High Patch Quality	-0.0675	0.0008
	Producer	Low Patch Quality	-0.00505	0.0639
	Scrounger	Low Patch Quality	-0.027	0.0035
<b>Flock B</b>	Producer	High Patch Quality	-0.00657	0.5175
	Scrounger	High Patch Quality	-0.0729	0.0018
	Producer	Low Patch Quality	0.00081	0.8233
	Scrounger	Low Patch Quality	-0.02976	0.0006

**Table 2.** Stable Equilibrium Frequency (SEF) ranges for Flocks A & B. Also indicated is whether there is a significant range overlap between both conditions for each flock ( $p < .05$ ).

	<u>High Patch Quality</u>	<u>Low Patch Quality</u>	<u>Range Overlap</u>
<b>Flock A</b>	7.4 to 1.2	7.3 to 2.0	Significant
<b>Flock B</b>	5.5 to 2.9	5.3 to 2.9	Significant

**Table 3.** Slopes of producer and scrounger payoff functions for experiment 2 and their corresponding p values for the test, slope  $\neq 0$ .

	<b>Tactic</b>	<b>Condition</b>	<b>Slope</b>	<b>p value</b>
<b>Flock 1</b>	Producer	Uncovered	-0.00667	0.1101
	Scrounger	Uncovered	-0.0673	0.0011
	Producer	Covered	-0.01152	0.0329
	Scrounger	Covered	-0.045	0.0007
<b>Flock 2</b>	Producer	Uncovered	-0.01895	0.0149
	Scrounger	Uncovered	-0.06914	0.0001
	Producer	Covered	-0.00195	0.3387
	Scrounger	Covered	-0.04005	0.0057
<b>Flock 3</b>	Producer	Uncovered	-0.00124	0.815
	Scrounger	Uncovered	-0.0581	0.0003
	Producer	Covered	-0.0029	0.7177
	Scrounger	Covered	-0.04505	0.0006



**Table 4.** Stable Equilibrium Frequency (SEF) ranges for Flocks 1-3. Also indicated is whether there is a significant range overlap between both conditions for each flock ( $p < .05$ ).

	<u>Uncovered Patches</u>	<u>Covered Patches</u>	<u>Range Overlap</u>
<b>Flock 1</b>	3.8 to 2.5	0.7 to -1.7	Non-significant
<b>Flock 2</b>	3.3 to 2.0	0.7 to -3.1	Non-significant
<b>Flock 3</b>	2.9 to 1.6	1.1 to -2.7	Non-significant

**Table 5.** Slopes of flock scrounger frequency adjustment functions for experiment 2 and their corresponding p values for the test, slope  $\neq 0$ .

	<b>Condition</b>	<b>Slope</b>	<b>p value</b>
<b>Flock 1</b>	Covered	-0.25079	0.0116
	Uncovered	0.07381	0.3197
<b>Flock 2</b>	Covered	-0.2937	0.0002
	Uncovered	0.1677	0.0016
<b>Flock 3</b>	Covered	-0.25595	0.0091
	Uncovered	0.099206	0.0456

**Table 6.** Aspin-Welch unequal-variance, two-tailed t-tests for whether flock scrounger frequencies on days eight and 16 are not significantly different from their respective SEF ranges.

	<u>Day</u>	<u>t value</u>	<u>p value</u>
<b>Flock 1</b>	8	-1.9139	0.088
	16	0.2820	0.784
<b>Flock 2</b>	8	-1.5499	0.180
	16	-0.9026	0.396
<b>Flock 3</b>	8	-1.8078	0.109
	16	-1.5680	0.149

## FIGURE CAPTIONS

**Figure 1.** The producer-scrouter game. At the equilibrium frequency of scrounging (SEF), both producers and scroungers receive equal payoffs.

**Figure 2.** Limitations of Giraldeau et al. (1994). The shaded region indicates the only sections of the producer and scrounger payoff functions they were able to generate.

**Figure 3.** View of the experimental apparatus as seen from above. Individuals can only search for patches containing strings on the producer side, and only search for discovered patches on the scrounger side. When calculating the producer and scrounger payoff functions a barrier between the sides prevented individuals from switching tactics during a trial.

**Figure 4.** Diagram of experimental food patch. Producers must land on the perch and pull the string in order to release the seeds from the food container. When approaching from the producer side, individuals can only feed after pulling the string. When approaching from the scrounger side, individuals can only feed after the string has been pulled. The arrow indicates the direction of the producing action.

**Figure 5.** Producer (solid lines) and scrounger (dashed lines) payoff functions for Flocks A & B. Error bars represent the standard error of the mean for each data point. These graphs show the high negative frequency-dependence of scrounger payoff on scrounger frequency.

**Figure 6a.** The percent scrounging of each bird in experiment 1: Flock A over six consecutive days in the high patch quality condition. Arrows indicate adoption of a pure strategy.

**Figure 6b.** The percent scrounging of each bird in experiment 1: Flock B over six consecutive days in the high patch quality condition. Arrows indicate adoption of a pure strategy. No data was obtainable for Birds C and E during day five.

**Figure 7a.** The percent scrounging of each bird in experiment 1: Flock A over eight consecutive days in the low patch quality condition. Arrows indicate adoption of a pure strategy.

**Figure 7b.** The percent scrounging of each bird in experiment 1: Flock B over eight consecutive days in the low patch quality condition. Arrows indicate adoption of a pure strategy.

**Figure 8.** Standard error of the mean values of flock scrounger frequencies over the adjustment periods for experiment 1. Only the high quality patch condition for both flocks show significant ( $p < .05$ ) negative slopes. This indicates that only for this condition do the birds become selective on the scrounger frequencies they choose.

**Figure 9.** Producer (solid lines) and scrounger (dashed lines) payoff functions for Flocks 1-3. Error bars represent the standard error of the mean for each data point. These graphs show the high negative frequency-dependence of scrounger payoff on scrounger frequency.

**Figure 10a.** The percent scrounging of each bird in experiment 2: Flock 1 over 16 consecutive days. Day 10 is the first measurement in the uncovered condition. Arrows indicate adoption of a pure strategy.

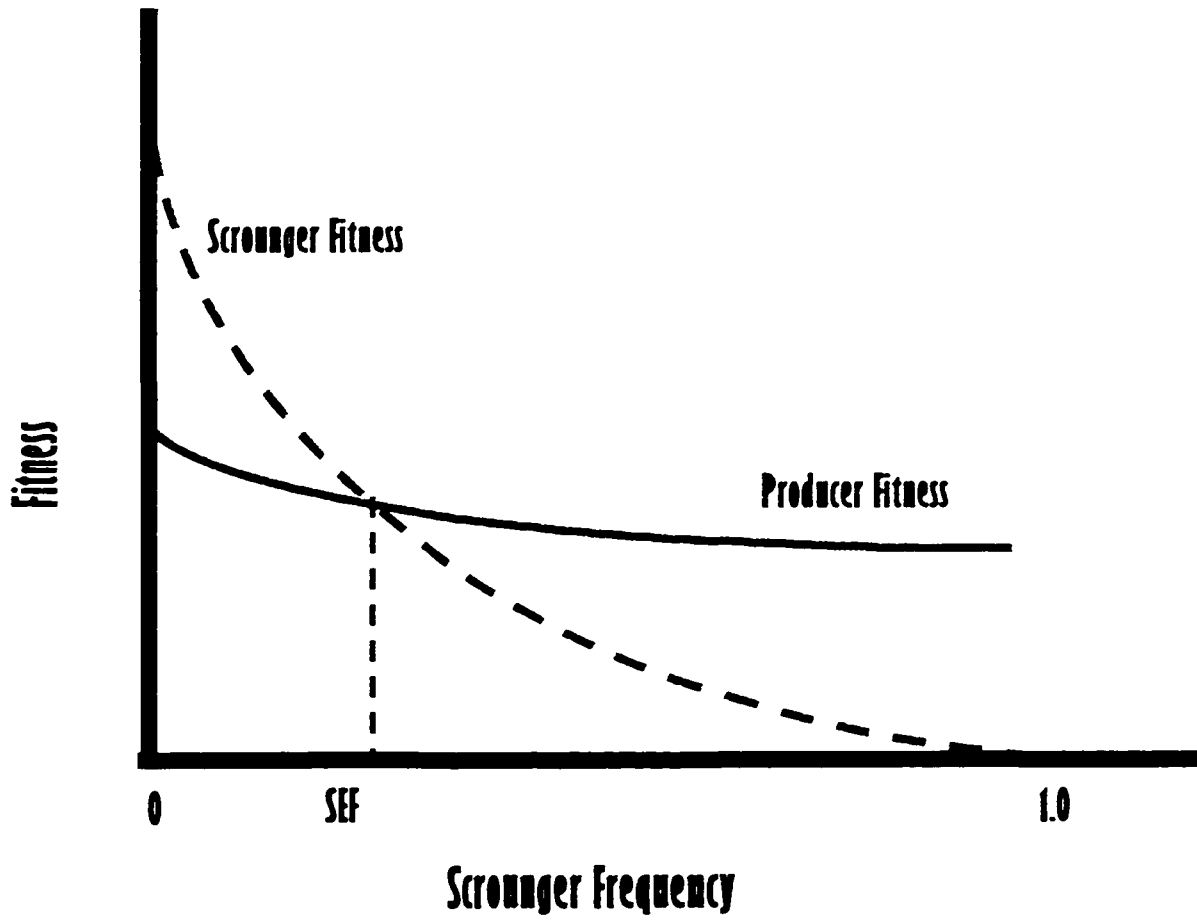
**Figure 10b.** The percent scrounging of each bird in experiment 2: Flock 2 over 16 consecutive days. Day 10 is the first measurement in the uncovered condition. Arrows indicate adoption of a pure strategy.

**Figure 10c.** The percent scrounging of each bird in experiment 2: Flock 3 over 16 consecutive days. Day 10 is the first measurement in the uncovered condition. Arrows indicate adoption of a pure strategy.

**Figure 11.** Scrounger frequency adjustment functions for experiment 2. All flocks are switched from the covered condition to the uncovered condition on day 9. The shaded regions represents the flocks' experimentally determined SEF ranges. Data points for days eight and 16 contain error bars representing the 95% confidence interval of each flock frequency mean.

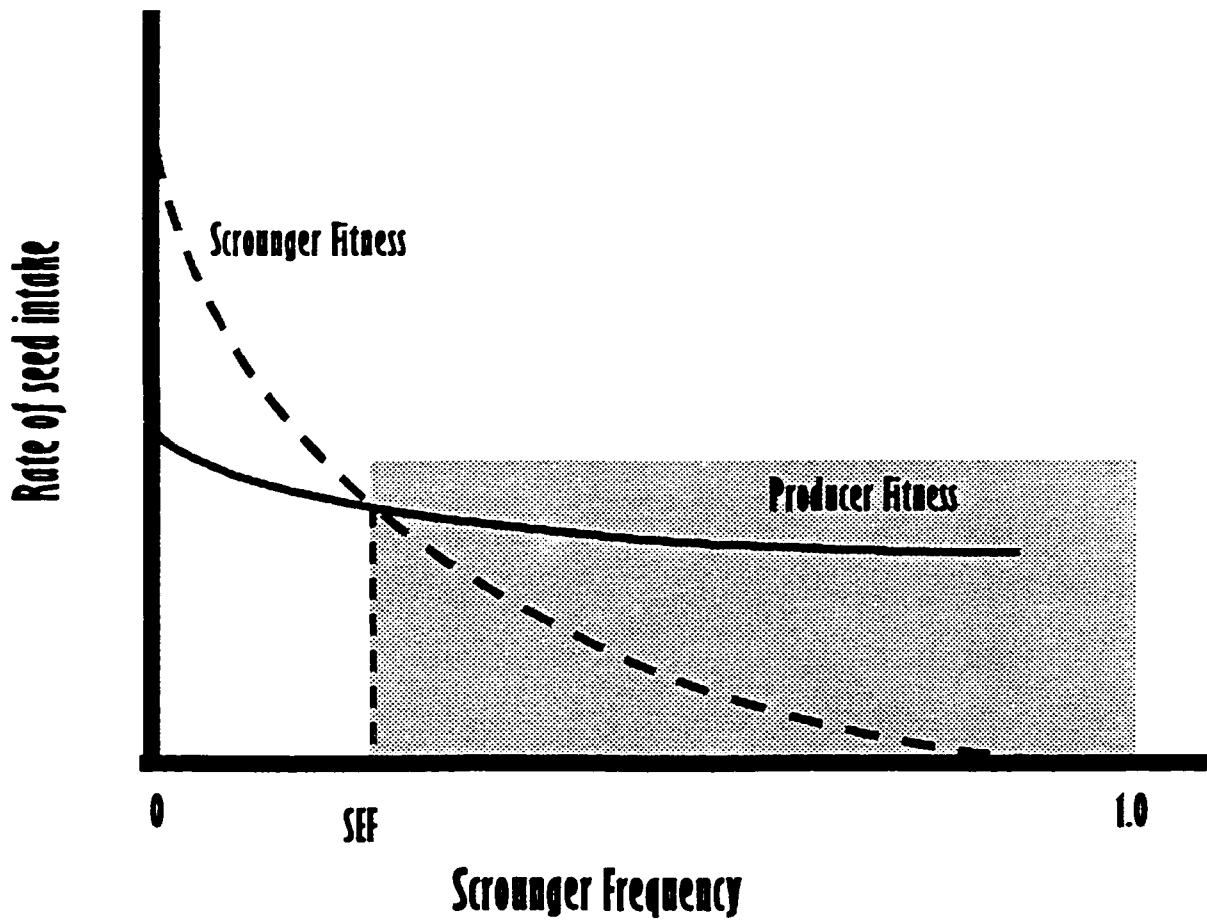
**Figure 12.** Standard error of the mean values of flock scrounger frequencies over the adjustment periods for experiment 2. Flocks 2 & 3 have significant ( $p < .05$ ) negative slopes indicating that the birds become much more selective on the scrounger frequencies they chose.

*Figure 1*

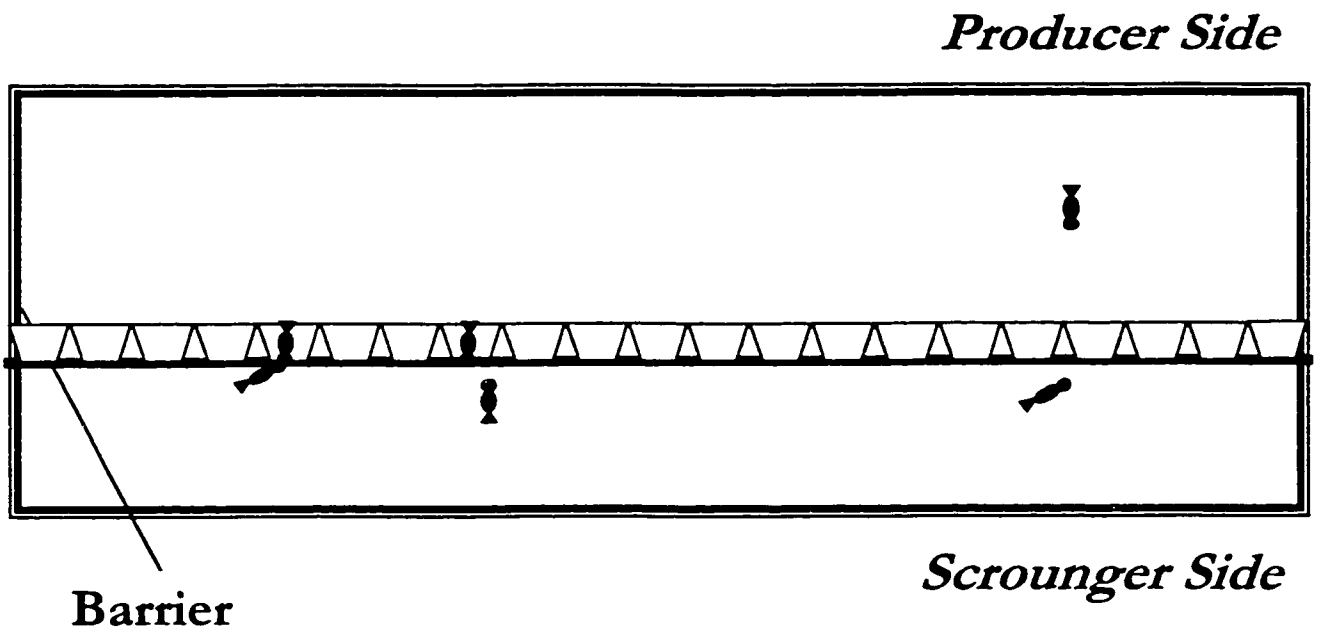




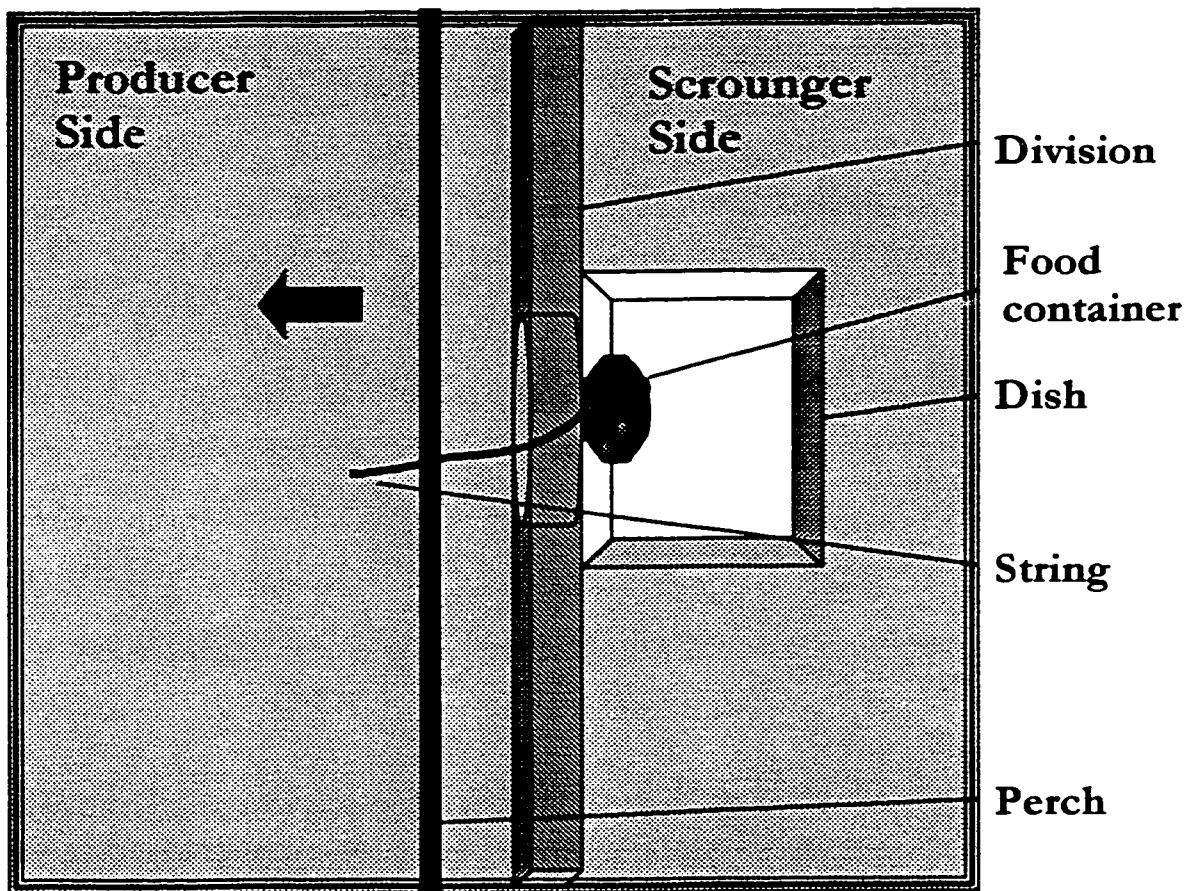
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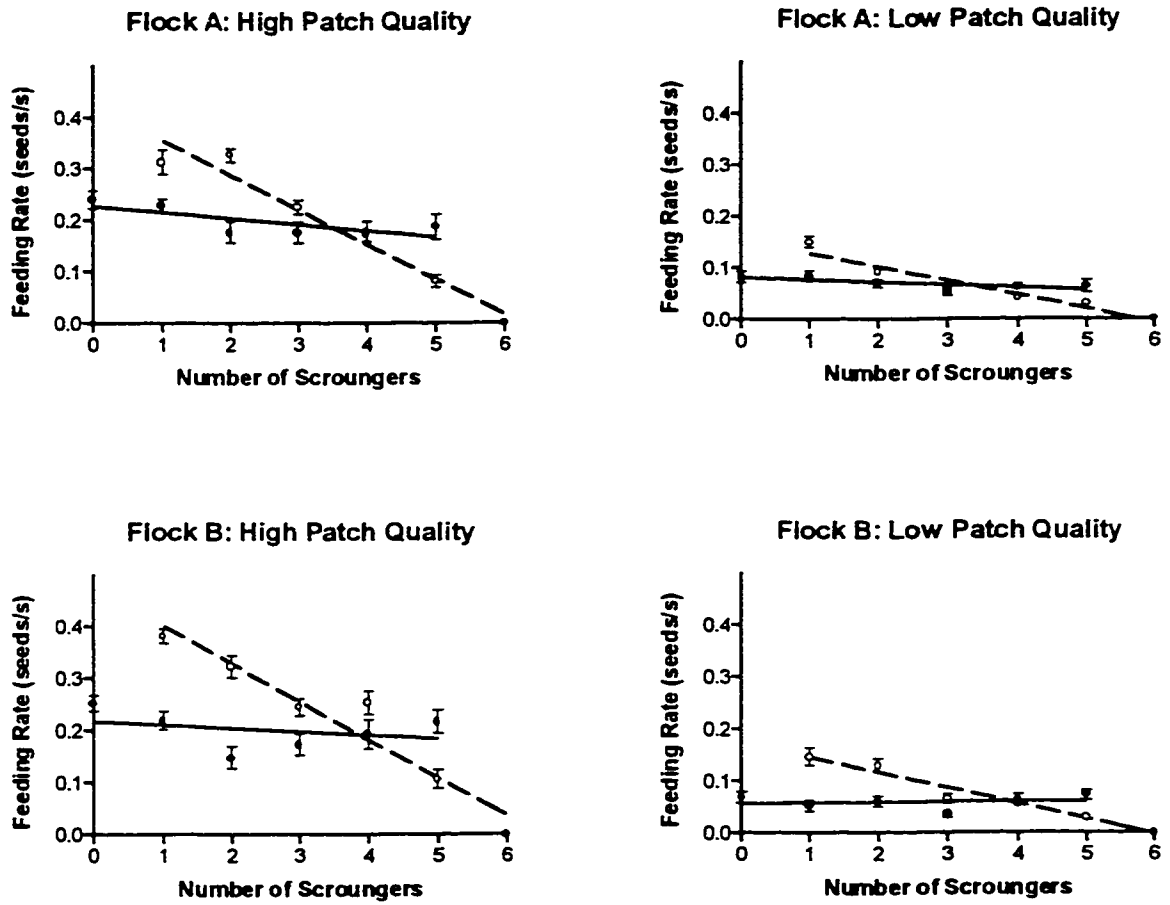
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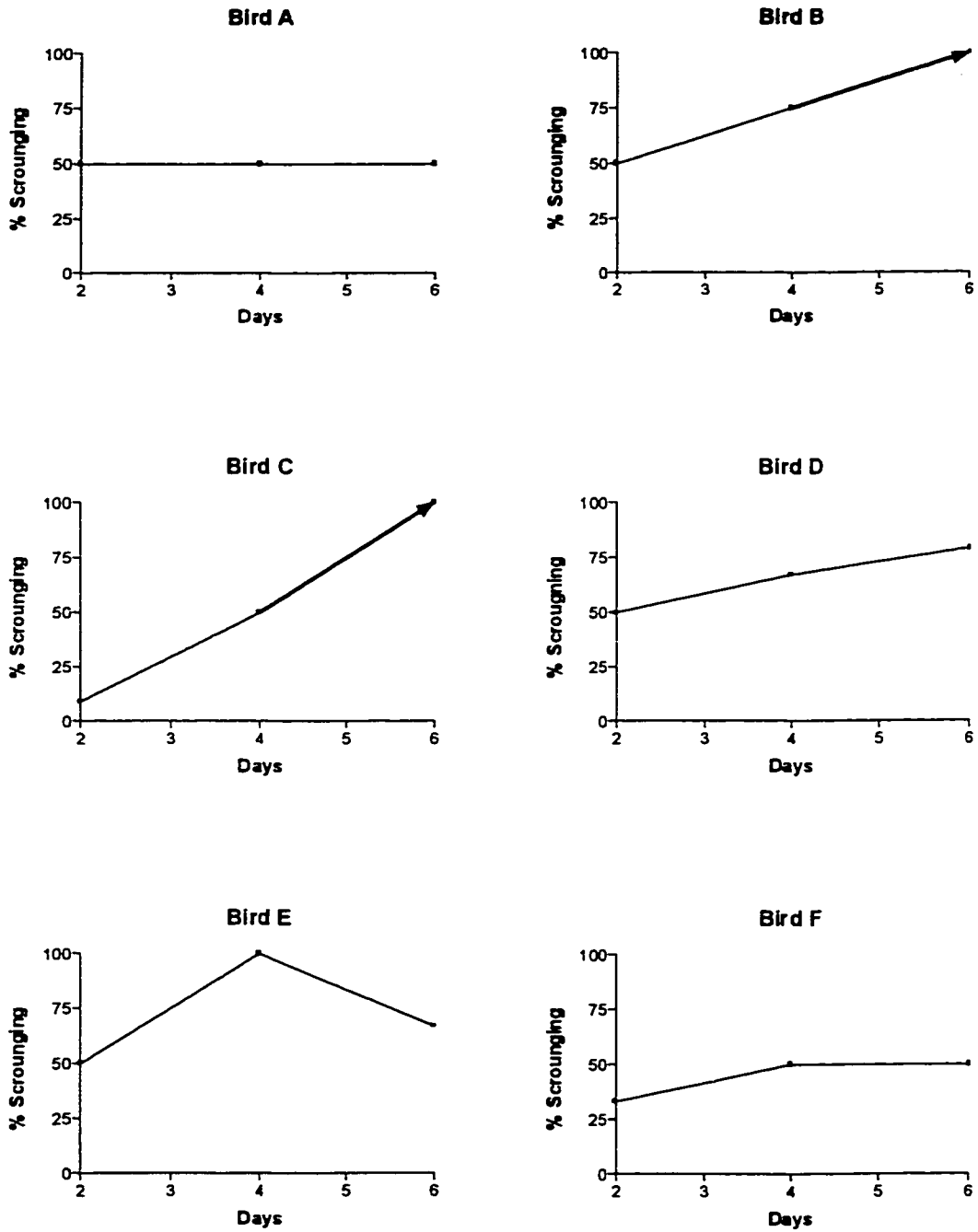
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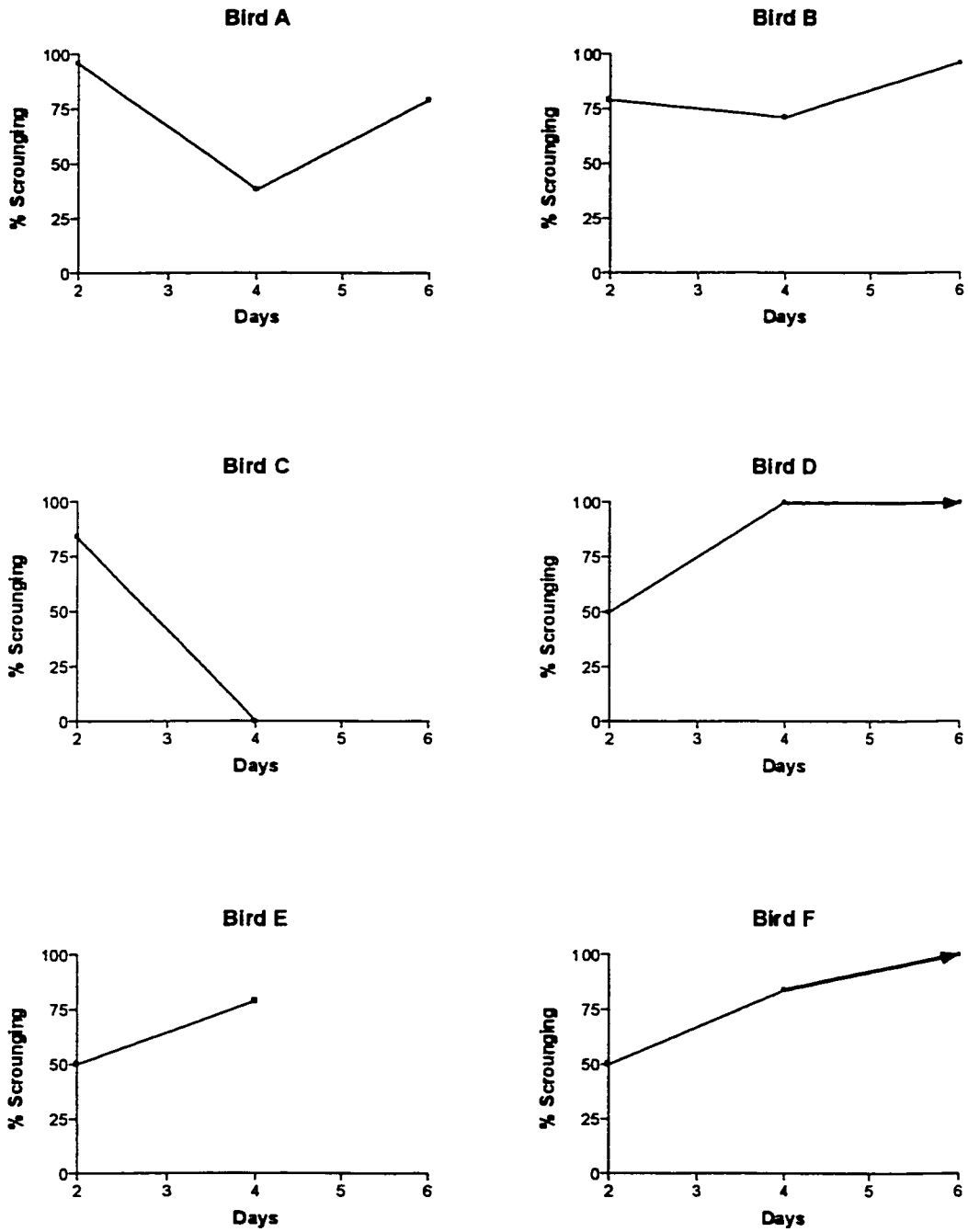
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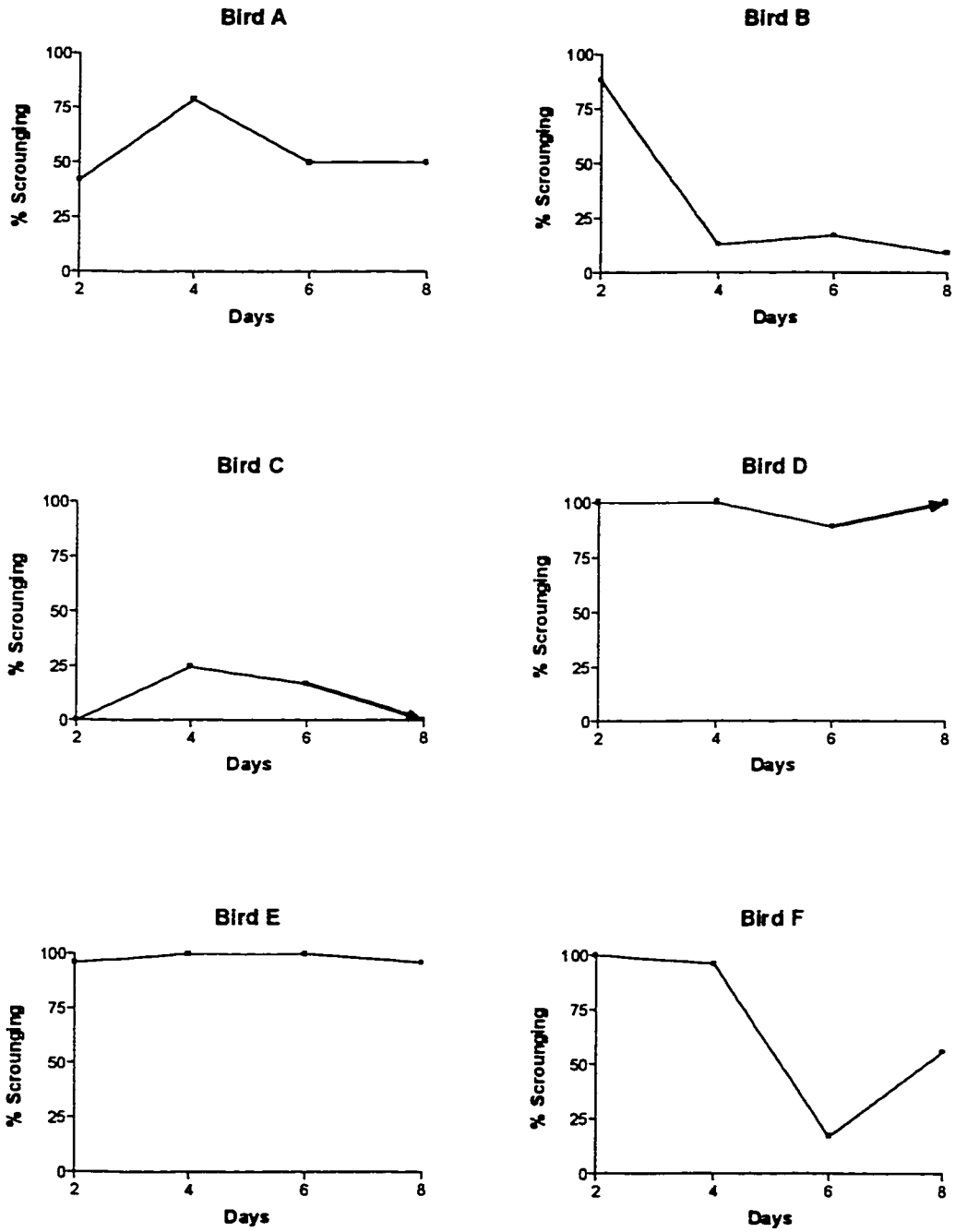
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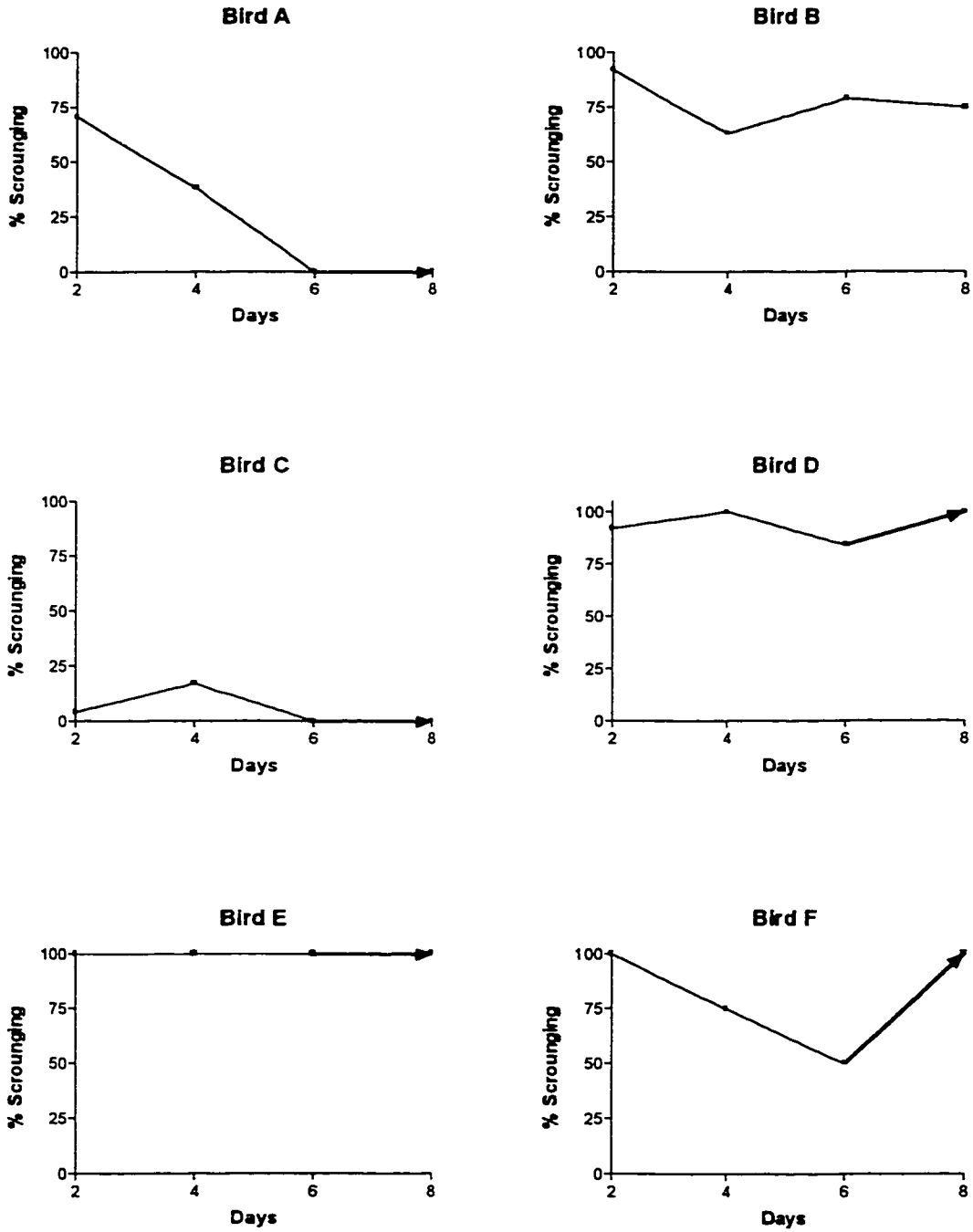
*Figure 6b*



*Figure 7a*



*Figure 7b*





*Figure 8*

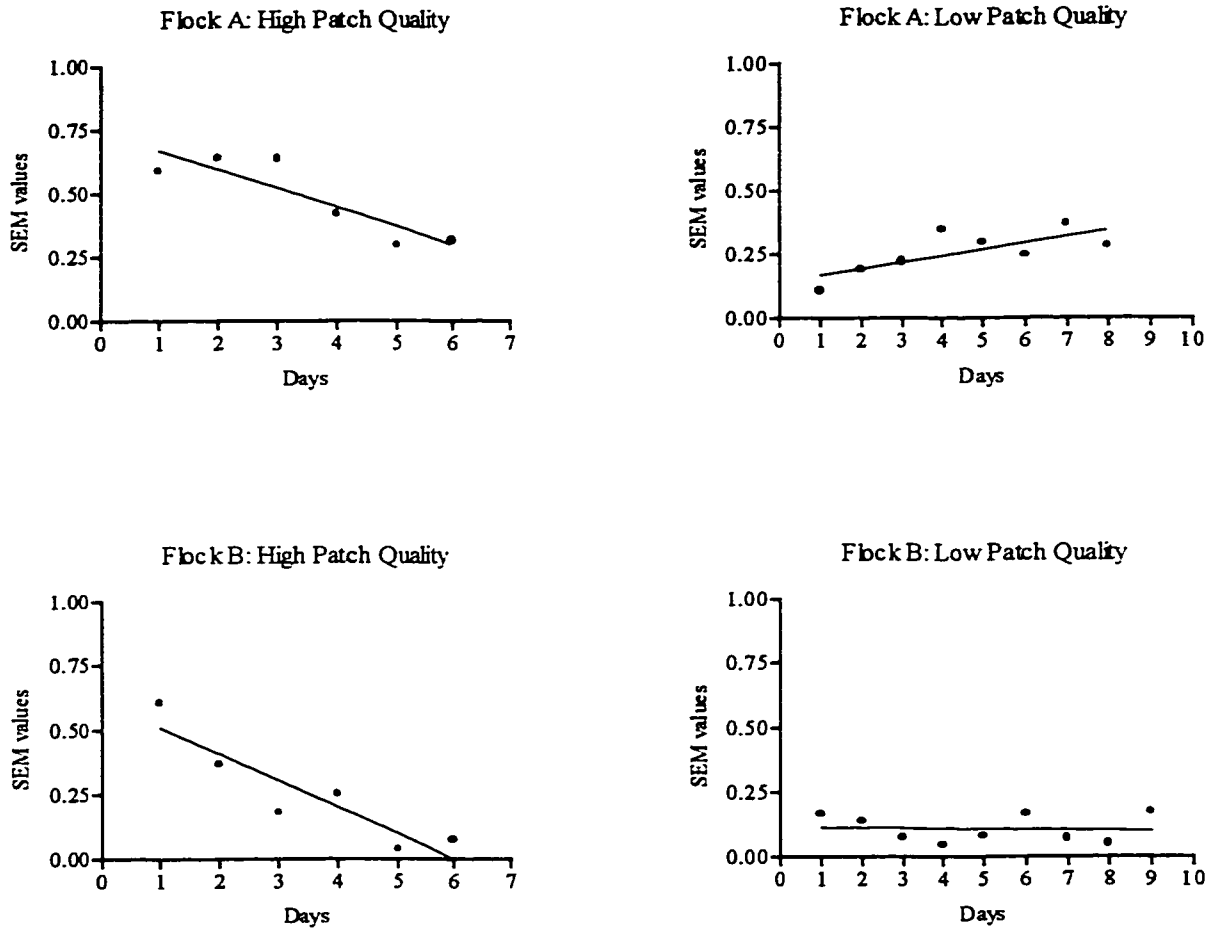
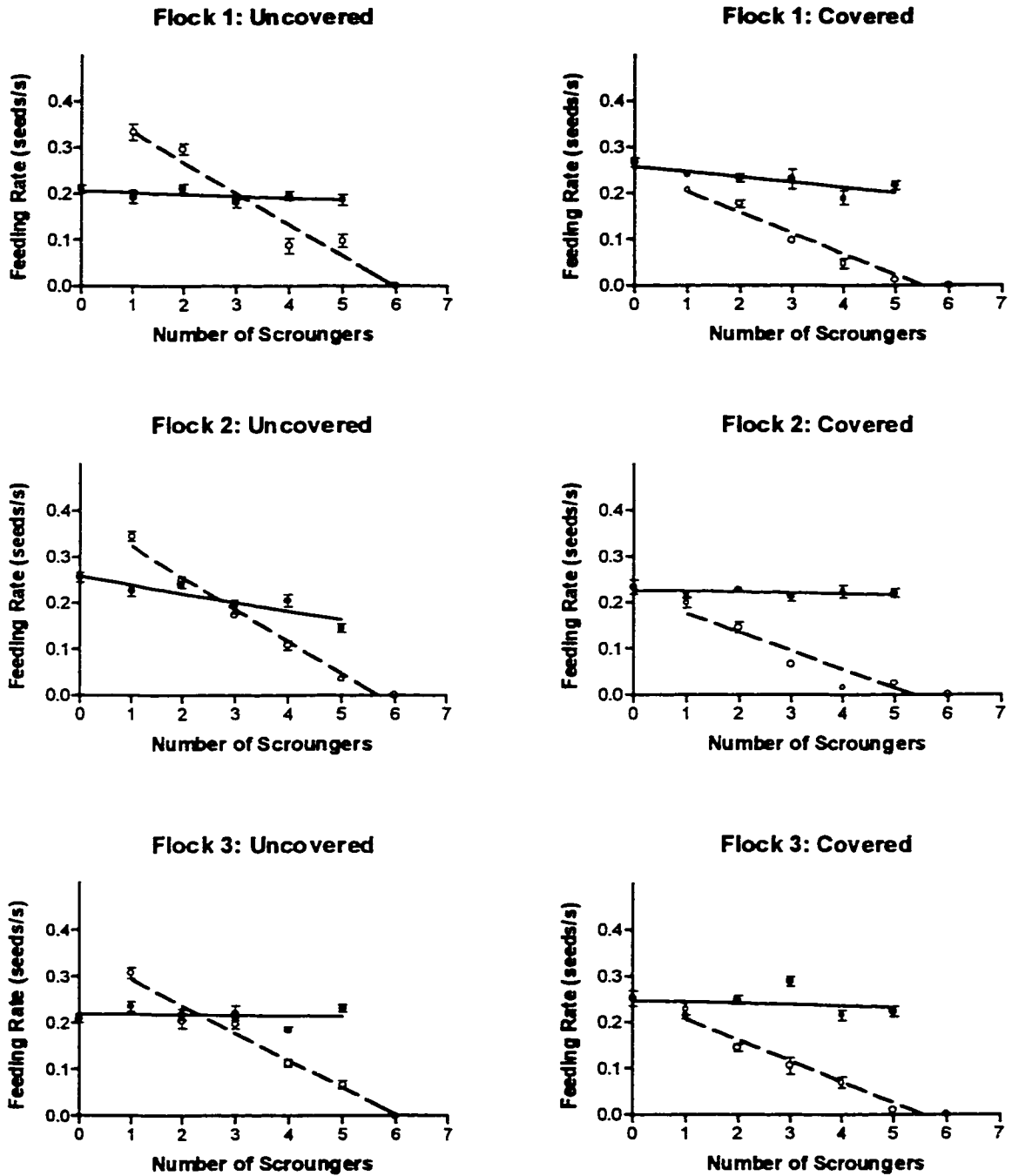
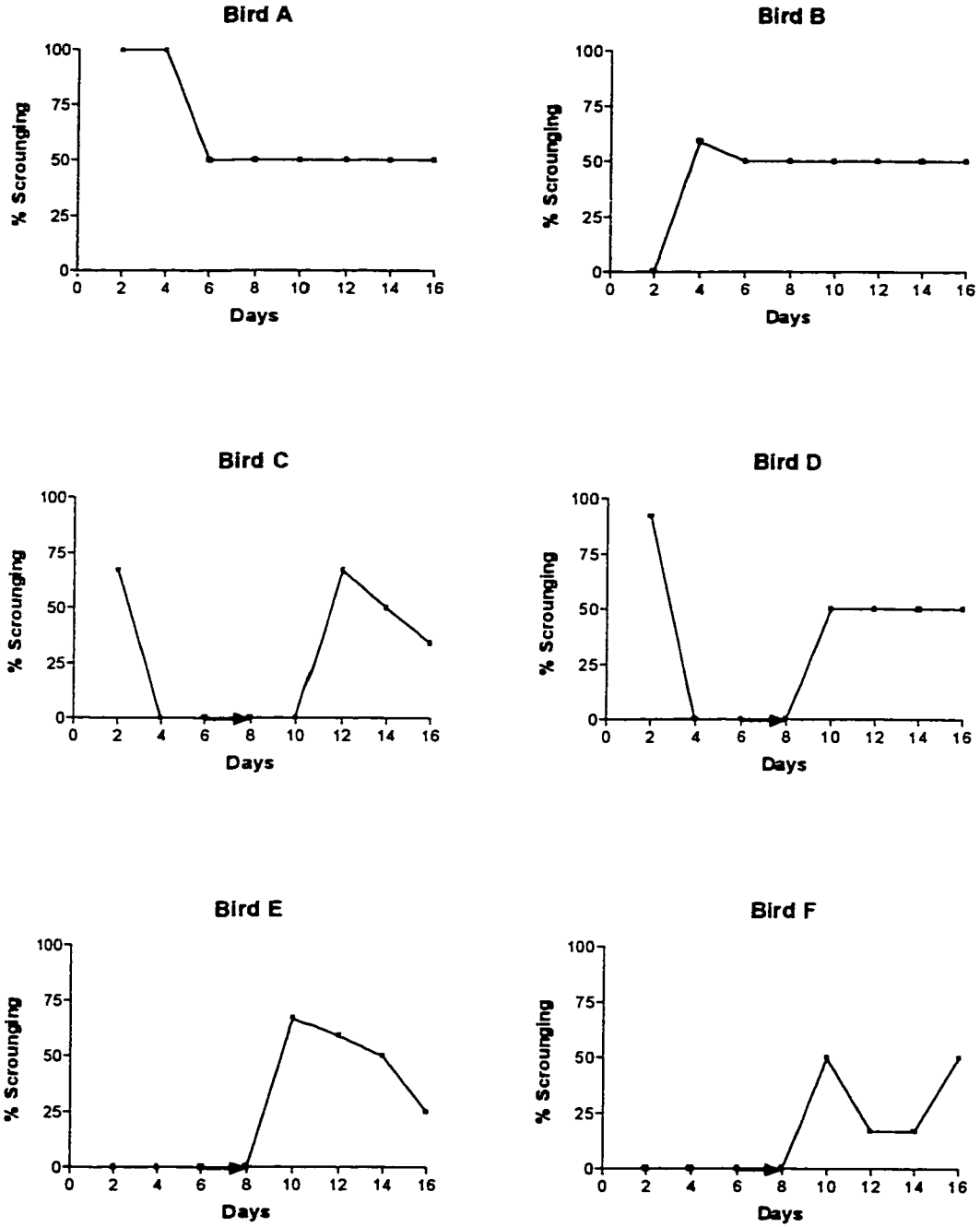


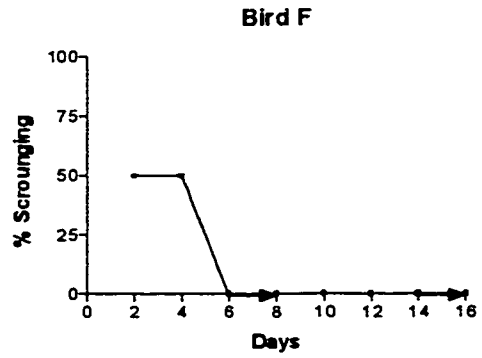
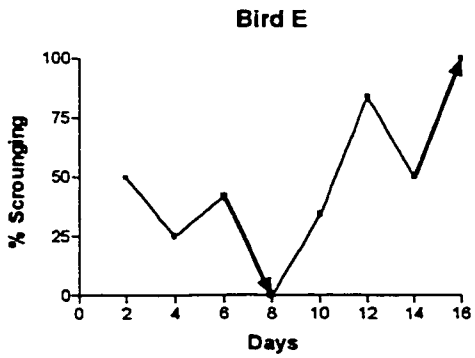
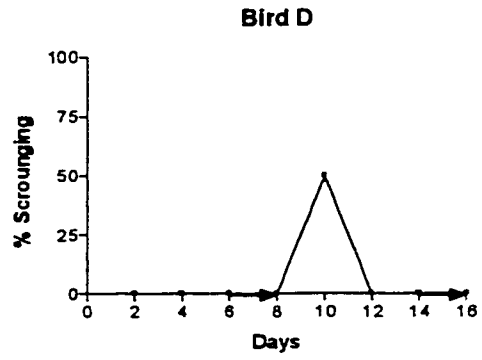
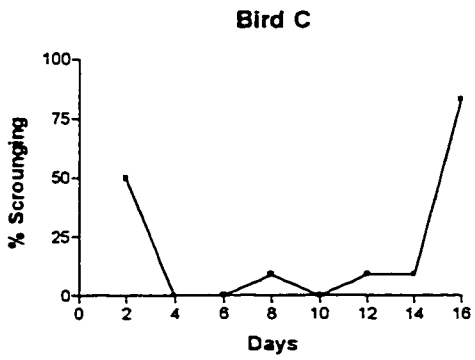
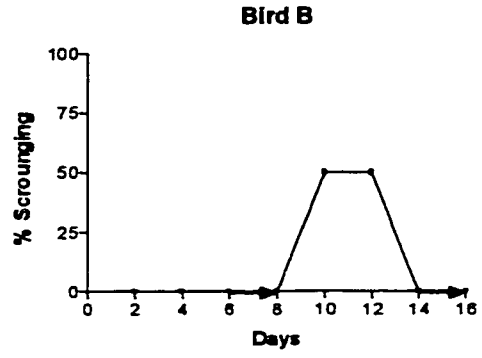
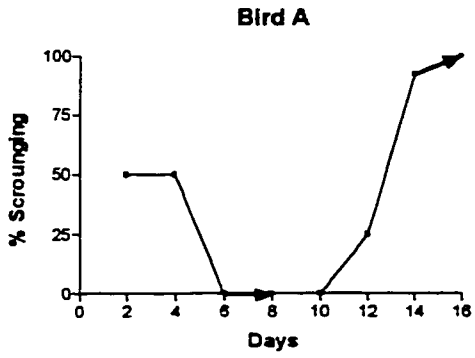
Figure 9



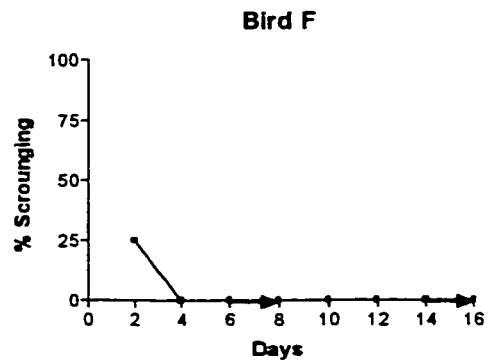
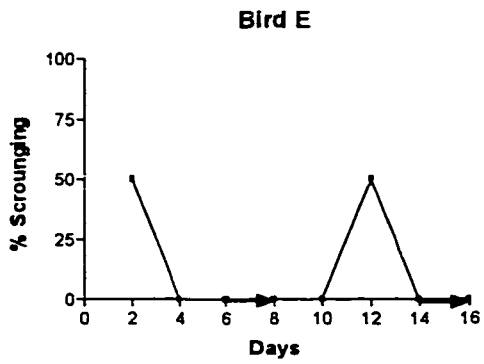
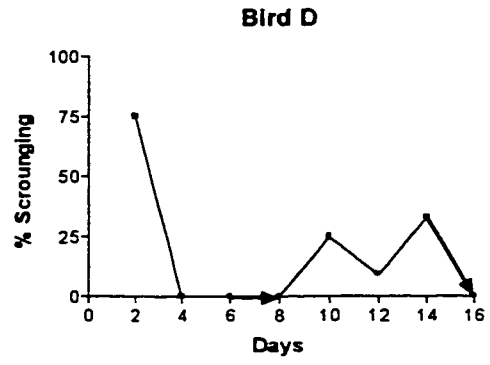
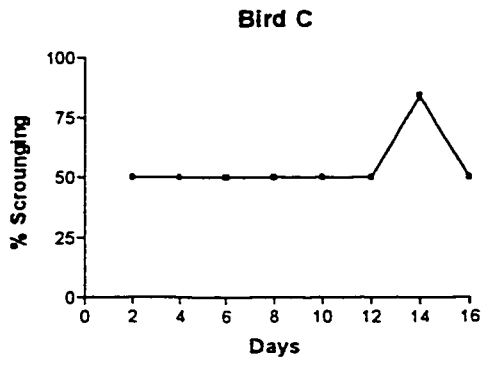
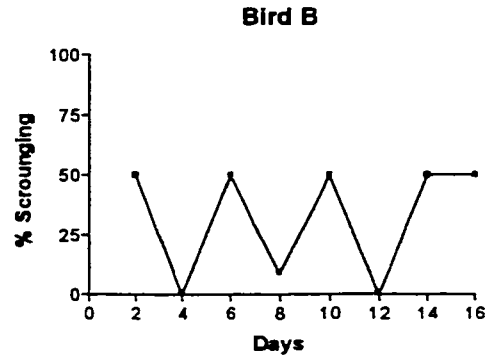
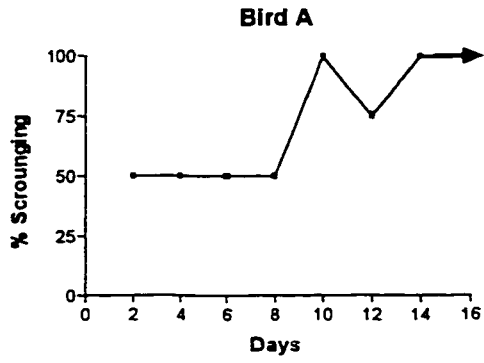
*Figure 10a*



*Figure 10b*

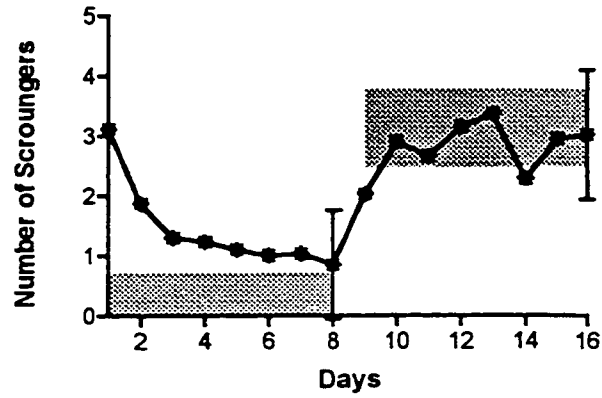


*Figure 10c*

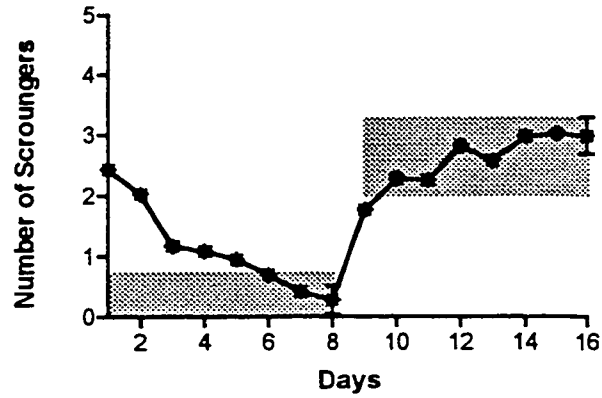


*Figure 11*

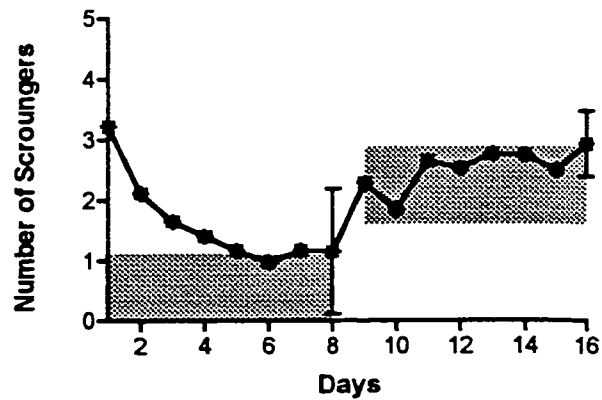
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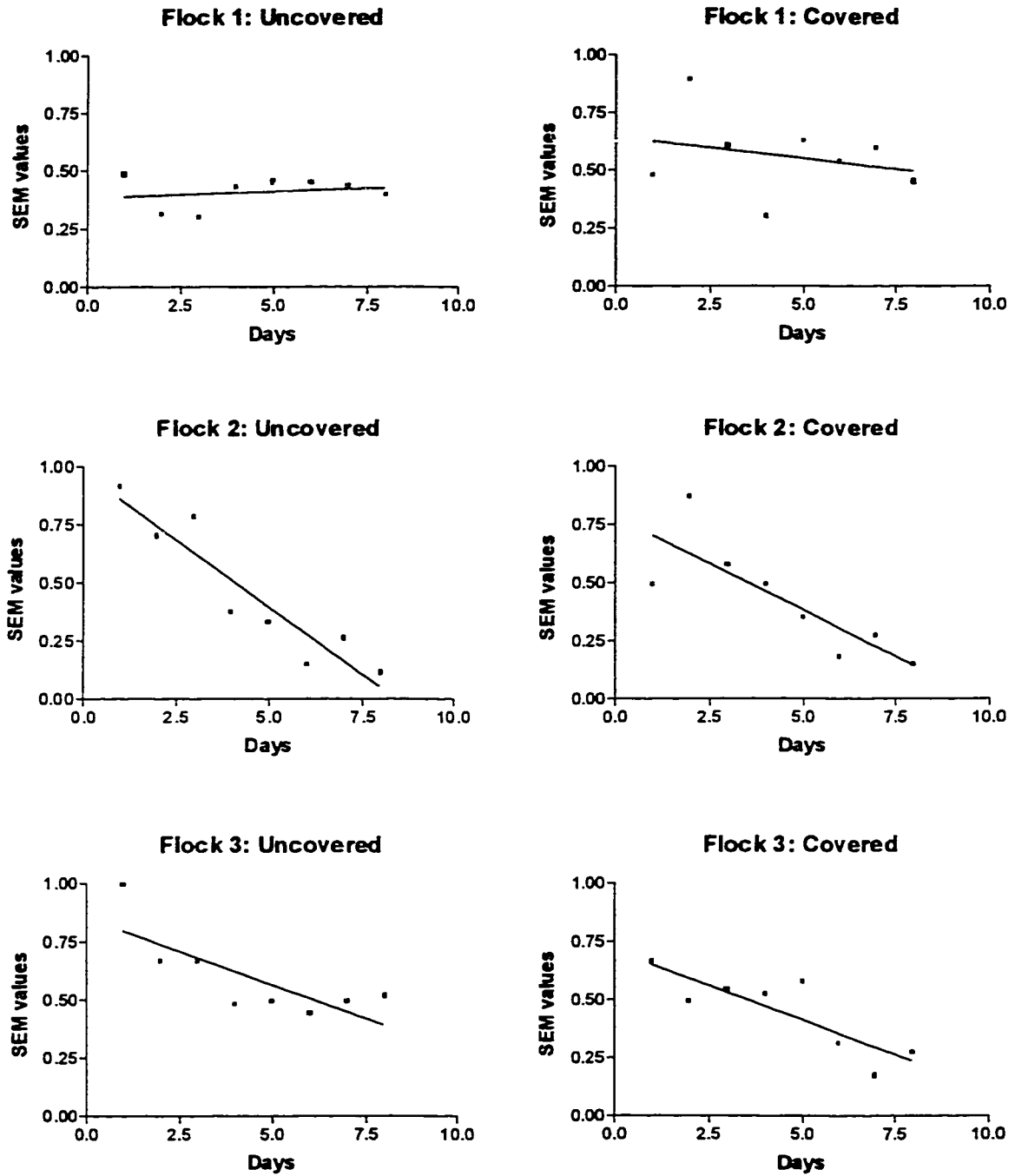
**Flock 2: Adjustment Curve**



**Flock 3: Adjustment Curve**



*Figure 12*



**CONCORDIA UNIVERSITY**

**School of Graduate Studies**

This is to certify that the thesis prepared

By: Kieron Mottley

Entitled: Experimental Evidence that Group Foragers can Converge on Predicted  
Producer-Scrounger Equilibria

and submitted in partial fulfillment of the requirements for the degree of

**Master of Science (Biology)**

Complies with the regulations of the University and meets the accepted standards with  
respect to originality and quality.

Signed by the final examining committee:

\_\_\_\_\_ Chair  
\_\_\_\_\_ Examiner  
\_\_\_\_\_ Examiner  
\_\_\_\_\_ Supervisor

Approved by \_\_\_\_\_  
Chair of Department or Graduate Program Director

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