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Testing Predictions of a Risk-Sensitive Scrounging Model
using European Starlings

Marten A. Koops

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

Testing Predictions of a Risk-Sensitive Scrounging Model using European Starlings

Marten A. Koops

Social foragers have the opportunity to exploit (scrounge) the food discovered by the foraging behaviour of other group members (producers). To date, studies of producing and scrounging have modelled the alternatives deterministically as a mean rate maximizing game. However, deterministic models ignore the stochastic nature of the foraging process, and ignore the effects that variance can have on the consequences of foraging decisions. Caraco & Giraldeau (1991) proposed a stochastic model of producing and scrounging to rectify this situation. When modelled stochastically, scrounging can be conceived of as a risk-averse foraging tactic; i.e., it can reduce the chances of an energetic shortfall by reducing the forager's variance in food intake. I tested this assumption, and the stochastic model's predictions that scrounging should increase with increasing food requirement and food density using wild caught starlings (*Sturnus vulgaris*) in an indoor aviary. When requirement was increased, there were no statistically detectable increases in scrounging. But, no relationship was found between scrounging and variance in food intake, so scrounging did not have the assumed effect on variance, and may, in fact, have been independent

of requirement. Increased food density, however, resulted in significant increases in scrounging, and provided evidence that scrounging and variance in intake were negatively related. Scrounging, at least in one of the two experiments, appeared to be a risk-averse foraging tactic and starlings responded in a risk-sensitive fashion.

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INTRODUCTION

Social Foraging

Many animals forage in groups for part or all of their life cycle (see Lott 1991 for a review). This behaviour results in a number of potential benefits and costs related either to foraging or predation (see reviews in Barnard & Thompson 1985; Pitcher 1986; Lott 1991). In the present study, I focus on one of the costs of group foraging: food lost to competitors (Clark & Mangel 1984; Giraldeau et al. 1991, in press; Vickery et al. 1991), which reduces the benefit of group foraging for all group members.

Exploitation of resources that others have made available has been called "scrounging" (Barnard & Sibly 1981), and may apply to inter- or intra-specific relations. Scrounging food has been observed in a vast number of avian species (also called kleptoparasitism, Brockmann & Barnard 1979), but has also been observed in mammals (Packer & Ruttan 1988), fish (Pitcher 1986) and invertebrates (Vollrath 1984). The extent to which social foraging provides benefits will depend on the frequency with which social foragers lose food to scroungers. So, scrounging frequency may, in a way, be a key factor in promoting or preventing the evolution of group foraging. Understanding the ecological and organismal characteristics that modulate the occurrence of scrounging will likely have consequences for the unravelling of the conditions promoting the evolution of sociality.

One approach to studying determinants of scrounging frequency is through modelling. However, conventional optimality models are of little use because the

behaviour of some individuals affects the benefits derived from the behaviour of others. Under these conditions, a game-theory approach is needed (Maynard Smith 1982).

Barnard & Sibly (1981) used game theory to propose a foraging game, in which individuals employ one of two alternative foraging strategies: "producer", expending time and energy to generate opportunities for resource exploitation; or "scrounger", taking advantage of the opportunities generated and usurps some or all of the resource (Barnard & Sibly 1981; Caraco & Giraldeau 1991; Vickery et al. 1991). The producer-scrounger (P-S) game assumes that the fitness of each strategy is dependent upon their frequency in the group. Thus, producer and scrounger are frequency dependent strategies (*sensu* Maynard Smith 1982).

A social foraging system leads to stable co-existence of producer and scrounger strategies when: (i) scroungers have a higher fitness than producers when scroungers are rare; and (ii) producers have a higher fitness than scroungers when scroungers are common (Parker 1984). The first condition insures that a rare scrounger mutant does better than producers, and consequently the strategy spreads in the group. As the scrounger strategy spreads, the fitness of both producers and scroungers decreases. However, the fitness of scroungers is expected to decrease at a faster rate than the fitness of producers. Not only does competition among scroungers increase, but as scroungers replace producers in the group, fewer feeding opportunities are generated per unit search time. The second point insures that at some point the fitnesses of the producer and scrounger strategies will be equal,

corresponding to a Nash equilibrium, that is, a state where no player can profit by altering its behaviour unilaterally.

This form of the P-S game assumes that the strategy played by an individual is determined either genetically or phenotypically. An individual can be a producer or scrounger based upon genes, or can play producer or scrounger at frequencies based upon some phenotypic characteristic such as age, size, sex, or dominance.

Alternatively, the frequency of the tactics can be based on assessment of payoffs (in some fitness currency) to each (Harley 1981; Maynard Smith 1982; Houston & Sumida 1987). If the frequency of tactics is based on assessment, then all individuals can be both producer and scrounger, but settle upon one or the other, or some mix, depending upon the local foraging conditions.

The P-S game has only been studied empirically in foraging systems. The P-S game has been used to study social foraging in house sparrows (*Passer domesticus*, Barnard & Sibly 1981), bald eagles (*Haliaeetus leucocephalus*, Hansen 1986), pigeons (*Columba livia*, Giraldeau & Lefebvre 1986), zebra finches (*Poephila guttata*, Giraldeau et al. 1991) and spice finches (*Lonchura punctulata*, Giraldeau et al. 1991, in press). To date, most P-S foraging models have assumed that mean intake (or mean intake rate) was the fitness currency that foragers were maximizing (Vickery et al. 1991). However, using such a deterministic modelling approach has limitations. For instance, by ignoring physiologically required intake levels, deterministic models ignore the chance that a forager may alter its decisions as a function of requirement (Caraco & Giraldeau 1991). Moreover, empirical research has shown that when

required intake levels are manipulated, foragers are responsive to the variance in food intake (Caraco et al. 1980; Caraco 1981, 1982, 1983). Only stochastic models deal with variance.

Risk-Sensitive Foraging

Caraco (1980) proposed, what would later be called the energy budget rule (Stephens & Krebs 1986). This rule states that when a forager expects to exceed its daily energetic requirements, it should be "risk-averse" (i.e., choose the foraging option with the lower variance in intake). But, when a forager expects to fall short of daily energetic requirements, it should be "risk-prone" (i.e., choose the foraging option with the higher variance in intake). The logic behind this rule is simple. If a forager has the choice between two foraging options with the same expected mean, but different variances, then variance will be the deciding factor between starvation and survival. Suppose a hypothetical forager, a small homeotherm, must ingest ten seeds before nightfall (the time horizon), and has the choice between two options. Both options offer the same mean intake. However, one option has a high variance (risk-prone option), and the other has a low variance (risk-averse option). If the forager has a requirement which is higher than the mean intake (Fig. 1A), then the probability of obtaining more food than required can be maximized by choosing the risk-prone option (as shown by the shaded area under the curve in Fig. 1A). However, if the forager's requirement is less than the expected intake (Fig. 1B), the chances of failing to meet the requirement can be minimized by choosing the risk-averse option (as

shown by the shaded area under the curve in Fig. 1B).

Sensitivity to variance in intake has been shown in a number of animals, ranging from bumble bees (*Bombus* sp., Real 1981; Waddington et al. 1981; Cartar & Dill 1990; Cartar 1991) and orb-weaving spiders (*Metepeira spinipes*, Gillespie & Caraco 1987; Uetz 1988) through small homeotherms such as white-crowned sparrows (*Zonotrichia leucophrys*, Caraco 1982, 1983) and common shrews (*Sorex araneus*, Barnard & Brown 1985a, b, 1987; Barnard et al. 1987) to larger birds such as pigeons (*Columba livia*, Hamm & Shettleworth 1987). The majority of risk-sensitive foraging studies have been run under laboratory conditions offering invariable and variable options, both providing the same mean intake. In most natural situations, animals will not be faced with a choice between two options with equal means and different variances. Instead, foragers will need to tradeoff between the preferred mean intake (i.e., maximizing mean intake), and the preferred variance. Experimentally, it has been shown that bumble bees (*Bombus pennsylvanicus*, Real et al. 1982), dark-eyed juncos (*Junco hyemalis*, Caraco & Lima 1985), rufous hummingbirds (*Selasphorus rufus*, Stephens & Paton 1986) and bananaquits (*Coereba flaveola*, Wunderle & Cotto-Navarro 1988) can tradeoff mean and variance in laboratory settings. A mathematical model which deals with the tradeoffs that foragers will make between the mean and variance of intake when minimizing the probability of starvation is the z-score model (Stephens 1981). The basic formulation is: $z = (R-x)/s$, where R is food intake required for survival, x is expected mean food intake and s is the expected standard deviation of intake. This model makes the same

predictions as the energy budget rule.

A Risk-Sensitive Scrounging Model

Caraco & Giraldeau (1991) proposed a risk-sensitive stochastic P-S model, based upon Stephens' (1981) z-score model. Foragers modify their scrounging frequency to obtain the mean and variance in intake which will minimize their probability of failing to meet their physiological requirement. The mean and variance of intake are proposed to be affected by the number of food items in a food clump, the rate at which producers expect to discover food clumps, the foraging time available, the producer's competitive efficiency (which is defined as the probability that the producer will obtain any given food item in the food clump discovered), and group size. The physiological requirement of scroungers is adjusted in relation to the producer's requirement by a cost of scrounging.

Predictions from their model develop from two assumptions. First, they assume that scrounging is determined by assessment. Individual foragers can either produce or scrounge, and the two tactics are played in the group at the frequency that will minimize an individual's probability of starvation. Second, scrounging is a risk-averse tactic. As scrounging increases, the variance in intake that an individual experiences decreases. From these two assumptions, we see that individuals can both produce and scrounge, and settle upon an incidence of scrounging based on the local foraging conditions. However, the incidence of scrounging that an individual expresses will influence its variance in intake, and hence its probability of starvation.

Caraco & Giraldeau's (1991) model makes a number of predictions. Scrounging should decrease when: (i) the cost of scrounging increases; (ii) the competitive efficiency of producers increases; (iii) the group size decreases; or (iv) the number of food clumps that producers expect to discover decreases. The predicted effect of changes in requirement is dependent on the competitive efficiency of producers. If producers have a competitive advantage, scrounging will decrease when requirement increases. However, if producers lack a competitive advantage, scrounging will increase when requirement increases.

In this thesis, I test the two risk-sensitive predictions of Caraco & Giraldeau's (1991) model using wild-caught starlings. The expected energy budget of a forager, and hence its proneness or aversion to variance, can be influenced by two factors: requirement and expected intake. I will test each of these factors separately in two experiments. Experiment 1 will deal with requirement, the effect of which is dependent upon the producer's competitive advantage. If producers have a competitive advantage and requirement increases, foragers should be risk-prone. Because scrounging is assumed to be a risk-averse tactic, the model predicts that starlings will reduce their scrounging in response to increased requirement. However, when producers lack a competitive advantage, more food is available for scroungers. Scrounging remains a risk-averse tactic, but the model predicts, in this case, that increasing requirement should prompt starlings to increase their scrounging, not so much in response to variance effects, but to increase mean intake. Thus, when producers lack a competitive advantage, the starlings should respond to the mean, and

tradeoff the preferred variance (i.e., higher variance when requirement is higher) for a preferred (i.e., increased) mean intake.

The second experiment will deal with expected intake. The starling's expected intake will be influenced by the number of food clumps that producers expect to discover (discovery rate times available foraging time). When expected number of food clump discoveries is low, foragers should be risk-prone, and scrounge less. When expected number of food clump discoveries is high, foragers should be risk-averse, and scrounge more. Testing these two predictions is the first step towards determining whether Caraco & Giraldeau's (1991) risk-sensitive P-S model can predict the use of scrounging alternatives in starlings.

GENERAL METHODS

Subjects

The European starling (*Sturnus vulgaris*) was successfully introduced into North America in 1890, and since then, has spread throughout Canada and the United States (Krebs 1978; Feare 1984). The starling is omnivorous, and commonly forages by probing in the ground with its bill, in single and mixed species flocks (Williamson & Gray 1975). Flocking provides starlings with anti-predatory (Powell 1974) as well as foraging benefits (Feare 1984). Recent work has shown that starlings will scrounge both information and food (Templeton 1993), and are sensitive to variance in intake (Reboreda & Kacelnik 1991). For these reasons, I believe starlings are an excellent model species for testing predictions about risk-sensitive scrounging.

The 13 starlings used in this study were captured as adults and have been kept indoors for periods of 9 to 24 months. Starlings were housed in groups of five in 1.1 x 0.95 x 0.6 m, galvanized wire mesh cages. They were kept at 22 °C (\pm 1 °C) on a 12 hour L:D cycle (lights on at 0600 hours EDST).

Outside experimental periods, starlings were fed a mixture of bread, turkey starter, "Eight-in-One" pellets for Mynah birds, canned dog food and cheese. The same food was used during the experiments, but gelatin was added to the mixture. Once the gelatin set, the mix was forced through a processor making food items that were 1 cm long and weighing approximately 0.14 g each (5 food items = 0.7 g).

Experiments were run in a 2.4 x 2.5 x 2.4 m indoor aviary. Flocks of seven starlings were used, and the foraging behaviour of focal starlings was recorded while they were feeding on experimental patches. I use the term "patch" in a broad sense to mean any recognizable location that has the potential of offering a localized concentration of food. Hence, patches, in the current context, can either contain food (a food patch) or contain no food (an empty patch). A single patch (19 x 21 cm) contained five holes (5 cm diameter, 1.5 cm deep), one hole in the centre of the patch, and one hole in each corner. Each hole was at least 1 cm from any other hole, and covered by opaque latex into which a 3 cm slit was made. The latex covers hid the food such that the starlings were forced to probe the holes of a patch in a manner similar to their natural foraging behaviour. To test the model's predictions, requirement was manipulated through periods of food deprivation, and the number of food patches that producers expected to discover was manipulated through food

density.

Training

Two starlings were trained simultaneously to feed from experimental patches prior to experiments. They were each placed in a separate cage (0.6 x 0.6 x 0.6 m), and allowed to collect food from patches without latex covers. Once the starling landed and ate the food presented in the patches within ten seconds, ten times in a row, the covers were replaced. During the next stage of training, the starling was presented with a single covered patch for ten seconds. This continued until the starling would land and eat the food in the patch within ten seconds of presentation.

Training then consisted in repeatedly presenting the starling with the following two contingencies: 1) a full patch (when one hole had food, all five holes in a patch had food); and 2) an empty patch (when one hole was empty, all five holes were empty). Two patches would be presented simultaneously. Half of the patches would contain food, half would not. The two patches would be presented for 15 seconds, then removed. Patches were presented every 15 minutes for four hours per day. A starling's training was complete when: (i) it ate all five food items in a patch, and moved to the next patch immediately, for ten consecutive presentations where a full patch happened to be visited first, and (ii) it left the empty patch after no more than two probes, for ten consecutive presentations where the empty patch happened to be visited first. To determine if the criteria were fulfilled, only the behaviour of the starling on the first patch visited was used since there were no other patches to visit

after the second patch. Complete training took 9 days ($SD = 5.0$, $n = 4$) per pair, on average.

Experiments

To minimize the number of subjects required to run the study, a core flock procedure (Giraldeau et al. in press) was used, where subjects were added to a core group of individuals whose behaviour was not recorded. Five starlings (three males and two females) were chosen to form the core flock. The core flock (as part of the treatment) controlled for the size of the foraging group and reduced any inter-flock variance that might add noise to the data. Two uniquely marked starlings were placed in the aviary with the core flock, forming a foraging group of seven starlings.

Fifteen patches were placed, touching each other to form a checkerboard pattern, on the floor of the aviary and covered by an opaque sheet of heavy black polythene. The sheet could be removed by a string and pulley system from behind a blind. The positions of food-containing patches were determined randomly, with the constraint that a patch could only be assigned food once per trial. If a patch was designated full, then each of its five holes contained one food item. Conversely, if the patch was empty, then none of its five holes contained food. The same number of patches were assigned food for each trial within a treatment.

The experiment consisted of observing each focal individual's allocation to producing and scrounging activities while they foraged in a flock on the patches described above. Producing was defined as probing in a patch that no other starling

was foraging in, regardless of the presence or absence of food.

Data was collected for scrounging under two operational definitions. The first, a general definition, defined scrounging as an attempt to probe at, eat from, or step onto a patch which one or more starlings were already occupying. Scrounging included both successful attempts (starling was able to probe a hole at the patch) and unsuccessful attempts (starling was prevented from probing). A starling was also considered to have scrounged if it stepped onto and probed a hole in a patch that another starling had just left (within two seconds). Scrounging is defined without regard for the presence or absence of food.

The second operational definition divided scrounging into four categories: (1) Copying, defined by Barnard & Sibly (1981) as "the interactor responding to some cue from another forager (not necessarily a successful find) by moving across to search in the immediate area around the forager" (p.546). The starling was counted as having copied if it foraged in a patch with the resident starling (producer); (2) Snatching, defined as "the taking [of] prey directly from the recipient's bill. Less commonly, dropped prey was also taken" (Barnard & Sibly 1981, p.546); (3) Displacement, where the starling forced the resident starling off the patch; and (4) Foiled Attempts, where the starling attempted to forage at a patch where another starling was present, but was prevented from doing so by the resident starling. Again, these behaviour patterns (with the exception of Snatching) are defined without regard for the presence or absence of food.

These four types of scrounging were grouped into two categories: (i) passive

scrounging, composed of Copying, since no aggression was apparent in this behaviour alone; and (ii) aggressive scrounging, composed of Snatching, Displacement, and Foiled Attempts. These three latter behaviour patterns involved aggression toward the resident starling (producer) by the scrounger, or vice versa.

Data on producing and scrounging were collected using the focal sampling method (Altmann 1974; Martin & Bateson 1986) to record the number of food clumps and the number of empty patches that a focal starling produced and scrounged. Patches were designated as food clumps or empty patches based upon the presence or absence of food when the focal starling was producing or scrounging at that patch. Data were collected from each focal starling over five of ten trials per day.

A trial started when the focal starling first landed on a patch, and ended after (i) 30 seconds, (ii) two or more starlings had left the patches, or (iii) the focal starling left the patches. Ten trials were run in a day, and were separated into four series of consecutive trials. Within each series, trials were run at 20 minute intervals. Series were separated by 40 minute intervals. The first series included four trials, the second series had three trials, the third series had two trials, and the fourth series had only one trial. The two focal starlings were randomly assigned to be observed on even or odd trials by a coin toss. This meant that data were collected from each focal starling on the first trial of two series. The last trial was run 2 hours before lights out, and then sufficient food was provided to allow the starlings to meet their daily energetic requirements.

All trials were videotaped. From the videotapes, the number of food items

obtained from each patch was recorded. This gave measurements of the mean number of food items eaten/patch by producing and scrounging, and the variance in the number of food items eaten/patch by each tactic. Data on passive and aggressive scrounging were also collected from videotape, while data on the incidence of producing and scrounging were recorded during trials on a lap top computer programmed as an event recorder. The incidence of scrounging is measured as the proportion of patches at which the focal starling scrounged (number patches scrounged/number patches visited).

Random Scrounging

There is the possibility that the starlings forage independently of one another, and the incidence of scrounging measured is actually a product of random encounters. To test this hypothesis, the Poisson distribution (Zar 1984) was used to calculate the incidence of random scrounging. This Poisson model assumes that starlings move randomly around the patches, and that each starling that landed on a patch had an equal chance of being the first and being called the producer. Based upon this Poisson model, the expected incidence of random scrounging was calculated to be 0.11.

EXPERIMENT 1: MANIPULATION OF REQUIREMENT

This first experiment tests the prediction that the incidence of scrounging will increase as requirement decreases when producers have a competitive advantage, and will

increase as requirement increases when producers lack a competitive advantage.

METHODS

I manipulated requirement through food deprivation and subjected starlings to two requirement levels. In the low requirement treatment, food deprivation started four hours before the beginning of trials. In the high requirement treatment, the starlings were food deprived 18 hours before the beginning of trials.

Trials were run with eight of the 15 patches containing food. Preliminary experiments indicated that with this food density, starlings would expect a positive energy budget (i.e., expect to gain weight) during the low requirement treatment, and would expect a negative energy budget (i.e., expect to lose weight) during the high requirement treatment (Koops, unpublished data).

The order of treatments was balanced. The starlings were given three days of trials but only data from the last two days were included in the analysis.

Data Analysis

To determine the competitive efficiency of producers, the number of food items eaten/patch by starlings from which focal starlings scrounged was measured from videotape. The mean number of food items eaten/patch was then divided by five (the number of food items available/patch), resulting in a number between zero and one that was used as a measure of competitive efficiency (probability of the producer obtaining any given food item in a food clump that it discovers). With a group size

of seven, Caraco & Giraldeau's (1991) model predicts that producers need a competitive efficiency greater than 0.59 to have a competitive advantage.

Eight focal starlings were tested in four pairs. To test the predictions of the model, a three way repeated-measures analysis of variance (ANOVAR) was run on SYSTAT (Wilkinson 1990). Two within subject factors: a treatment factor (low and high requirement), and a trial factor (five trials per starling per treatment); and one between subject factor to test for an effect of core flock experience. Any non-significant factors were dropped from the ANOVAR. When the assumption of compound symmetry was mildly violated (Huynh-Feldt epsilon close to 1), the Huynh-Feldt corrected p-value was used (Potvin et al. 1990). Proportional data were arcsine square root transformed. The probability of making a type II error (β) is provided for all t-tests for which $p > 0.05$, using the equations provided in Zar (1984).

RESULTS

General Foraging Behaviour

Starlings foraged on the patches simultaneously, starting a trial by landing on separate patches (i.e., starting as producers). The focal starlings for instance, started a trial by scrounging in only 0.088 of the trials. The first starlings to leave were usually members of the core flock (which usually left together), and one of the two focal starlings was invariably the last starling on the patches.

Trials lasted an average of 25.3 s (SD = 3.66, n = 8) and 27.8 s (SD =

2.74, $n = 8$) in low and high requirement treatments respectively (ANOVAR, $F_{1,7} = 3.56$, $p = 0.10$). Time of day had no effect on trial duration (ANOVAR, $F_{4,28} = 0.60$, Huynh-Feldt corrected $p = 0.62$).

Focal starlings visited patches at a mean rate of 0.32 patches/s (SD = 0.059, $n = 8$) in the low requirement treatment, and 0.38 patches/s (SD = 0.080, $n = 8$) in the high requirement treatment, a significant increase (ANOVAR, $F_{1,7} = 9.12$, $p = 0.019$). The patch visitation rate, however, did not change significantly over the course of the day (ANOVAR, $F_{4,28} = 0.032$, $p = 0.99$).

Focal starlings fed at a mean rate of 0.19 food items/s (SD = 0.034, $n = 8$) and 0.18 food items/s (SD = 0.046, $n = 8$) in the low and high requirement treatments respectively ($t_7 = 0.65$, $p = 0.54$, $\beta = 0.066$). The starlings' average intake rate (0.18 food items/s, SD = 0.034, $n = 8$) for the two treatments was significantly lower than would be expected if all group members shared food equally over the duration of the trial (0.22 food items/s, $t_7 = 2.85$, $p = 0.025$).

The Rewards of Producing

When a focal starling produced, it obtained a mean of 0.54 food items/patch (SD = 0.23, $n = 8$) and 0.49 food items/patch (SD = 0.18, $n = 8$) in the low and high requirement treatments respectively. The amount obtained was not affected by the requirement ($t_7 = 0.81$, $p = 0.44$, $\beta = 0.081$). When the focal starlings successfully produced a food clump (i.e., produced a patch where food was present), they obtained similar amounts in both treatments: 2.46 food items/clump (SD = 0.47, $n = 8$) for

low requirement and 2.60 food items/clump ($SD = 0.65$, $n = 8$) for high requirement ($t_7 = 0.47$, $p = 0.66$, $\beta = 0.049$).

Scrounging or Random Encounters on the Patches?

Scrounging incidence was not merely the result of random encounters of starlings on the patches. The incidence of scrounging observed in the low requirement treatment was 0.27 ($SD = 0.14$, $n = 8$), which was significantly higher than the 0.11 predicted for random encounters ($t_7 = 3.14$, $p = 0.016$). The incidence of scrounging in the high requirement treatment was 0.31 ($SD = 0.16$, $n = 8$) which was also significantly higher than the 0.11 predicted for random encounters ($t_7 = 3.44$, $p = 0.011$).

Additional evidence that scrounging incidence is not reflecting random encounters is that the incidence of scrounging was not correlated with the patch visitation rate in either the low requirement treatment ($r = 0.14$, $p = 0.75$, $n = 8$) or the high requirement treatment ($r = -0.35$, $p = 0.40$, $n = 8$). Even when data from the two treatments were pooled there was no significant correlation ($r = -0.075$, $p = 0.78$, $n = 16$).

The Rewards of Scrounging

The amount of food obtained by scrounging decreased from 0.57 food items/patch ($SD = 0.21$, $n = 8$) to 0.38 food items/patch ($SD = 0.24$, $n = 8$) as requirement increased ($t_7 = 2.33$, $p = 0.052$, $\beta = 0.50$). Successful scrounging events yielded

1.35 food items/patch (SD = 0.68, n = 8) and 1.14 food items/patch (SD = 0.59, n = 8) in low and high requirement treatments respectively ($t_7 = 1.86$, $p = 0.10$, $\beta = 0.33$).

For focal starlings, rewards (food items/patch) provided by producing and scrounging (described above) were statistically indistinguishable in both low ($t_7 = 0.24$, $p = 0.82$, $\beta = 0.037$) and high ($t_7 = 0.86$, $p = 0.42$, $\beta = 0.088$) requirement treatments. However, when only successful events were considered, focal starlings obtained more food items/patch from producing than scrounging in both low ($t_7 = 2.96$, $p = 0.021$) and high ($t_7 = 7.15$, $p < 0.001$) requirement treatments.

Passive scrounging by focal starlings yielded 0.68 food items/scrounge (SD = 0.63, n = 8) and 0.29 food items/scrounge (SD = 0.18, n = 8) in the low and high requirement treatments respectively ($t_6 = 2.07$, $p = 0.084$, $\beta = 0.37$). Aggressive scrounging by focal starlings yielded 0.55 food items/scrounge (SD = 0.41, n = 8) and 0.32 food items/scrounge (SD = 0.31, n = 8) in the low and high requirement treatments respectively ($t_6 = 0.90$, $p = 0.40$, $\beta = 0.081$). Scrounging passively and aggressively provided focal starlings with the same rewards in the low requirement ($t_6 = 0.65$, $p = 0.54$, $\beta = 0.056$) and high requirement ($t_6 = 0.017$, $p = 0.99$, $\beta = 0.027$) treatments.

Successful passive scrounging provided focal starlings with 1.52 (SD = 0.71, n = 8) and 1.12 (SD = 0.64, n = 8) food items/scrounge in the low and high requirement treatments respectively, values which do not differ ($t_7 = 1.27$, $p = 0.24$, $\beta = 0.16$). Successful aggressive scrounging provided focal starlings with 1.27 (SD

= 0.84, $n = 8$) and 0.99 (SD = 0.70, $n = 8$) food items/scrounge for low and high requirement treatments, with no treatment effect ($t_7 = 0.96$, $p = 0.37$, $\beta = 0.10$). Successful passive and aggressive scrounging provided the focal starlings with the same number of food items in the low requirement treatment ($t_7 = 0.80$, $p = 0.45$, $\beta = 0.079$) and in the high requirement treatment ($t_7 = 0.39$, $p = 0.71$, $\beta = 0.044$).

Testing the Model

Does variance in food intake decrease when scrounging increases?

The major assumption of the model is that scrounging decreases the variance in food intake. For each focal starling, both treatment and time of day were non-significant factors contributing to the variance in food intake/patch. Observations from each trial, for each individual, therefore, can be considered independent of one another. Thus, a correlational analysis of the incidence of scrounging and the variance in food intake/patch is valid. Only two of the eight focal starlings showed a significant correlation between incidence of scrounging and the variance in food intake/patch (Fig. 2). One of these showed an unexpected positive correlation, whereas the other showed a negative correlation (as predicted by the model). Variance ratio tests between the two treatments for each focal starling showed that variance in food intake/patch did not decrease significantly as scrounging increased (Table 1), with the exception of one focal starling.

Similar results were found when the incidence of aggressive scrounging was used for the correlation, except that only one correlation was significant (bird 5, $r = -0.75$, $p = 0.012$, $n = 10$). The variance in food intake/patch was significantly explained by time of day (bird 7) and treatment (bird 8), suggesting that the correlation between incidence of aggressive scrounging and variance in intake/patch is not valid for these two starlings.

Do producers have a competitive advantage?

When a focal starling scrounged, the producer of the patch obtained an average of 2.10 food items/clump ($SD = 0.68$, $n = 8$) in the low requirement treatment, and 2.18 food items/clump ($SD = 1.02$, $n = 8$) in the high requirement treatment. These values (2.10 and 2.18) convert into competitive efficiencies of 0.42 and 0.44 respectively, values that are not significantly different from each other ($t_7 = 0.23$, $p = 0.83$, $\beta = 0.036$). Averaging across treatments gives a competitive efficiency of 0.42, which is significantly lower than the critical competitive efficiency of 0.59 ($t_7 = 3.34$, $p = 0.012$). Producers, therefore, did not have a competitive advantage.

Does incidence of scrounging increase with requirement?

The observed incidence of scrounging was not affected by the order in which focal starlings received the treatments (Fisher exact test, $p = 0.21$), the experience of the core flock (ANOVAR, $F_{1,4} = 4.15$, $p = 0.10$), or the time of day (ANOVAR, $F_{4,16} = 0.48$, $p = 0.75$). The incidence of passive scrounging was not affected by the

treatment order (Fisher exact test, $p = 0.34$), the experience of the core flock (ANOVAR, $F_{3,4} = 4.91$, $p = 0.079$), or the time of day (ANOVAR, $F_{4,16} = 1.87$, $p = 0.17$). The incidence of aggressive scrounging was not affected by the treatment order (Fisher exact test, $p = 0.50$), or time of day (ANOVAR, $F_{4,16} = 2.73$, $p = 0.066$), however, the core flock experience (ANOVAR, $F_{3,4} = 9.24$, $p = 0.029$) did affect the incidence of aggressive scrounging, but no straight forward pattern emerges: scrounging increased slightly over the first three focal pairs, but declined abruptly in the fourth pair.

The non-significant factors were dropped from further analyses, and the treatment effects on the incidence of scrounging and the incidence of passive scrounging were tested using paired-sample t-tests. Any treatment effect on the incidence of aggressive scrounging was tested using a two-way ANOVAR (with factors treatment and core flock experience).

There was no significant increase in the incidence of scrounging (Table 2), passive (Table 3), or aggressive (Table 4) scrounging as requirement increased. None of the starlings showed a significant increase in any scrounging between treatments (see Tables 2, 3, and 4). However, a significant number of focal starlings (7/8) increased their incidence of aggressive scrounging with requirement (one-tailed binomial, $p = 0.035$).

DISCUSSION

My measurement of scrounging appeared to represent actual scrounging decisions of the starlings. The incidence of scrounging was considerably higher than would have been expected if random encounters between starlings had been recorded. If starlings had foraged independently of one another, encounters would have been less frequent. Furthermore, if scrounging resulted from unintentional encounters with other foragers, the incidence of scrounging would have been more strongly related to the rate of patch visitation. Since neither were observed, starlings appeared to be foraging socially.

Producers from which focal starlings scrounged obtained, on average, 42 percent of the food in clumps they discovered. This amount is insufficient, according to the model, to give producers a competitive advantage. As assumed, the competitive efficiency of producers was not affected by the manipulation of requirement.

Daily food requirement, however, had an effect on the returns from scrounging. When scrounging, focal starlings obtained less food in the high requirement treatment. Since requirement had no effect on the competitive efficiency of producers, lower scrounging rewards suggests that as requirement increased, there could have been more scrounging competitors, and hence a greater likelihood of being displaced from a patch by another scrounger. Scrounging, therefore, may have increased enough in the group to have a significant effect on the returns from scrounging, but with no effect on the incidence of scrounging in the focal starlings. It would be worth investigating the possibility that core starlings adjust their scrounging

more readily than focal starlings.

When, as was true in the present case, producers lack a competitive advantage, the model predicts that scrounging increases with requirement. My results do not support this prediction. Not only was there no significant increase in the incidence of scrounging, but the number of focal starlings that did increase their scrounging was not significant. Narrowing my definition of scrounging to aggressive scrounging only, provides no indication of a significant increase in scrounging. However, a significant number of focal starlings increased their aggressive scrounging with requirement. Aggressive scrounging may be a better index of the starlings' scrounging decisions because it clearly excluded cases where individuals just happened to be foraging on the same patch (a random encounter).

Although I failed to find an increase in scrounging with requirement, the model's prediction may not be falsified for a number of reasons. First, the power of the comparison of the mean incidences of scrounging between treatments was unimpressive. The probability of making an error by concluding no effect of requirement (β) is 0.18, an unacceptably high value for such a conclusion (Peterman 1990). Second, when building their model, Caraco & Giraldeau (1991) assumed that increased scrounging on the part of a forager would result in a decreased variance in food intake. I used two separate analyses to test this assumption. The first, a correlational analysis did not indicate the existence of a negative correlation between the incidence of scrounging and variance in food intake/patch, within individuals. Either the assumption was wrong, or, more likely, the data range was insufficient to

test the assumption. The second analysis, a variance ratio test, supported the conclusions of the former, showing that variance did not change with the incidence of scrounging. The two analyses together failed to provide evidence that scrounging influences variance in food intake. If scrounging was not related to variance in food intake, then there is no reason to believe that requirement should have had any effect on the incidence of scrounging. Under the present conditions therefore, the model's prediction remains untested.

Requirement may not be a strong factor in a forager's scrounging decision. When numerically analyzing their model, Caraco & Giraldeau (1991) found that when producers lacked a competitive advantage, the incidence of scrounging did increase with requirement, but that "the level of scrounging [was] essentially independent of requirement" (p.573). When the producer's competitive efficiency is low, there should be a high proportion of scroungers in the group, so that the level of scrounging becomes essentially independent of requirement. Thus, the non-significant increases in scrounging I observed may not be surprising, and may, in fact, have been quantitatively consistent with the model's prediction.

My results suggest that when scroungers have a competitive advantage, requirement may have little effect on scrounging. Two points relating to this prediction need to be emphasized. Because the model's prediction is sensitive to the scroungers' competitive advantage, it could be tested by manipulating competitive advantage rather than requirement. Competitive advantage may be manipulated by using an experimental apparatus that gives the producer an advantageous spot for

obtaining more food from a food clump. Alternatively, one may use a species where, unlike the starlings, the producer has a clear competitive advantage.

An actual manipulation of physiological requirement, such as that induced by treatments at ambient temperatures of 5 and 25 °C, as in Caraco et al. (1990), would be a superior manipulation of requirement. My manipulation of requirement, through periods of food deprivation, simulated conditions following a poor morning of foraging (high requirement treatment), and following a successful morning of foraging (low requirement treatment). In effect, the starlings' physiological requirement remained the same, but food deprivation changed the amount of food required to maintain body weight during the time period remaining. Food deprivation was, nonetheless a meaningful manipulation. When requirement was increased, patch visitation rate increased. If more food is needed, then it makes sense to increase search rate. This suggests that manipulation of food deprivation did influence the foraging behaviour of the starlings, and the lack of a significant shift in scrounging can not be attributed to an ineffective manipulation, or undetectable change in conditions, but rather to the proposed independence of scrounging and requirement.

The lack of evidence supporting the assumption that scrounging is risk-averse suggests that scrounging may be independent of requirement, as indicated by Caraco & Giraldeau's (1991) numerical analysis, though the proportion of scrounging in my groups was not as high as their simulation predicts. Thus, the results of the present experiment do not constitute a strong test of the model's prediction. A more powerful test of the model may involve its prediction concerning expected patch encounter

rates, because, according to Caraco & Giraldeau's simulation, scrounging incidence should be considerably more sensitive to that factor.

EXPERIMENT 2: MANIPULATION OF FOOD DENSITY

This second experiment tests the prediction that the incidence of scrounging will increase when the number of food clumps producers expect to discover increases.

METHODS

The number of food clumps that producers expected to discover was manipulated by changing the number of food-containing patches per trial (density of food). In the low food density treatment, 5/15 patches contained food, and, in the high food density treatment, 10/15 patches contained food. This increased amount of food available for discovery should effectively increase the starlings' rate of discovery (and intake).

The model's prediction, however, deals with the number of food clumps producers expect to discover, which is a product of the discovery rate and the available foraging time. By holding foraging time constant, an increased rate of discovery will increase the number of food clumps that producers expect to discover.

After the starlings had settled in the aviary, they were given one day of training trials followed by one day of testing trials for each treatment. Again, the order of treatments was controlled, with half the starlings experiencing the low food density first, and half experiencing the high food density first. Starlings were given two days of trials under each treatment condition, but only data from the second day

of trials for each treatment were included in the analysis. Data were analyzed in the same manner as for the first experiment.

RESULTS

General Foraging Behaviour

Focal starlings started trials by scrounging in only 0.062 of the trials. The duration of trials was not affected by the food density, lasting 27.07 s (SD = 2.54, n = 8) in the low food density treatment and 27.83 s (SD = 1.78, n = 8) in the high food density treatment (ANOVAR, $F_{1,7} = 0.44$, $p = 0.58$). Trial duration did not change over the day (ANOVAR, $F_{4,28} = 0.37$, $p = 0.83$).

When foraging on the patches, focal starlings had a patch visitation rate of 0.40 patches/s (SD = 0.048, n = 8) in the low food density treatment, and decreased patch visitation to 0.34 patches/s (SD = 0.038, n = 8) in the high food density treatment (ANOVAR, $F_{1,7} = 29.47$, $p = 0.001$). The patch visitation rate was not affected by the time of day (ANOVAR, $F_{4,28} = 2.45$, $p = 0.069$).

Food intake rate of focal starlings increased from 0.15 food items/s (SD = 0.033, n = 8) to 0.24 food items/s (SD = 0.043, n = 8) when the food density was increased ($t_7 = 8.67$, $p < 0.001$). The intake rates in each treatment were not significantly different from the 0.13 food items/s expected in the low food density treatment ($t_7 = 1.53$, $p = 0.17$, $\beta = 0.24$), nor the 0.26 food items/s expected in the high food density treatment ($t_7 = 1.05$, $p = 0.33$, $\beta = 0.12$) if all foragers shared

food equally over the duration of the trial.

Scrounging or Random Encounter on the Patches?

The incidence of scrounging was not merely the result of random encounters of starlings on the patches. The incidence of scrounging observed in the low food density treatment (0.30, SD = 0.17, n = 8) was significantly higher than the 0.11 predicted for random encounters ($t_7 = 3.12$, $p = 0.017$). The incidence of scrounging in the high food density treatment (0.40, SD = 0.16, n = 8) was also higher than the 0.11 predicted for random encounters ($t_7 = 5.18$, $p = 0.001$).

The incidence of scrounging was not correlated with the rate of patch visitation in either the low food density treatment ($r = 0.47$, $p = 0.24$, n = 8) or the high food density treatment ($r = 0.27$, $p = 0.52$, n = 8). Even when the data from the two treatments were pooled, there was no correlation ($r = 0.12$, $p = 0.65$, n = 16).

The Rewards of Producing and Scrounging

When all patches are considered, patch production provided starlings with less than one food item per patch (Table 5). Not surprisingly, the mean number of food items obtained by producing increased significantly when food density increased (Table 5, $t_7 = 4.66$, $p = 0.002$). The same is true for scrounging (Table 5, $t_7 = 2.01$, $p = 0.084$, $\beta = 0.38$). The number of food items obtained by producing and scrounging were not significantly different in the low ($t_7 = 1.06$, $p = 0.32$, $\beta = 0.12$) or high ($t_7 = 0.94$, $p = 0.38$, $\beta = 0.098$) food density treatments (Table 5).

The amount of food obtained by passive scrounging was not affected by food density (Table 5, $t_7 = 0.74$, $p = 0.49$, $\beta > 0.10$). Neither was the amount of food obtained by aggressive scrounging affected by food density (Table 5, $t_7 = 1.03$, $p = 0.34$, $\beta = 0.11$). Scrounging mode (i.e., passive versus aggressive) did not provide starlings with different numbers of food items/scrounged patch in either the low ($t_7 = 1.18$, $p = 0.28$, $\beta = 0.14$) or the high ($t_6 = 1.78$, $p = 0.13$, $\beta > 0.25$) food density treatments (Table 5).

When starlings successfully produced, they obtained roughly half of the food items in a patch (Table 5). The number of food items obtained by successful producing was not affected by the food density (Table 5, $t_7 = 0.18$, $p = 0.86$, $\beta = 0.035$). When starlings successfully scrounged, they obtained about a third of the food items in a patch (Table 5), with no effect of food density ($t_7 = 0.80$, $p = 0.45$, $\beta = 0.078$). Comparisons of the amount of food obtained by successful producing and scrounging demonstrated that starlings obtained significantly more food by successfully producing than successfully scrounging in both the low ($t_7 = 3.41$, $p = 0.011$) and high ($t_7 = 2.60$, $p = 0.036$) food density treatments (Table 5).

The number of food items obtained by successful passive scrounging was not affected by food density (Table 5, $t_6 = 0.78$, $p = 0.48$, $\beta > 0.05$). The same can be said for successful aggressive scrounging (Table 5, $t_4 = 2.12$, $p = 0.10$, $\beta > 0.25$). When comparing the amounts of food obtained by successful passive versus successful aggressive scrounging, aggressive scrounging provided significantly more food to the starlings than passive scrounging in the low food density treatment (Table 5, $t_4 =$

3.29, $p = 0.03$). However, no such effect of scrounging mode was apparent in the high food density treatment (Table 5, $t_5 = 0.58$, $p = 0.59$, $\beta > 0.05$).

Testing the Model

Did the increase in food density increase the producers' rate of discovery?

In the low food density treatment, focal starlings produced food clumps at a rate of 0.044 food clumps/s (SD = 0.013, $n = 8$), and this rate increased significantly to 0.063 food clumps/s (SD = 0.020, $n = 8$) in the high food density treatment ($t_7 = 3.18$, $p = 0.016$). Thus, increasing the food density did increase the producers' rate of discovery.

Does incidence of scrounging increase with food density?

Neither the order in which the focal starlings received the treatments (Fisher exact test, $p = 1.00$), the experience of the core flock (ANOVAR, $F_{3,4} = 3.42$, $p = 0.13$), nor the time of day (ANOVAR, $F_{4,16} = 0.59$, $p = 0.68$) affected the incidence of scrounging. The same was true for the incidence of passive scrounging for treatment order (Fisher exact test, $p = 0.34$), experience of the core flock (ANOVAR, $F_{3,4} = 1.76$, $p = 0.29$), and time of day (ANOVAR, $F_{4,16} = 0.26$, $p = 0.90$), as well as for the incidence of aggressive scrounging for treatment order (Fisher exact test, $p = 1.00$), core flock experience (ANOVAR, $F_{3,4} = 3.59$, $p = 0.12$), and time of day (ANOVAR, $F_{4,16} = 0.65$, $p = 0.64$). The non-significant factors, therefore, were dropped from further analyses, so that treatment effects were tested using paired

sample t-tests.

Directional changes in the incidences of scrounging were consistent with the model's prediction in 8/8 focal starlings (one-tailed binomial, $p = 0.0039$). Furthermore, the incidence of scrounging increased significantly with increased food density (Table 6, $t_7 = 3.09$, $p = 0.009$). Analysis by scrounging mode revealed that incidence of aggressive scrounging was considerably higher than the incidence of passive scrounging in the low ($t_7 = 2.63$, $p = 0.034$) and high ($t_7 = 4.75$, $p = 0.002$) food density treatments (Table 6). Moreover, food density had no significant effect on the incidence of passive scrounging (Table 6, $t_7 = 1.82$, $p = 0.94$, $\beta = 0.32$), but the incidence of aggressive scrounging increased significantly with food density (Table 6, $t_7 = 3.89$, $p = 0.003$).

Does variance in food intake decrease when scrounging increases?

For each focal starling, treatment and time of day were non-significant factors contributing to the variance in food intake/patch. One focal starling showed a significant negative correlation between the incidence of scrounging and the variance in food intake/patch (Fig. 3). Similar conclusions were reached when the incidence of aggressive scrounging alone was used, but in that case no significant correlations were found.

Since the mean number of food items/patch obtained by scrounging increased significantly, this change in the mean may be hiding any changes in variance. If the assumption that scrounging is risk-averse is correct, coefficient of variation (CV) of

intake/patch should decrease as scrounging increases. The mean CV in the low food density treatment was 2.64 (SD = 0.34, n = 8), and CV decreased significantly to 1.82 (SD = 0.15, n = 8) in the high food density treatment ($t_7 = 6.43$, $p < 0.001$). This shows that variance in food intake was negatively related to the incidence of scrounging.

DISCUSSION

The results provide strong evidence that I was truly recording the starlings' scrounging decisions. For instance, the incidence of scrounging was higher than would be expected if the starlings were simply moving independently of one another. In addition, if starlings had been foraging independently, the incidence of scrounging would have been positively related to the rate of patch visitation, but no such correlation was found. In fact, when scrounging increased, the rate of patch visitation decreased. Thus, I can conclude that these starlings were foraging socially.

The results provide support for Caraco & Giraldeau's (1991) risk-sensitive producer-scrounger model. When I manipulated the number of food clumps that producers expected to discover, starlings scrounged significantly more, as predicted by the model. The results also show that the assumption of the model was met. The coefficient of variation (CV) which scales variance to the mean, may allow a better comparison between treatments. We expect the CV in intake per patch to decrease from the low to the high food density treatments due to the increase in scrounging, and indeed, the CV of a significant number of focal starlings decreased when food

density was increased. Thus, the model's assumption that scrounging provided a risk-averse option was verified.

In a rich habitat, starlings expressed a higher incidence of scrounging than in a poor habitat. This difference was obtained while keeping flock size constant. However, in more natural settings, increased food density may have even greater effects on scrounging than expected on the basis of food density alone due to the attraction of more foragers. Both models of Caraco & Giraldeau (1991) and Vickery et al. (1991) predicted that increased group size leads to increased scrounging, and group size effects are supported by field observations of oystercatchers (*Haematopus ostralegus*, Ens & Goss-Custard 1984). Thus, group size effects may compound food density effects, leading to even larger differences in the incidence of scrounging between rich and poor habitats.

The starlings behaved according to both the assumption and the prediction of the risk-sensitive producer-scrounger model, that as the expected number of encountered food clumps increases, foragers become risk-averse and consequently scrounge more.

GENERAL DISCUSSION

The lack of support for the assumption that scrounging is risk-averse (in experiment 1) suggests that scrounging was independent of requirement, as per Caraco & Giraldeau's (1991) numerical analysis. As a result, experiment 1 failed to test the prediction that as requirement increases risk-sensitive starlings should scrounge more.

Experiment 2, however, provided support for both the prediction that scrounging should increase with the expected number of food clumps, and the assumption that scrounging is risk-averse.

Use of Assessment

Caraco & Giraldeau's (1991) model assumes that individuals decide on their incidence of scrounging by assessment. Individuals, therefore, are expected to employ both tactics in order to assess allocation of foraging effort to each tactic. The stable outcome of assessment and allocation in accordance to local foraging conditions is expected to be equal payoffs to each tactic (Maynard Smith 1982). My results show that starlings changed their scrounging decision in response to local foraging conditions (changes in food density). Moreover, equality of rewards obtained from producing and scrounging, coupled with the absence of any specialist producers or scroungers are consistent with the assumption that starlings base their scrounging decision on some form of assessment. Other studies have also provided evidence of assessment in the context of producing and scrounging. Giraldeau & Lefebvre (1986) found that when producers were removed from a flock of pigeons, scroungers switched to producing, and when the producers were returned to the flock, they switched back to scrounging. And, Giraldeau et al. (in press) showed that spice finches could increase their allocation to scrounging when producing became energetically more costly.

Competitive Advantage

Producers lacked a competitive advantage in both experiments, even against focal starlings that scrounged relatively infrequently, and therefore, were likely to be socially subordinate. The producers' lack of a competitive advantage is not surprising given that we would normally expect that dominant starlings would scrounge from subordinate starlings. Feare & Inglis (1979) found that in a captive flock of starlings, dominance was not correlated with either sex or weight. Rather, starlings that initiate an agonistic encounter were most likely to be dominant over their opponent (aggressive scrounging was initiated by the scroungers in my experiments). Furthermore, Caraco et al. (1989) found that when pairs of dark-eyed juncos (*Junco hyemalis*) had the opportunity of foraging independently, dominants would often follow subordinates, and initiate bouts of social foraging (scrounging). They also found, as I did, that the amount of time spent foraging socially was dependent upon the availability of food. Field studies of kleptoparasitism in water birds have also shown that dominants are most likely to scrounge (Ens & Goss-Custard 1984, Ens et al. 1990).

However, if dominants do most of the scrounging, it does not explain why even infrequent scroungers have a competitive advantage over producers. One possibility is that scroungers had a competitive advantage at patches due to a position effect. Hansen (1986) found, for instance, that bald eagles which scrounged while positioned in the air may be more likely to win the food. When aggressively scrounging, starlings often displaced the resident starling with a peck or squawk from

the side or behind. Two observations suggest that scrounging starlings may have had a position advantage. First, foiled scrounging attempts were infrequent. Producers very rarely defended a patch. Second, whenever a producer did defend a patch (aside from situations considered foiled attempts), it was first displaced, and then turned to displace the scrounger. Thus, the resident starling may have been in a positional disadvantage relative to the scrounger.

Passive vs Aggressive Scrounging

Analysis of scrounging modes has led to paradoxical results. For instance, aggressive scrounging was considerably more frequent than passive scrounging, yet yielded the same amount of food as passive scrounging, and appeared to require more effort. It follows that the most frequently used scrounging mode yielded the lower net benefit. One possible explanation for this result is that aggressive scrounging provided some unmeasured benefit to its user. For example, the small size of the foraging flocks may have allowed starlings to identify one another. As a result, starlings which scrounged aggressively may have been able to produce with a lower chance of being scrounged from by subordinate starlings, if dominance is transferrable between tactics.

No model to date has looked at alternative forms of scrounging (or kleptoparasitism). If the use of aggressive versus passive scrounging was itself frequency-dependent then, stable incidences of aggressive and passive scrounging should occur when the two tactics provide equal food intakes. If such a game within

a game were taking place, it would require foragers to decide upon how much foraging effort to allocate to scrounging, then, to determine how much of that scrounging effort should be aggressive versus passive. Manipulation of food density had a significant effect on aggressive scrounging, but no effect on passive scrounging. This may indicate that different ecological conditions promote different forms of scrounging. Or, passive scrounging may simply be the result of random encounters rather than scrounging decisions.

Risk-Sensitive vs Mean Maximizing

My results suggest that the decision to use scrounging may be dependent upon its effect on the variance in intake. The fact that scrounging may also reduce mean intake, suggests that some foragers may need to tradeoff their preferred mean and variance in food intake (Real et al. 1982, Caraco & Lima 1985, Stephens & Paton 1986). Ens et al. (1990) found that scrounging in curlews (*Numenius arquata*) can be explained on the basis of maximizing the net rate of energy gain, suggesting that variance is not needed to explain all instances of scrounging. However, the mean does not explain all cases. Kushlan (1978) examined scrounging (called robbing) by great egrets (*Casmerodius albus*). Based upon a cost-benefit analysis of the two foraging options available to the egrets (produce or scrounge), he found that use of scrounging was less than optimal and he could not determine the adaptive significance of scrounging.

Vickery et al. (1991) proposed a deterministic model of producing and

scrounging that also includes the producer's rate of food clump discovery. However, Vickery et al.'s model predicts that the incidence of scrounging will not be influenced by food density. My observation that starlings increase their incidence of scrounging in response to increased food density suggests that the starlings' responses cannot be explained in a mean maximizing context.

Contributions to Risk-Sensitive Foraging Theory

Scrounging reduces the mean intake of foraging group members (Giraldeau et al. 1991, in press, Vickery et al. 1991), and has therefore, been pictured as an inevitable cost of social foraging. However, scrounging may not only be a cost of social foraging. My results demonstrate that scrounging is a risk-averse option, so that under conditions of positive expected energy budgets, scrounging provides reduced variance in intake, and hence, may be beneficial. This also provides a mechanism for why group foraging is proposed to be a risk-averse foraging option (Caraco & Pulliam 1984; Pulliam & Caraco 1984). The effect of scrounging on a forager's probability of starvation may provide at least part of an explanation for why scrounging occurs, and suggests that scrounging's negative effect on sociality may have been overestimated.

Previous theoretical work on risk-sensitive foraging (Houston & McNamara 1985, McNamara & Houston 1992) has suggested that a forager's sensitivity to variance should be affected by proximity of the time horizon. If a forager must meet its requirement before nightfall, and is falling short, the forager may not be risk-prone

all day, but rather switch to a risk-prone tactic during a critical period just before dusk. I found no effect of time of day suggesting either that starlings were not working with a daily time horizon, or that the manipulation of requirement was not strong enough to put the starlings into dire trouble.

Reboreda & Kacelnik (1991) used starlings in their experiment on risk-sensitivity, and showed that starlings are sensitive to variance in both food intake, and time delay from the moment of choice until food was available. Caraco & Giraldeau's (1991) model does not consider any effect of variance in time delay, nor do my experiments control for time delays. A number of animals are known to prefer shorter time delays and variable over fixed time delays (Kagel et al. 1986). My data suggest that successful scrounging opportunities arose more frequently (with shorter delays between scrounging opportunities) than successful producing discoveries. More foraging effort is devoted to producing than scrounging (as indicated by mean incidences of scrounging between 0.27 and 0.40 in the two experiments), and successful producing events provide more food than successful scrounging events. Yet, on average, producing and scrounging provided the same amount of food. Thus, scrounging provided proportionally more success than producing, and successful scrounging must occur more frequently than successful producing. Scrounging, therefore, may be used to decrease delays between feeding events, as suggested by Thompson et al. (1974). If this were so, foragers may have changed their allocation of foraging effort to scrounging based upon variability in time delay as well as variability in intake. Future studies should take this possibility into consideration.

Conclusions

I have shown, as Caraco & Giraldeau's (1991) model assumes, that an individual's incidence of scrounging can have a significant effect upon its variance in intake. Predictions stemming from this assumption are that the amount of food discovered and the amount of food required will affect the incidence of scrounging expressed by individuals. I have provided support for the prediction that food density will influence scrounging, but found that the incidence of scrounging may be independent of requirement. The effect of food density on scrounging means that a stochastic model of producing and scrounging is needed to explain fully the important aspects of social foraging. However, until the effect of requirement in situations where producers have the competitive advantage has been tested, we cannot determine whether requirement is needed.

Deterministic models fail to predict the effect of factors such as food density upon scrounging, suggesting that the modelling approach used by Caraco & Giraldeau (1991) is appropriate for explaining the incidence of scrounging and factors that influence its expression. If other aspects of Caraco & Giraldeau's (1991) stochastic producer-scrounger model prove to be wrong, then modification must keep the stochastic elements if we hope to understand scrounging and social foraging.

REFERENCES

- Altmann, J. 1974. Observational study of behavior: sampling methods. Behaviour, 49, 227-265.
- Barnard, C.J. & Sibly, R.M. 1981. Producers and scroungers: a general model and its application to captive flocks of house sparrows. Anim. Behav., 29, 543-550.
- Barnard, C.J. & Brown, C.A.J. 1985a. Risk-sensitive foraging in common shrews (*Sorex araneus* L.). Behav. Ecol. Sociobiol., 16, 161-164.
- Barnard, C.J. & Brown, C.A.J. 1985b. Competition affects risk-sensitivity in foraging shrews. Behav. Ecol. Sociobiol., 16, 379-382.
- Barnard, C.J. & Thompson, D.B.A. 1985. Gulls and Plovers: The Ecology of Mixed Species Feeding Groups. London: Croom Helm.
- Barnard, C.J., Brown, C.A.J., Houston, A.I., & McNamara, J.M. 1985. Risk sensitive foraging in common shrews: an interruption model and the effect of mean and variance in reward rate. Behav. Ecol. Sociobiol., 18, 139-146.
- Brockmann, H.J. & Barnard, C.J. 1979. Kleptoparasitism in birds. Anim. Behav., 27, 487-514.
- Caraco, T. 1980. On foraging time allocation in a stochastic environment. Ecology, 61, 119-128.
- Caraco, T. 1981. Energy budgets, risk and foraging preferences in dark-eyed juncos (*Junco hyemalis*). Behav. Ecol. Sociobiol., 8, 213-217.

- Caraco, T. 1982. Aspects of risk-aversion in foraging white-crowned sparrows. Anim. Behav., 30, 719-727.
- Caraco, T. 1983. White-crowned sparrows (*Zonotrichia leucophrys*): foraging preferences in a risky environment. Behav. Ecol. Sociobiol., 12, 63-69.
- Caraco, T., Martindale, S. & Whittam, T.S. 1980. An empirical demonstration of risk-sensitive foraging preferences. Anim. Behav., 28, 820-830.
- Caraco, T. & Lima, S.L. 1985. Foraging juncos: interaction of reward mean and variability. Anim. Behav., 33, 216-224.
- Caraco, T., Barkan, J.L., Brisbib, L., Lima, S., Mohan, A., Newman, J.A., Webb, W. & Withiam, M.L. 1989. Dominance and social foraging: a laboratory study. Anim. Behav., 38, 41-58.
- Caraco, T., Blanckenhorn, W.U., Gregory, G.M., Newman, J.A., Recer, G.M. & Zwicker, S.M. 1990. Risk-sensitivity: ambient temperature affects foraging choice. Anim. Behav., 39, 338-345.
- Caraco, T. & Giraldeau, L.-A. 1991. Social foraging: producing and scrounging in a stochastic environment. J. theor. Biol., 153, 559-583.
- Caraco, T. & Pulliam, H.R. 1984. Sociality and survivorship in animals exposed to predation. In: A New Ecology: Novel Approaches to Interactive Systems. (Ed. by P.W. Price, C.N. Slobodchikoff & W.S. Gaud). pp. 279-309. New York: John Wiley & Sons.
- Cartar, R.V. 1991. A test of risk-sensitive foraging in wild bumble bees. Ecology, 72, 888-895.

- Cartar, R.V. & Dill, L.M. 1990. Why are bumble-bees risk-sensitive foragers?
Behav. Ecol. Sociobiol., 26, 121-127.
- Clark, C.W. & Mangel, M. 1984. Foraging and flocking strategies: information in an uncertain environment. Am. Nat., 123, 626-641.
- Ens, B.L. & Goss-Custard, J.D. 1984. Interference among oystercatchers, *Haematopus ostralegus*, feeding on mussels, *Mytilus edulis*, on the Exe estuary. J. Anim. Ecol., 53, 217-231.
- Ens, B.J., Esselink, P. & Zwarts, L. 1990. Kleptoparasitism as a problem of prey choice: a study on mudflat-feeding curlews, *Numenius arquata*. Anim. Behav., 39, 219-230.
- Feare, C. 1984. The Starling. Oxford: Oxford University Press.
- Feare, C.J. & Inglis, I.R. 1979. The effects of reduction of feeding space on the behaviour of captive starlings *Sturnus vulgaris*. Ornis Scand., 10, 42-47.
- Gillespie, R.G. & Caraco, T. 1987. Risk-sensitive foraging strategies of two spider populations. Ecology, 68, 887-899.
- Giraldeau, L.-A. & Lefebvre, L. 1986. Exchangeable producer and scrounger roles in a captive flock of feral pigeons: a case for the skill pool effect. Anim. Behav., 34, 797-803.
- 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. & Templeton, J.J. 1991. Food scrounging and diffusion of foraging skills in pigeons, *Columbia livia*: the importance of tutor and observer rewards. Ethology, 89, 63-72.
- Giraldeau, L.-A., Soos, C. & Beauchamp, G. In Press. A test of the producer-scrounger foraging game in captive flocks of spice finches, *Lonchura punctulata*. Behavioral Ecology Sociobiology.
- Hansen, A.J. 1986. Fighting behavior in bald eagles: a test of game theory. Ecology, 67, 787-797.
- Hamm, S.L. & Shettleworth, S.J. 1987. Risk aversion in pigeons. J. Exp. Psychol.: Anim. Behav. Proc., 13, 376-383.
- Harley, C.B. 1981. Learning the evolutionarily stable strategy. J. theor. Biol., 89, 611-633.
- Houston, A. & McNamara, J. 1985. The choice of two prey types that minimises the probability of starvation. Behav. Ecol. Sociobiol., 17, 135-141.
- Houston, A.I. & Sumida, B.H. 1987. Learning rules, matching and frequency dependence. J. theor. Biol., 126, 289-308.
- Kagel, J.H., Green, L. & Caraco, T. 1986. When foragers discount the future: constraint or adaptation? Anim. Behav., 34, 271-283.
- Krebs, C.J. 1978. Ecology: The Experimental Analysis of Distribution and Abundance. New York: Harper & Row Publishers.
- Kushlan, J.A. 1978. Nonrigorous foraging by robbing egrets. Ecology, 59, 649-653.

- Lott, D.F. 1991. Intraspecific variation in the social systems of wild vertebrates.
Cambridge: Cambridge University Press.
- Martin, P. & Bateson, P. 1986. Measuring Behaviour: an introductory guide.
Cambridge: Cambridge University Press.
- Maynard Smith, J. 1982. Evolution and the Theory of Games. Cambridge: Cambridge
University Press.
- McNamara, J.M. & Houston, A.I. 1992. Risk-sensitive foraging: a review of the
theory. Bull. Math. Biol., 54, 355-378.
- Packer, C. & Ruttan, L. 1988. The evolution of cooperative hunting. Am. Nat., 132,
159-198.
- Parker, G.A. 1984. The producer/scrounger model and its relevance to sexuality. In:
Producers and Scroungers: Strategies of Exploitation and Parasitism (Ed. by
C.J. Barnard), pp. 127-153. New York: Chapman and Hall.
- Peterman, R.M. 1990. Statistical power analysis can improve fisheries research and
management. Can. J. Fish. Aquat. Sci., 47, 2-15.
- Pitcher, T.J. 1986. Functions of shoaling behaviour in teleosts. In: The Behaviour of
Teleost Fishes (Ed. by T.J. Pitcher), pp. 294-337.
- Potvin, C., Lechowicz, M.J. & Tardif, S. 1990. The statistical analysis of
ecophysiological response curves obtained from experiments involving repeated
measures. Ecology, 71, 1389-1400.

- Powell, G.V.N. 1974. Experimental analysis of the social value of flocking by starlings (*Sturnus vulgaris*) in relation to predation and foraging. Anim. Behav., 22, 501-505.
- Pulliam, H.R. & Caraco, T. 1984. Living in groups: is there an optimal group size? In: Behavioural Ecology: An Evolutionary Approach. (Ed. by J.R. Krebs & N.B. Davies). pp.122-147. Sunderland, Massachusetts: Sinauer Associates Inc.
- Real, L. 1981. Uncertainty and pollinator-plant interactions: the foraging behavior of bees and wasps: a novel approach. Ecology, 62, 20-26.
- Real, L., James, O. & Silverfine, E. 1982. On the trade-off between the mean and the variance in foraging: effect of spatial distribution and color preference. Ecology, 63, 1617-1623.
- Reboreda, J.C. & Kacelnik, A. 1991. Risk sensitivity in starlings: variability in food amount and food delay. Behav. Ecol., 2, 301-308.
- Stephens, D.W. 1981. The logic of risk-sensitive foraging preferences. Anim. Behav., 29, 628-629.
- Stephens, D.W. & Paton, S.R. 1986. How constant is the constant of risk-aversion? Anim. Behav., 34, 1659-1667.
- Stephens, D.W. & Krebs, J.R. 1986. Foraging Theory. Princeton: Princeton University Press.
- Templeton, J.J. 1993. The use of personal and public information in foraging flocks of European starlings. Unpublished PhD Thesis, Concordia University.

- Thompson, W.A., Vertinsky, I. & Krebs, J.R. 1974. The survival value of flocking in birds: a simulation model. J. Anim. Ecol., 43, 785-820.
- Uetz, G.W. 1988. Group foraging in colonial web-building spiders: evidence for risk-sensitivity. Behav. Ecol. Sociobiol., 22, 265-270.
- Vickery, W.L., Giraldeau, L.-A., Templeton, J.J., Kramer, D.L. & Chapman, C.A. 1991. Producers, scroungers, and group foraging. Am. Nat., 137, 847-863.
- Vollrath, F. 1984. Kleptobiotic interactions in invertebrates. In: Producers and Scroungers: Strategies of Exploitation and Parasitism (Ed. by C.J. Barnard), pp. 61-94. New York: Chapman and Hall.
- Waddington, K.D., Allen, T. & Heinrich, B. 1981. Floral preferences of bumblebees (*Bombus edwardsii*) in relation to variable vs. fixed rewards. Anim. Behav., 29, 779-784.
- Wilkinson, L. 1990. SYSTAT: The System for Statistics. Evanston, IL: SYSTAT, Inc.
- Williamson, P. & Gray, L. 1975. Foraging behavior of the starling (*Sturnus vulgaris*) in Maryland. Condor, 77, 84-89.
- Wunderle, J.M., Jr. & Cotto-Navarro, Z. 1988. Constant vs. variable risk-aversion in foraging bananaquits. Ecology, 69, 1434-1438.
- Zar, J.H. 1984. Biostatistical analysis. 2nd edn. Englewood Cliffs, NJ: Prentice-Hall, Inc.

Table 1. Variance in food intake/patch for each focal starling in the low requirement (low R) and high requirement (high R) treatments, the degrees of freedom (df) for each treatment (high R, low R), the F from the variance ratio test. $F = s^2_{\text{low R}} \div s^2_{\text{high R}}$ for all birds except birds 4 & 7, where the F ratio is inverted due to these two starlings decreasing their scrounging as requirement increased (see Table 2). All $p \geq 0.10$, except bird 8 where $0.05 > p > 0.025$.

Bird	Variance in food intake/patch		df	F
	low R	high R		
1	0.35	0.22	3,4	1.59
2	0.31	0.080	4,4	3.88
3	0.10	0.057	4,4	1.75
4	0.040	0.068	4,4	1.70
5	0.017	0.032	4,4	0.53
6	0.11	0.42	4,4	0.26
7	0.15	0.055	4,4	0.37
8	0.068	0.0094	4,4	7.23 *

Table 2. The mean incidences of scrounging (SD) for each focal starling in the low (low R) and high (high R) requirement treatments, the t value of a one-tailed paired sample t-test for comparing individual means across requirement, associated degrees of freedom (df), the p value and the probability of making a type II error (β). The means of all focal birds are presented in the last line.

Bird	Mean incidence of scrounging in		t	df	p	β
	Low R	High R				
1	0.27 (0.19)	0.38 (0.19)	0.54	3	0.31	>0.05
2	0.14 (0.16)	0.21 (0.12)	1.70	4	0.082	>0.25
3	0.24 (0.08)	0.31 (0.17)	1.00	4	0.19	>0.10
4	0.36 (0.09)	0.23 (0.14)	-1.52	4	0.90	>0.25
5	0.33 (0.18)	0.43 (0.21)	0.70	4	0.26	>0.10
6	0.56 (0.13)	0.62 (0.20)	1.07	4	0.17	>0.10
7	0.13 (0.13)	0.11 (0.10)	-0.30	4	0.61	>0.05
8	0.16 (0.05)	0.20 (0.05)	1.08	4	0.17	>0.10
All:	0.27 (0.14)	0.31 (0.16)	1.35	7	0.11	0.18

Table 3. The mean incidences of passive scrounging (SD) for each focal starling in the low (low R) and high (high R) requirement treatments, the t value of a one-tailed paired sample t-test for comparing individual means across requirement, associated degrees of freedom (df), the p value and the probability of making a type II error (β). The means of all focal birds are presented in the last line.

Bird	Mean incidence of scrounging in		t	df	p	β
	Low R	High R				
1	0.17 (0.20)	0.22 (0.16)	0.32	3	0.38	>0.05
2	0.08 (0.17)	0.15 (0.13)	1.59	4	0.094	>0.25
3	0.10 (0.14)	0.14 (0.13)	0.83	4	0.23	>0.10
4	0.04 (0.06)	0.06 (0.05)	1.42	4	0.11	0.25
5	0.05 (0.11)	0.00 (0.00)	-1.00	4	0.81	>0.10
6	0.04 (0.10)	0.04 (0.06)	-0.12	4	0.55	0.05
7	0.13 (0.13)	0.08 (0.08)	-0.84	4	0.78	>0.10
8	0.10 (0.08)	0.10 (0.04)	-0.12	4	0.55	>0.05
All:	0.09 (0.05)	0.10 (0.07)	0.64	7	0.27	0.06

Table 4. The mean incidences of aggressive scrounging (SD) for each focal starling in the low (low R) and high (high R) requirement treatments, the t value of a one-tailed paired sample t-test for comparing individual means across requirement, associated degrees of freedom (df), the p value and the probability of making a type II error (β). The means of all focal birds are presented in the last line, with the results from the ANOVAR including core flock experience.

Bird	Mean incidence of scrounging in		t	df	p	β
	Low R	High R				
1	0.10 (0.15)	0.16 (0.12)	0.58	3	0.30	> 0.05
2	0.03 (0.08)	0.06 (0.06)	0.94	4	0.20	> 0.10
3	0.14 (0.11)	0.21 (0.19)	0.55	4	0.31	> 0.05
4	0.32 (0.10)	0.17 (0.16)	-1.58	4	0.91	> 0.10
5	0.28 (0.18)	0.44 (0.21)	1.26	4	0.14	> 0.10
6	0.52 (0.12)	0.59 (0.22)	1.11	4	0.16	> 0.10
7	0.00 (0.00)	0.03 (0.04)	1.55	4	0.098	> 0.25
8	0.06 (0.06)	0.10 (0.04)	1.19	4	0.15	> 0.10
All:	0.18 (0.18)	0.22 (0.20)	$F_{1,4} = 1.67$		$p = 0.27$	

Table 5. The mean (SD, n) number of food items obtained per patch that has been produced and scrounged in the low and high food density treatments. Scrounging is further subdivided into passive and aggressive scrounging. Presented first are data from all patches visited, then just the data from successful patches (i.e., food present).

Treatment	Producing	Scrounging	Aggressive	Passive
(i) all patches				
Low	0.43 (0.11, 8)	0.36 (0.21, 8)	0.30 (0.41, 8)	0.62 (0.60, 8)
High	0.80 (0.27, 8)	0.61 (0.33, 8)	0.47 (0.29, 8)	0.92 (0.70, 8)
(ii) successful patches				
Low	2.55 (0.54, 8)	1.46 (0.61, 8)	1.97 (0.58, 5)	1.29 (0.49, 7)
High	2.52 (0.52, 8)	1.64 (0.61, 8)	1.67 (0.57, 8)	1.83 (0.75, 6)

Table 6. The mean (SD) incidences of scrounging for starlings tested in the low and high food density treatments. Scrounging is further broken down into aggressive and passive modes.

	Low	High
Scrounging	0.30 (0.17)	0.40 (0.16)
Aggressive	0.24 (0.17)	0.36 (0.17)
Passive	0.06 (0.03)	0.05 (0.03)

FIGURE CAPTIONS

Figure 1. Frequency distributions of two foraging options with the same mean intake, but different variances in intake. (a) If required intake is greater than expected intake, then the probability of exceeding the requirement can be maximized by choosing the risk-prone option (as shown by shading). (b) If required intake is less than expected intake, then the probability of failing to meet the requirement can be minimized by choosing the risk-averse option (as shown by shading).

Figure 2. The standard deviation (SD) of food intake/patch plotted against the incidence of scrounging for each focal starling in experiment 1, with the correlation coefficients (r), significance levels (p), and sample sizes (n). The model assumes that the variance in food intake decreases as scrounging increases.

Figure 3. The standard deviation (SD) of food intake/patch plotted against the incidence of scrounging for each focal starling in experiment 2, with the correlation coefficients (r), significance levels (p), and sample sizes (n). The model assumes that the variance in food intake decreases as scrounging increases.





