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An empirical investigation of risk-sensitivity in foraging flocks of Nutmeg Mannikins
(Lonchura punctulata)

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ABSTRACT

An empirical investigation of risk-sensitivity in foraging flocks of Nutmeg Mannikins
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Gi-Mick Wu

Foraging in a group allows for the exploitation of other individuals' food findings, often modeled as a producer-scrounger game. Producer-scrounger games assume that searching for food patches (producer) and for exploitation opportunities (scrounger) are mutually exclusive tactics, and predict that the proportion of scrounger in a group should reach a stable equilibrium where both tactics provide equal payoffs. A stochastic producer-scrounger model assumes that scrounger reduces the variability of intake and that animals minimize the probability of incurring an energy shortfall (risk-sensitive). Consequently, it predicts that the proportion of scrounger at SEF should depend on the animals' energy requirement. In experiment one, I tested the crucial assumption that producer yields a more variable intake than scrounger. I observed flocks of Lonchura punctulata foraging for hidden patches of seeds on a board, in an indoor aviary. At a short time scale, producer yielded a more variable intake than scrounger in 17/20 birds. Based on the cumulative probability distributions of intake rates, scrounger frequency should decline with decreasing energy reserves, the opposite predicted by the stochastic model. In experiment two 7/8 birds reduced their use of scrounger with decreasing energy reserves. I conclude that L. punctulata is sensitive to the variability of intake rate (risk-sensitive), but that the current stochastic producer-scrounger model does not apply to these birds.

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INTRODUCTION

Social foraging

Many animals gather into foraging groups for a number of reasons. They may be forming groups by simple aggregation at food patches (see Giraldeau & Caraco 2000 for a review) or because of advantages inherent to groups. Groups can reduce the risk of predation because of a dilution of predation-risk among group members, an increase in vigilance due the whole group scanning for predators, the group having a confusion effect on predators, or concerted defense against predators (see Pulliam & Millikan 1982 and Quenette 1990 for reviews). Evidence for anti-predatory advantages of groups has been found in fishes, birds and mammals (see Elgar 1989 and Quenette 1990 for reviews). In a group, individuals have the opportunity to join and exploit the food findings of others (Pulliam & Millikan 1982; Beauchamp & Giraldeau 1996). This can have many consequences on the foraging behavior of group members and on the outcome of foraging. Models that analyze the decision to join foraging groups (information-sharing models) assume that all individuals in a group search for food patches and monitor joining opportunities simultaneously, so that they share the patches discovered by the group equally. This can result in an increase in feeding rate (Thompson et al. 1974; Clark & Mangel 1984), a reduction in the variance of feeding rate (Thompson et al. 1974; Clark & Mangel 1984; Ruxton et al. 1995; Beauchamp & Giraldeau 1996), but can also decrease feeding rate (Clark & Mangel 1984; Hake & Ekman 1988; Ruxton et al. 1995). Foraging advantages of groups have been shown in many taxa (for reviews, see Pulliam & Millikan 1982; Clark & Mangel 1986; Giraldeau & Caraco 2000). However, it may not

always be possible to search for food and monitor conspecifics at the same time. For example, a bird that is probing the soil for insects in a field of tall grass may not be able to monitor conspecifics at the same time. There is evidence in some studies of birds that these two foraging modes are incompatible alternatives, between which individuals alternate (Giraldeau & Lefebvre 1986; Giraldeau et al. 1990). When this is the case, the greater the number of individuals searching for food patches, the greater the reward (payoff) for individuals that search for joining opportunities. Since the payoff of scrounger is frequency-dependent, the solution to this paradigm should be derived using game theory (Maynard-Smith 1982), in this case a producer-scrounger game (Barnard & Sibly 1981; Caraco & Giraldeau 1991; Vickery et al. 1991).

Producer-scrounger game

In a producer-scrounger game, searching for food patches (producer) and searching for joining opportunities (scrounger) are incompatible foraging tactics. The game assumes that an individual will obtain a larger amount of food when finding a patch than when joining one. This benefit, the finder's advantage (Vickery et al. 1991) can be due to the finder of a patch having access to the food before others can join in or to a positional advantage (Giraldeau et al. 1990; Ward & Enders 1985). The payoff structure of the producer-scrounger game (Figure 1) is such that producer pays more than scrounger when rare in the group and vice versa. This is because when scrounger is rare, it can exploit the discoveries of many searching individuals. The proportion of scrounger in the group will therefore increase. As scrounger becomes more common, the competition for food at every patch will increase, reducing the payoff of both producer

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and scrounger. More importantly though, as the proportion scrounger increases, fewer individuals will be searching. Thus, the number of patches available to join will decrease, thereby greatly reducing the payoff of scrounger. The payoff curves of producer and scrounger will cross at an intermediate frequency of scrounger and result in an equilibrium frequency of scrounger that will be stable because no individual can increase its payoff by changing strategy (Nash equilibrium, Giraldeau & Caraco 2000). Mottley and Giraldeau termed this a stable equilibrium frequency (SEF) of scrounger. This SEF can be the result of natural selection, and thus also be an evolutionary stable strategy (ESS, Maynard-Smith 1982). Equally, it can result from phenotypically plastic individuals adjusting to their foraging conditions. The SEF of scrounger at equilibrium increases with increasing group size (Barnard & Sibly 1981; Vickery et al. 1991) and with decreasing finder's share (Vickery et al. 1991).

A number of studies have provided evidence for mean rate-maximizing producer-scrounger models (Barnard & Sibly 1981, Vickery et al. 1991). Giraldeau et al. (1994) trained a number of Nutmeg Mannikins (Lonchura punctulata) to find seeds that were hidden in an array of holes drilled in a board (grid). Trained birds were called producer-specialists, and untrained birds, scrounger-specialists because they could not find food. The experimenters varied the proportion of scrounger-specialists in flocks of birds foraging on the grid. An increase in the proportion of scrounger-specialist resulted in a decrease in seed intake for all birds, and slightly more so for scrounger-specialists, hence providing evidence for the negative frequency-dependence of the payoffs to producer and particularly to scrounger. Mottley and Giraldeau (2000) observed L. punctulata foraging in an apparatus that spatially separated producer and scrounger tactics. The apparatus

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consisted of two adjacent compartments, of which only one (producer compartment) allowed the birds to make food patches become available by pulling on a string. Once available, food patches were accessible from both compartments. The experimenters could vary the proportion of scrounger in the apparatus precisely by changing the number of birds in each compartment, while keeping the total number of birds in the apparatus constant. When there were relatively few birds in the scrounger compartment, birds in the scrounger compartment obtained more seeds per trial than those in the producer compartment. With few birds in the producer compartment on the other hand, the reverse was observed. In addition, when the birds were allowed to switch compartments freely, the frequency of scrounger in the flock stabilized near the SEF predicted by Vickery et al. (1991). Coolen et al. (2001) observed L. punctulata foraging for seeds on a grid. They determined that the orientation of a bird's head while it was hopping indicated whether it was playing producer or scrounger. Hopping with the head down was correlated with patch finding (producer), and hopping with the head up with patch joining (scrounger). The experimenters then varied the finder's share by changing the number and size of food patches (clumpiness) while keeping the total food density constant. Birds settled on a higher rate of scrounger and hopped with the head up proportionately more when the finder's share was decreased as predicted by Vickery et al. (1991). The previous studies suggest that mean rate-maximizing producer-scrounger games are applicable, at least in small birds.

Mean rate-maximizing producer-scrounger models are deterministic in that they assumes a forager always obtains the same payoff for any given decision and set of conditions; it ignores the risk or the uncertainty associated with the outcome of a decision

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(not the risk of predation). Assuming normally distributed reward sizes, risk is proportional to the variability in the size of a reward (Stephens & Krebs 1986). Producer only yields food by finding, while scrounger yields food if any other individual finds a patch. Thus, producer yields either no reward, when no food is found and relatively large rewards (finder's advantage plus a share of the remaining food), when food is found. Scrounger on the other hand, yields relatively small rewards (only a share of the remaining food) every time any forager finds food. Hence, producer is commonly assumed to be more risky and to yield a more variable food intake than scrounger (Caraco & Giraldeau 1991; Barta & Giraldeau 2000). Differences in the variability of rewards can influence a forager's preference between options that have similar means rewards are equal, a response termed risk-sensitivity (Caraco 1980; Stephens 1981; Stephens & Krebs 1986).

Risk-sensitive foraging theory

Risk-sensitivity is based on the relationship between reward size and the forager's fitness (Jensen's inequality, Stephens & Krebs 1986; Bateson & Kacelnik 1998). A forager that has a choice should avoid alternatives that lead to higher variability in reward sizes when fitness is a concave-down function of reward size, because the potential loss of increasing variability is greater than its potential gain (Figure 2a). Inversely, when fitness is a concave-up function of reward size, a forager should prefer variability (Figure 2b). Many studies have demonstrated risk-proneness or risk-aversion in insects, fishes, birds, and mammals that were given the choice between a variable and a constant foraging option (see Kacelnik & Bateson 1996 for review). A simple preference or

aversion for variability however can be an artifact of the animal's way of assessing mean rates of intake, so that even mean rate-maximizers can display a preference or aversion for variability (McNamara & Houston 1992; Kacelnik & Bateson 1996). If an animal's apparent risk-sensitivity was due to its method of assessing mean intake rates, then one could expect it to be in a constant direction (always risk-prone or risk-averse). Demonstrating a shift from risk-aversion to risk-proneness or vice versa in the same animals would therefore constitute strong support for risk-sensitive theory. The energy budget rule predicts the conditions under which an animal should switch from risk-aversion to risk-proneness and hence can be useful to test risk-sensitive theory (Caraco 1980; Stephens 1981; McNamara & Houston 1982; Kacelnik & Bateson 1996).

Energy budget rule

Consider an animal that must store sufficient energy to survive the coming night or any other time period, during which it cannot forage. Fitness could then be measured by the animal's probability of meeting its energy requirements for the coming night (Caraco 1980; Stephens 1981; McNamara & Houston 1987). An increase in intake variance increases the probability of the intake being lower or higher than the average. When an animal's average intake slightly exceeds its expected energy requirements, a decrease in intake can result in starvation, while an equal increase in intake would not affect its survival probability much. Thus, the potential loss from an increased variability of intake is greater than its potential gain. Conversely, when an animal's average intake is just short of the expected requirement, a decrease in intake will be insignificant, since it expects to starve, while an equal increase in intake could mean surviving the coming

night. In this case, the potential loss from an increased variability of intake is less than its

potential gain. Therefore, risk-proneness should be anticipated when animals expect a

negative energy budget and risk-aversion when they expect a positive energy budget

(Caraco 1980; Stephens 1981). The energy budget rule is expected to occur in small

homeotherms (Stephens 1981; Kacelnik & Bateson 1996), since their high energy

requirements make them more likely to starve than large animals or ectotherms (Calder

1974; Stuebe & Ketterson 1982). Evidence for the energy budget rule has been found in

fishes (Young et al. 1990; Croy & Hughes 1991), small birds (Caraco et al. 1980; Caraco

1981, 1983; Moore & Simm 1986; Caraco et al. 1990) and in small mammals (Barnard &

Brown 1985; Zabludoff et al. 1988; Lawes & Perrin 1995). In most of the previous

studies foragers were given discrete choices between constant and variable options with

equal mean rewards. In a producer-scrounger game however, the intake from producer

and scrounger are frequency-dependent so that changing the proportion of scrounger in

the group will affect their mean and variability of intake rates.

Stochastic producer-scrounger

Caraco and Giraldeau (1991) proposed a stochastic producer-scrounger model

based on the energy budget rule to predict the proportion of scrounger in a group of risk-

sensitive foragers. They modeled a group of foragers consisting of pure-producer or pure-

scrounger individuals. The model assumes that producer yields a more variable intake

than scrounger for the reasons mentioned previously. It also assumes that individuals

minimize the probability of their energy intake falling short of their physiological

requirement and finds the SEF proportion of scrounger in the group accordingly. It

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predicts that the energy requirement of the animals should affect the SEF proportion of scrounger in a group. More specifically, it predicts that the effect of energy requirements should depend on producer's competitive efficiency (θ): the proportion of a patch going to its producer. Above a critical θ, the proportion of scrounger should decrease with increasing requirement; below the critical θ, it should increase with increasing requirement. The critical θ is defined by $(1-\theta)=G^{-1/2}$, where G is the size of the group (Caraco & Giraldeau 1991). This prediction distinguishes the stochastic model from mean rate-maximizing models since the latter predict no effect of energy requirements on the proportion of scrounger at SEF. Despite the implications of this novel idea, there has only been one published study that attempted to test the stochastic producer-scrounger model. Koops and Giraldeau (1996) looked for effects of energy budget on the use of scrounger in starlings (Sturnus vulgaris). The experimenters manipulated the food deprivation of the birds to change their energy requirements. Food deprivation only had a non-significant effect on the birds' use of scrounger. Further testing will help determine the prevalence of risk-sensitivity in groups of animals foraging in a producer-scrounger context. In addition, identifying a system where risk-sensitive producer-scrounger occurs will also allow testing other predictions of the stochastic producer-scrounger model (Caraco & Giraldeau 1991) and of dynamic stochastic producer-scrounger models (Barta & Giraldeau 2000).

Objectives

In one experiment, I attempt to verify the crucial assumption of the stochastic producer-scrounger model (Caraco & Giraldeau 1991) that producer yields a more

variable intake than scrounger. I refer to producer and scrounger as foraging tactics (Vickery et al. 1991; Caraco & Giraldeau 1991; Giraldeau & Caraco 2000) rather than individuals with fixed phenotypes (Ranta et al. 1996, 1998). Koops and Giraldeau (1996) showed using S. vulgaris that the standard deviation of intake per patch was higher in the food density treatment where there was less joining, suggesting that scrounger reduces the variability of intake of the birds. However, the observers could not distinguish a starling playing producer from one playing scrounger until a food patch was actually found. Hence, they could not account for variability due to patch encounter rates, so that their measure of variability was incomplete. Moreover, they could not measure the intake rate of each tactic separately, so they could not compare the variability of intake of producer and scrounger directly. I use L. punctulata and use the orientation of the birds' head while hopping (Coolen et al. 2001) to account for their use of producer and scrounger tactics. I can therefore measure the overall intake rates from producer and from scrounger separately, and compare their overall variability directly. I also use the cumulative probability distribution of the birds' intake rates to estimate the probability that it will fall short of a given required intake rate from each tactic.

In a second experiment, I test for effects of the birds' energy requirements on their use of scrounger by manipulating food deprivation. This study differs from Koops and Giraldeau's (1996) study, because I record the search effort of birds rather than the number of patches (outcome) they obtain from each tactic. The search effort actually measures what the birds intend to do. The result of a foraging bout on the other hand, depends in part on the birds' search effort, but is also constrained by foraging conditions. Thus, changes in a foraging strategy such as an increased proportional use of scrounger

are not always translated into equivalent changes in the outcome of a foraging bout. In addition, I use smaller birds, since they are more likely to be risk-sensitive than starlings (Kacelnick & Bateson 1996).

EXPERIMENT 1: PAYOFFS OF PRODUCER AND SCROUNGER TACTICS

Methods

Study subject

Nutmeg Mannikins (L. punctulata) are small granivorous birds weighing on average (± SE, n = 8) 13.7 ± 0.2g. In the wild, they feed mostly by hopping on the ground or climbing tall grasses and twigs in search of the seeds of grasses and weeds (Immelmann 1965). The sexes are monomorphic. They are extremely social birds at all times of the day and throughout the year.

I observed three flocks of seven birds as they foraged in an indoor aviary (195 cm x 305 cm, and 240 cm high) kept at 22-24°C. Birds were randomly selected from a flock of 97 commercially purchased wild-caught adult birds. Each bird was identified with a unique combination of color leg bands. During experiments, each bird was marked on the top of the head and the tip of the tail using acrylic paint to facilitate identification. The birds experienced a 12L:12D photoperiod throughout the study. They had access to a mixture of millet seeds ad libitum between experiments and water at all times.

Foraging apparatus

The birds foraged on a grid consisting of two boards joined to form a 2.0 m x 1.2 m surface. Each board contained 99 wells of a similar color to the seeds (mean diameter and depth ($\pm$SE) of 1.32 $\pm$ 0.02 cm and 0.83 $\pm$ 0.01 cm, respectively) spaced on average ($\pm$SE) at 10.16 $\pm$ 0.05 cm intervals. The grid was elevated at a height of 92 cm and the birds were videotaped with a color Sony Handicam held approximately at their eye level. Outside of experimental periods, a sheet of paper covered the grid.

Training

After a flock had been placed in the aviary for seven to 10 days, I trained the birds to search for white millet seeds placed in the grid's wells. Birds were food deprived for 15h (12h overnight) and trained 3h after the lights turned on. At the beginning of a trial, I removed the paper cover and placed seeds in randomly selected wells while the birds remained perched. Once I left the aviary, the birds flew down from their perches onto the grid. The trial ended after 3 min of foraging or 1 min after all the birds flew back to their perches, after which I vacuumed any remaining seeds and seed husks. Initially, I dispersed a small handful of seeds around the center of the grid. In the following trials, an increased fraction of the seeds were placed in the wells. Once the birds were searching in the wells, they were exposed to a dispersed food distribution (three seeds placed in each of 60 randomly selected wells) and then to a clumped food distribution (10 seeds placed in each of 20 randomly selected wells). Training consisted of six trials per day at 30 min intervals. Under the dispersed food distribution, birds easily found seed-containing wells

(patches) and often depleted them before other birds could join in. This means the finder's share was large in this condition so that the SEF of producer should be high. After three days of training in the dispersed food distribution, all birds could find at least five patches per trial in three consecutive trials. The clumped food distribution allows for more profitable joining than the previous treatment, because patch finders obtain a much smaller proportion of the patch before the arrival of joiners. Hence the SEF of scrounger should be higher. After three days of training in the clumped food distribution, all birds had joined at least three patches in three consecutive trials, and training was considered complete.

Testing

Testing started the day following the completion of training. The birds were food deprived as for training. Testing consisted of six trials per day at 30 min intervals. For each trial, a randomly predetermined focal bird was videotaped from behind a one-way glass. Each bird was observed no more than once per day. Observations started when at least five of the seven birds (including the focal bird) were on the grid and were suspended when there were fewer than five birds on the grid, and when the focal bird left the grid. To reduce the effect of patch depletion, an observation ended after 3 min unless: a) a trial was suspended for more than 1 min, or b) 1 min elapsed without a patch finding.

The birds were tested on consecutive days. In order to obtain sufficient data, flocks 1, 2 and 3 were tested for 15, 22, and 19 days, respectively, because a number of trials were too short and discarded. Tests for flock 1 and 2 were interrupted during two

consecutive days, after which the next two days of testing were discarded. Tests for flock 3 were interrupted one day, after which the following day of testing was discarded.

Behavior patterns

The birds' behavior patterns were entered into a computer running the Observer 3.0 event recorder software (±0.1s) from the video records. Eight behavior patterns were noted: 1) finding a patch; 2) joining a patch; 3) eating a seed from a patch the bird found; 4) eating a seed from a patch the bird joined; 5) hopping with the head up; 6) hopping with the head down; 7); standing with the head up 8) standing with the head down. A bird's head orientation was based on an imaginary line going from its eye to its nostrils. It was up when this line pointed to the horizon or higher, and down otherwise (Coolen et al., 2001). Birds rarely flew (<0.1% of the time) while foraging on the grid, so I excluded flights from observations.

I assumed that a bird had found a patch as a result of playing producer when it was the first to feed at a patch, and that it had played scrounger if it fed from a patch that was already attended by another bird. A bird was assumed to have eaten one seed every time it pecked in a patch followed immediately by 0.5s or more of husking behavior. Husking behavior was usually accompanied by pieces of husk falling out of the bird's beak.

A series of hops was treated as continuous when individual hops were separated by less than 1s. A bird remaining stationary for more than 1s was recorded as standing. Hops were later categorized into search and pursuit hops (sensu Coolen et al. 2001). Hopping with the head up was considered searching using scrounger, and hopping with

the head down searching using producer. For producer, the two hops immediately preceding a patch finding were defined as pursuit and treated separately from search. For scrounger, pursuit consisted of the continuous series of hops of the same head orientation immediately preceding a patch joining. The rate of hopping was calculated from the frequency and duration of hops. I calculated the patch encounter rate (patches/s) and the intake rates (seeds/s) for producer and scrounger separately, where the time investment consisted in the sum of searching, pursuing, and feeding recorded for each tactic.

Analysis

Observations were confined to the first 60s of each trial, while fine-scale estimates of mean and variability of intake rates for each tactic were calculated from short intervals. One 10s interval of time invested in each of producer and scrounger was randomly selected from each trial to calculate intake rates for producer and scrounger, respectively. I also plotted the cumulative probability distribution of the calculated intake rates to estimate the birds' probability of incurring an energy shortfall by using producer and scrounger tactics. I defined a bird's probability of incurring an energy shortfall (PIES) as the probability that a bird's actual intake rate (I) falls short of the intake rate required (I_R) to meet its energy requirements. All statistical tests were two-tailed.

Results

General

Results are based on a total of 182 trials yielding 335.6 minutes of foraging for 21 birds. Only 14 trials (8%) included pauses, which together lasted 5.8 minutes, leaving a

total of 329.8 minutes of observation time. The birds flew down on the grid and foraged on average (± SE, n = 21) 110.4 ± 14.2s per trial. They spent 52.9 ± 6.6% of their time feeding in patches, 39.3 ± 6.6% hopping, and 7.8 ± 5.1% standing. During the average trial, a bird obtained 9.6 ± 5.1 seeds from 1.9 ± 1.1 discovered patches, and 7.7 ± 4.4 seeds from 3.1 ± 1.9 joined patches.

Behavioral indicators of tactic use

The proportion of time a bird had its head up while hopping (excluding pursuits) was a strong predictor of the proportion of patches it joined (Partial correlation, controlling for flock: r=0.706, df=18, p=0.001, Figure 3). A two-way repeated measures ANOVA testing for tactic (producer/scrounger) and hop type (search/pursuit) with flock as a between subject factor, showed that the rate of hopping was higher for pursuit than for search ($F_{1,18}$=12.46, p=0.002, Figure 4). Also, the rate of hopping was higher for scrounger than for producer ($F_{1,18}$=16.65, p=0.001), but the effect was greater for pursuit than for search (Interaction: $F_{1,18}$=9.34, p=0.007).

Payoffs of producer and scrounger tactics

Scrounger yielded a significantly higher mean patch encounter rate (0.162 ± 0.007 patches/s) than producer (0.075 ± 0.003 patches/s; ANOVAR for tactic with flock as a between subject factor: $F_{1,18}$=153.28, p<0.001). On the other hand, a patch that was found yielded significantly more seeds (5.0 ± 0.2 seeds) than one that was joined (2.6 ± 0.1 seeds; ANOVAR for tactic with flock as a between subject factor: $F_{1,18}$=198.85,

p<0.001). One bird was excluded from the analysis of payoffs, because it played

scrounger too rarely to obtain sufficient data for a comparison of tactics. The mean (±SE)

seed intake rates of 0.210 ± 0.019 seeds/s for producer and 0.248 ± 0.014 seeds/s for

scrounger did not differ significantly (ANOVAR testing for tactic and flock effects:

$F_{1,18}$=2.46, p=0.135, 1-β=0.316). The variability of intake rates as measured by the mean

(±SE) coefficient of variation, was higher for producer (1.00 ± 0.02) than for scrounger

(0.55 ± 0.01). This pattern was consistent for 17/20 birds and significantly so for four

birds, when comparing the coefficients of variation of intake rate (Miller 1991) for each

bird. A binomial probability test reveals that producer was more variable than scrounger

for a greater number of birds than expected by chance (p<0.01).

The cumulative probability distribution of intake rates (Figure 5) shows that birds

had a higher probability of obtaining a low intake rate (0.1 & 0.2 seeds/s) by playing

producer than scrounger. On the other hand, producer also yielded high intake rates (0.4

seeds/s to 0.6 seeds/s) more often than scrounger. These differences are shown by the

significant interaction between the two factors (tactic and intake rate) in a two way

ANOVAR ($F_{6,108}$=4.35, Greenhouse-Geisser corrected p=0.001). Post-hoc comparisons

show that the difference was only significant for the lowest intake rate of 0.1 seeds/s

(Wilcoxon: Z=3.24, n=20, p=0.001) after a Bonferroni correction. Neither tactic yielded

intake rates above 0.7 seeds/s.

Discussion

Behavioral indicators of tactic use

I was able to obtain estimates of the birds' seed intake rates for producer and scrounger tactics using the birds' head orientation while hopping as an indicator of tactic use. The relevance of those estimates however, is strongly dependent on the validity of head orientation as a predictor of tactic use. The strong association between the proportion of time spent hopping with the head up and the proportion of patches that were joined confirms the findings of Coolen et al. (2001) using the proportion of hops with the head up. The consistency between the two studies shows that head up and head down are good predictors of foraging tactic in L. punctulata. In addition, the analysis of hopping rates provided further support for this claim by showing that birds hopped at a higher rate with the head up than with the head down while searching, highlighting the functional difference between the two foraging search modes. The slower hopping recorded for birds searching with the head down (playing producer), may be due to hidden seeds being harder to detect than a feeding conspecific. It follows that birds may need to slow down when playing producer to increase the probability of detecting cryptic seeds (e.g. Gendron & Staddon 1983, Pyke 1981, Speakman 1986). However, why birds searching with the head up (playing scrounger) hop at all is intriguing because they could save energy by remaining stationary while searching. When animals scan for predators, they often slow down or remain stationary altogether (McAdam & Kramer 1998). One likely explanation is that birds attempt to stay near the center of the flock when playing scrounger, thereby minimizing their distance to as many potential finders as possible (Barta et al. 1997). Flynn and Giraldeau (1999) recorded the position of individuals in

flocks of L. punctulata and found that birds playing mostly scrounger tended to remain near the center of the flock as shown by their relatively small inter-individual distance. In any case, hopping with the head up and with the head down seem appropriate to measure the time invested in scrounger and producer tactics, respectively.

Payoffs of producer and scrounger tactics

The birds' mean intake rates from producer and scrounger did not differ significantly as predicted by mean rate-maximizing producer-scrounger models (Barnard & Sibly 1981; Vickery et al. 1991). However, the low power of the test does not exclude the possibility that this experiment failed to detect a real difference (type II error).

The intake rate of a bird was more variable when playing producer than scrounger as assumed in the stochastic producer-scrounger model (Caraco & Giraldeau 1991). In addition, a bird had a higher patch encounter rate from scrounger than from producer, so that scrounger yielded a lower probability of not obtaining any food at all. Both results show that producer is more risky than scrounger. These results confirm Koops & Giraldeau's result (1996) suggesting that producer was more variable than scrounger. It is important to note that the differences in variability of intake rate between producer and scrounger were calculated from 10s intervals. Since the birds in my experiments were foraging for less than 8 min for the first 4h of the day, a 10s interval may not be insignificant. In the wild, the birds are more likely to use a longer time scale (McNamara & Houston 1982, 1986). Over a longer time scale, there are a larger number of sequential plays, so that the intake rates of longer intervals will tend to approach the mean intake rate (Houston & McNamara 1985; Banschbach & Waddington 1994). The intake rate of

longer intervals would therefore be less variable than those of short intervals. Using 10s

intervals allowed me to detect a difference in variability of seed intake rate between

producer and scrounger. Whether that difference is taken into account in the birds' choice

of foraging strategy (proportional use of scrounger) can be answered by manipulating the

energy requirements of the birds. Only if the difference in variability of intake rate is

biologically significant will the energy requirements of the birds affect their foraging

strategy (Kacelnik & Bateson 1996). Showing that energy requirements of the birds have

no effect on their foraging strategy would support the hypothesis that the foraging

strategy of the birds maximizes their mean intake rate (Barnard & Sibly 1981; Vickery et

al. 1991).

The cumulative probability distribution of intake rates was higher for producer in

low intake rates and higher for scrounger in high intake rates. If we treat the given intake

rates as possible I_R's to avoid an energy shortfall, the cumulative probability distribution

can be used to estimate the birds' PIES for given I_R's (sensu Ekman & Hake 1988). This

result therefore shows that when I_R was low, PIES was lower for scrounger than for

producer, and when I_R was high the reverse was true (Figure 5). This pattern is consistent

with the one predicted if producer was more variable than scrounger (Pulliam & Millikan

1982; Ekman & Hake 1988). The difference between tactics is small for high I_R's though.

If the payoffs curves were overlapping for high I_R's, we would expect no effect of

changes in I_R on scrounger use, since producer and scrounger would yield equal PIES for

those I_R's. If, on the other hand, we accept that the curves differ, certain predictions can

be made concerning the effect of I_R on scrounger use. Conventional risk-sensitive

foraging theory would predict that in order to minimize PIES, the birds should play

scrounger exclusively when I_R is below the value for which the two curves cross, and

producer exclusively in the other case (Figure 5). In a producer-scrounger game however,

the magnitude of payoffs are frequency-dependent. An increase in the use of producer

(due to increasing I_R) would increase the mean intake rate of scrounger (Figure 1),

making scrounger more advantageous (lower PIES). Thus, an increase in I_R should

increase the frequency of producer until producer and scrounger yield equal PIES at the

new I_R (Figure 6). I compare the prediction of this simple shortfall-minimizing model to

those of the current stochastic producer-scrounger model (Caraco & Giraldeau 1991).

Predictions of the stochastic producer-scrounger game

As mentioned previously, Caraco & Giraldeau's model (1991) predicts that the

effect of energy requirement on the proportional use of scrounger depends on the

competitive efficiency of producer at a patch of food. For a group size of seven as used in

my study, the critical θ is equal to 0.59. The mean ($\pm SE$) θ of 0.50 ± 0.17 for the birds in

this study was significantly lower than the critical value (Combined probabilities of 2-

tailed, one-sample t-tests for each flock: $\chi^2=22.841$, df=6, p<0.005). Thus, the stochastic

producer-scrounger model predicts that under the conditions of my experiment,

increasing physiological requirements should increase the frequency of scrounger, which

is opposite to what I predict from the cumulative probability distribution of intake rates in

experiment one.

In the next experiment, I test the three alternative hypotheses regarding the effect

of energy requirement on the proportion of scrounger: 1) no effect as predicted by mean

rate-maximizing models (Barnard & Sibly 1981; Vickery et al. 1991); 2) decreasing

scrounger with increasing requirement (this manuscript); and 3) increasing scrounger with increasing requirement (Caraco & Giraldeau 1991). I make two assumptions about the predictions of Caraco & Giraldeau's model (1991).

First, I assume that the competitive efficiency of producer is a characteristic of the tactic itself rather than of producer individuals, so that a bird will have a competitive efficiency of 0.50 when playing producer and (1-0.50)/S when playing scrounger, where S is the number of scrounger in the group. This is because the birds in my experiment alternate between tactics (mixed strategy), while the stochastic model only varied the proportion of pure producer individuals and pure scrounger individuals. Competitive efficiency can be a characteristic of the tactic if it is determined by the advantage that an individual playing producer obtains by being the first to arrive at a patch. This is the case if for example, the producer of a patch starts feeding before others join in or if the producer gains a positional advantage allowing it to feed faster than others (Ward & Enders 1985; Giraldeau et al. 1990; Vickery et al. 1991). The second assumption deals with the nature of the energy requirements of the birds. Increasing animals' physiological requirements will increase the food intake rate that is necessary to meet the level of reserves required to survive the night. Another way of doing so is to decrease the level of their energy reserve levels before they forage so that they will require a higher food intake rate to meet the same energy requirements. Thus, both manipulations have equivalent effects on the energy budget of the animals, and on the food intake rate required to survive the night. I assume that increasing physiological requirements or decreasing the level of energy reserves have the same effect on scrounger use.

In the next experiment, I observe L. punctulata foraging in the same condition as the previous experiment, but under two different levels of energy reserves.

EXPERIMENT 2 MANIPULATION OF ENERGY RESERVE LEVELS

Methods

Measuring daily food requirement

I estimated the daily food requirement (grams of seeds) of eight L. punctulata randomly chosen from the same flock of 97 birds as used in experiment one. The birds were kept singly in cages (30 cm x 30 cm, and 34 cm high) during the 14 days of measurement. The birds had visual and auditory contact with another bird during testing and could feed from feeders that hung outside cages to prevent spillage from falling into the cage. Each bird's feeder was replaced by a fresh feeder containing 10.00g of white millet daily, 2h after the lights turned on. The used feeder was cleared of its empty husks weighed and replenished for the next feeder change. The birds were weighed daily at the same time the feeders were changed.

Manipulation of energy reserve levels

Two flocks, each composed of seven randomly selected individuals, were kept in an aviary and trained to forage on a grid as described in experiment 1, with the exception that they were given 14 days to habituate to the aviary.

Birds were tested as in experiment one, but at a rate of four trials per day. During the last half (6h) of the day preceding testing, the birds were subjected to either of two feeding schedules in order to manipulate their energy reserve level: 50% or 100% of their normal feeding rate for that period to generate the low and high energy reserve level treatments, respectively. All the birds were then food deprived 14h (12h overnight and 2h morning) before testing the following day. Testing always ended after 1.5h, and was followed 0.5h later, by 2h of ad libitum feeding (Figure 7). Birds were tested on consecutive days for each energy reserve level treatment, and the treatment order was balanced across birds. After the first treatment, birds were allowed 7 days of ad libitum feeding and were subject to 3 days of training before being tested in the second treatment.

Analysis

I selected four birds randomly in each flock as focal birds, and recorded the same behavior patterns as in the previous experiment. Observations were also confined to the first 60s. I used ANOVARs to test for effects of energy reserve levels. The small sample size did not allow me to include flocks as between subject factors, but visual inspection of the data revealed no obvious differences between flocks. Arcsine-square root transformations were performed on proportions and log transformations on other data

when the assumption of normality was violated (Zar 1996). When the latter failed, rank

transformations were used (Potvin & Roff 1993). Again, all tests were two-tailed.

Results

General

A bird weighed on average ($\pm$ SE, n = 8) 13.7 $\pm$ 0.2g and ate 3.7 $\pm$ 0.3g of millet

per day. Results of flock foraging are based on 163 trials yielding 310.9 min of foraging

for all 8 birds. The birds foraged as in the previous experiment except that trials were

interrupted much more frequently. A total of 71 trials (44%) included pauses that lasted a

total of 30.4 minutes. Removing the pauses left 280.5 minutes of observation time. The

birds flew down on the grid and foraged (X $\pm$ SE, n = 8) for 114.4 $\pm$ 2.8s per trial. They

spent 49.9 $\pm$ 2.4% of their time feeding in patches, 37.4 $\pm$ 2.7% hopping, and 12.7 $\pm$ 2.3%

standing.

Effects of energy reserve levels

Birds hopped at a higher rate when food deprived to a greater extent (three -way

ANOVAR testing for tactic, hop type, and treatment: $F_{1,6}$=12.09, p=0.013; Figure 8a-d).

There was no significant interaction among factors. Birds also consumed more seeds per

trial on average ($\pm$SE, n=8) in the low reserve treatment (20.3 $\pm$ 1.3) than in the high

reserve treatment (18.1 $\pm$ 1.2; ANOVAR: $F_{1,6}$=6.699, p=0.041).

The proportion of time spent playing scrounger declined by 33% from the high

reserve treatment (0.27 ± 0.06) to the low reserve treatment (0.18 ± 0.04), but the

difference was not statistically significant (ANOVAR: $F_{1,6}=3.458$, $p=0.112$, $1-\beta=0.347$).

The decline in scrounger use with decreasing energy reserve levels was observed in 7/8

birds (Binomial Test: $p=0.070$). The mean seed intake rate of scrounger increased with

decreasing energy reserve levels, but not significantly so (paired t-test: $t=1.133$, $df=6$,

$p=0.300$, Figure 9). The cumulative probability distribution of intake rates shows that the

I_R at which producer and scrounger yield equal PIES increased slightly from the high

(Figure 10a) to the low (Figure 10b) energy reserve level treatment, but a three-way

ANOVAR (tactic, intake rate, and treatment) revealed no significant effect of treatment

or any interactions between treatment and any other factor.

Discussion

Mean rate-maximizing producer-scrounger models (Barnard & Sibly 1981;

Vickery et al. 1991) predict no effect of energy reserve levels on scrounger use, while the

stochastic model (Caraco & Giraldeau 1991) predicts an increase in scrounger with

decreasing energy reserve levels for my experiment. My simple shortfall minimization

hypothesis predicted a decline of scrounger with decreasing energy reserve levels as

suggested in experiment two. This result can have a number of implications. It suggests

that L. punctulata may react to changes in energy budget and thus, that they are risk-

sensitive foragers. The violation of some assumptions of the stochastic producer-

scrounger model (Caraco & Giraldeau 1991) may weaken the relevance of experiment

two as a test of the model. Finally, the effect of energy reserve levels on scrounger use

was non significant, but I suspect that its weakness is due to the small sample size and an insufficient manipulation of the birds' energy reserve levels. I discuss these implications below.

The non significant decline in scrounger with decreasing energy reserve levels suggests that the birds became more risk-prone with increasing energy requirements. This effect is consistent with other studies of risk-sensitivity, in which the experimenter manipulated the energy requirement (or energy reserves) of fishes (Young et al. 1990; Croy & Hughes 1991), birds (Caraco et al. 1980; Caraco 1981, 1983; Caraco et al. 1990), and mammals (Barnard & Brown 1985; Zabludoff et al. 1988; Lawes & Perrin 1995), but see (Kacelnik & Bateson 1996; Abreu & Kacelnik 1999). Thus, it seems that the birds' pattern of risk-sensitivity was consistent with the general agreement, even though they were engaged in a producer-scrounger game. However, it is not clear why this pattern differs from the one predicted by the stochastic producer-scrounger model (Caraco & Giraldeau 1991).

It is possible that experiment two violated some assumptions of the stochastic producer-scrounger model (Caraco & Giraldeau 1991) so that it may not constitute a strong test of the model. The assumptions that patches are discovered sequentially and that they are exploited instantaneously were violated. While this could have affected the payoffs of producer and scrounger tactics, experiment one showed that producer still yielded more variable intake rates than scrounger as assumed in the model. Therefore, the violation of the above assumptions should not affect the qualitative predictions of the model. At most, one would expect a change in the magnitude of the effect of energy budget. The only other test of the stochastic producer-scrounger model on starlings

(Koops & Giraldeau 1996) violated the same assumptions, and yielded results that were qualitatively consistent with the stochastic producer-scrounger model (Giraldeau & Caraco 2000). The discrepancy between Koops & Giraldeau's study (1996) and my study could be due to important interspecific differences. For example, aggression was prevalent in starlings, but absent in my study. It is not clear though, how aggression can affect the effect of energy requirements on scrounger use. Further studies of risk-sensitivity in producer-scrounger games are needed to determine whether one pattern of risk-sensitivity is more common than the other, and why.

The use of energy reserve levels instead of physiological requirements to manipulate the energy budget of the birds has also been viewed as problematic (Caraco & Giraldeau 2000). Caraco & Giraldeau (2000) argued that if risk-sensitivity evolved in response to changes in physiological requirement, then animals may not respond similarly to equivalent changes in energy reserve levels. While physiological requirements can be affected by unpredictable weather (Kacelnik & Bateson 1996), energy reserve levels can be affected by the temperature during the previous night (Blem 1990), interruptions in foraging (Barnard et al. 1985), or unpredictable foraging success (McNamara & Houston 1992; 1985; Blem 1990). In fact, many experimental studies have shown animals to be risk-sensitive in response to food deprivation (Caraco et al. 1980; Caraco 1981, 1983; Barnard & Brown 1985; Young et al. 1990; Croy & Hughes 1991; Lawes & Perrin 1995). Thus, I argue that risk-sensitivity is as likely to have evolved in response to either or both source of change in energy budget. In addition, any significant length of time with an unpredicted increase in physiological requirement is likely to be accompanied by decreased energy reserve levels. My result suggests that L. punctulata

are likely risk-sensitive to changes in energy reserve levels. Future studies could determine whether these birds are also sensitive to changes in physiological requirements by varying the temperature at which the birds are kept (e.g. Caraco et al. 1990; Ha 1991)

One possible reason for the weakness of the effect of energy reserve levels is the small sample size used in experiment two. Given the differences observed between treatments in this experiment, 40 birds would be required to obtain a statistical power of 0.80. Another possible reason is that birds might have eaten more during the period of ad libitum feeding to compensate for the increased food deprivation. The fact that they ate more seeds during trials suggests that they likely did so during the ad libitum feeding period also. The birds could also have lowered their body temperature during the night to reduce their energy requirement when food deprived to a greater extent as shown in other species of birds (Ketterson & King 1977; Stuebe & Ketterson 1982). Since birds increased their seed intake and hopping rate during trials from high to low energy reserve level treatments, there was likely a treatment effect, but its extent is not clear. Future studies could benefit from a more rigorous control of the birds' total food intake as well as their energy budget. For example, one could keep a daily record of the birds' food intake and adjust the amount of food given to them in each treatment.

GENERAL DISCUSSION

This study provides weak support for risk-sensitive producer-scrounger games. Experiment one shows that the producer-scrounger game allows animals to choose between a risk-prone (producer) and a risk-averse (scrounger) alternative, at least for

short time intervals. Experiment two suggested that the risk difference between tactics that was observed in experiment one was biologically significant, since there was a tendency for the birds to reduce their use of scrounger, the least variable alternative, with decreasing energy reserve levels. In addition, this result suggests that risk-sensitive models may be more applicable than mean rate-maximizing models for the birds in this study, since the latter models do not predict the observed effect. On the other hand, the inconsistency between the prediction of the stochastic producer-scrounger model and the observed effect suggests that the current risk-sensitive model does not describe accurately the behavior of these birds. I discuss possible implications of the above two experiments.

Payoffs of producer and scrounger

Experiment one is the first direct comparison of producer and scrounger payoffs in unconstrained animals. Barnard & Sibly (1981) used house sparrows (Passer domesticus) to compare the food intake rates of searchers and copiers, birds that tended to find food patches and that tended to join food patches, respectively. Mottley & Giraldeau (2000) used an apparatus to separate the two tactics spatially and measured the intake rates from each side, but it is not clear that birds in the producer compartment did not attempt to use scrounger (unsuccessfully) and vice versa. Koops & Giraldeau (1996) compared the food intake of birds within found (producer) and joined (scrounger) patches, but had no way of identifying the tactic used between patches. Thus, part of the time invested in either or both tactics was left out. With the use of head orientation of hopping birds, I could account for all the time invested in producer and in scrounger tactics in unconstrained birds and show that producer was a more risky foraging tactic

than scrounger as is generally assumed (Caraco & Giraldeau 1991; Barta & Giraldeau 2000). Although experiment one was successful at comparing the mean intake rates of producer and scrounger directly, it could not show their equality. Studies with much larger sample sizes would be required to show equal payoffs with reasonable certainty.

The use of head orientation also allowed me to compare the variability of intake rates for producer and scrounger, and show that producer yielded a more variable intake rate than scrounger. As mentioned, the differences in variability are most likely very small and not necessarily biologically important. If it were the case the birds would be mean rate-maximizers and energy reserve levels would have no effect on the proportional use of scrounger. The energy reserve level treatments in experiment two caused a non significant change in the birds' use of scrounger, suggesting that the difference in variability may have been biologically significant. This suggests that very small differences in variability between foraging options can be biologically significant to foragers as argued previously (McNamara & Houston 1986) especially when the differences concern their survival (Barkan 1990).

The payoffs that I measured are specific to this study. By changing the conditions in which the birds forage, the difference in variability of intake rate between producer and scrounger may be greater or less than observed here. Conditions that yield greater differences in variability of intake rate between alternatives should facilitate risk-sensitivity in animals (Shafir and Trivaks 2000). When the conditions call for a low frequency of producer (small finder's share), birds playing scrounger should have limited joining opportunities and thus benefit from little reduction in risk. When conditions favor a high frequency of producer on the other hand (large finder's share), scrounger should

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provide a considerable reduction in risk. A dynamic stochastic producer-scrounger model (Barta & Giraldeau 2000) predicts average daily proportions of scrounger that differ from those of mean rate-maximizing models mostly when finder's share is high, but low enough to allow some scrounger to be profitable. Future studies should look for effects of finder's share and group size on the risk difference between producer and scrounger foraging tactics, as well as compare the effects of energy budget changes in different foraging conditions.

This study suggests that L. punctulata foraging in a producer-scrounger context may be risk-sensitive. It is not inconsistent however, with previous studies in L. punctulata that support the mean rate-maximizing producer-scrounger model (Giraldeau et al. 1994; Mottley & Giraldeau 2000; Coolen et al. 2001), since the latter do not constitute evidence against risk-sensitive producer-scrounger games. The stochastic producer-scrounger model also predicts the negative frequency-dependence shown in Giraldeau et al. (1994) as support for mean rate-maximizing models. The decrease in scrounger frequency with increasing finder's share in Coolen et al. (2001) is also a common prediction of both mean rate-maximizing and stochastic models. Mottley & Giraldeau (2000) showed that the birds in their apparatus stabilized near the SEF of scrounger predicted by a mean rate-maximizing model (Vickery et al. 1991), but it was not compared to the SEF predicted by the stochastic model (Caraco & Giraldeau 1991). Thus, tests of mean rate-maximizing producer-scrounger models do not provide evidence against the stochastic producer-scrounger model so far. Only tests of distinctive predictions from both types of models (Koops & Giraldeau 1996; this study) will allow one to discern the applicability of the two types of models. My study shows that L.

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punctulata may be risk-sensitive, but this result cannot be generalized to all situations, since patterns of risk-sensitivity may change during periods of growth (McNamara & Houston 1992), reproduction (McNamara et al. 1991; Schmitz 1992), and migration (Bednekof & Houston 1994).

Effect of energy reserve levels on scrounger use

Experiment two showed a tendency for the birds to reduce their use of scrounger with decreasing energy reserve levels, so it provides weak evidence for risk-sensitive producer-scrounger games. However, this effect was contrary to the one that the current stochastic producer-scrounger model (Caraco & Giraldeau 1991) predicts for my experiments. I discuss possible factors that may have caused this inconsistency.

The stochastic producer-scrounger model assumes a single continuous foraging period until the non-foraging period (e.g. night). This was not the case in experiment two, since, many of the trials were interrupted, because the birds suddenly flew up to their perches when a noise was heard. When a trial was interrupted, the birds could not feed until the next trial (30min later). At times they remained perched during two consecutive trials, so that they could not feed for 60min. The 13.7g birds were food deprived for 14h in addition to a reduced food intake in the low energy reserve level treatment. A study on black-capped chickadees showed that the 12g birds accumulated sufficient energy reserves for survival overnight and a few hours in the morning (Chaplin 1974). The apparently unpredictable interruptions were thus likely substantial for the already food deprived birds in my study. Such unpredictable interruptions in the foraging period of animals can affect their patterns of risk-sensitivity (Barnard et al. 1985; Houston &

McNamara 1985; McNamara & Houston 1992), since minimizing the probability of starving during an unpredictable interruption rather than during the distant period of non-foraging (e.g. night) will increase the animals overall survival. Barnard et al. (1985) predict that the risk-proneness of animals should depend on the required energy reserves to survive a potential interruption. It is not clear though how unpredictable interruptions would affect the predictions of the stochastic producer-scrounger model. Future models should investigate the effect of energy budget on scrounger using a dynamic producer-scrounger model (e.g. Barta & Giraldeau 2000) that includes unpredictable interruptions in the foraging period.

Summary

This study provides weak evidence for risk-sensitivity in the producer-scrounger game in small birds. Experiment one provides empirical evidence that producer is risk-prone and scrounger risk-averse for short time intervals. While the difference between the two tactics should be much smaller for longer, more biologically significant time periods, the tendency for energy reserve levels to affect scrounger use in experiment two suggests that it is likely biologically significant. Experiment two also supports risk-sensitivity since mean rate-maximizing models predict no effect of energy reserve levels on scrounger use. Experiment two shows a tendency for the birds to reduce their use of scrounger with decreasing energy reserve levels as predicted by a simple shortfall minimizing hypothesis from experiment one. This pattern of risk-sensitivity is consistent with general tests of risk-sensitivity, but opposite to the prediction of the stochastic producer-scrounger model (Caraco & Giraldeau 1991) and to a study using S. vulgaris

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(Koops & Giraldeau 1996). Further studies of risk-sensitive producer-scrounger games are needed to understand the factors that affect the pattern of risk-sensitivity in producer-scrounger groups.

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FIGURE LEGENDS

Figure 1.   Payoff to producer (solid line) and to scrounger (dashed line) tactics as a function of the proportion of scrounger in the group. Scrounger has a higher payoff than producer when rare and vice versa. Where the payoff functions cross, no individual can gain by changing strategy; the group is at SEF.

Figure 2.   Relationship between fitness and reward size. When fitness is a concave-down function of reward size (a), the potential loss of fitness from a decrease in reward size is greater than the potential gain of an equal increase in reward size ($\lambda > \gamma$). Individuals can gain by being risk-averse. When fitness is a concave-up function of reward size (b), the potential loss of fitness from a decrease in reward size is inferior to the potential gain of an equal increase in reward size ($\lambda < \gamma$). In this case, individuals can gain by being risk-prone.

Figure 3.   Relationship between the proportion of patches that were joined by a bird and the proportion of time it spent searching with the head up. Each of the 21 points represents the average of one bird for 6 to 10 trials. The proportion of joining increased with the proportion of time searching with the head up ($p=0.001$).

Figure 4   Hopping rate of search and pursuit for producer (blank) and for scrounger (dashed). The rate of hopping for pursuit was higher than that for search ($p=0.002$). It was

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also higher for scrounger than for producer (p=0.001), more so for pursuit than for search (interaction: p=0.007)

Figure 5   Cumulative probability distribution of intake rates for 10s intervals. Each point represents the average proportion of intervals (n=20), in which the intake rate for producer (filled triangles and solid line) and scrounger (open squares and dashed line) was lower than a given intake rate. The cumulative probability distribution at low intake rates (0.1 & 0.2 seed/s) was lower for scrounger than for producer, but only significantly so for an intake rate of 0.1 seed/s (p=0.001). For high intake rates (0.3 – 0.6 seed/s), it was non-significantly higher for scrounger than for producer.

Figure 6   Hypothetical curves for PIES as a function of I_R for producer (solid line) and scrounger (dashed line) tactics. a) For a given I_R (R1), the proportion of scrounger in the group should stabilize when producer and scrounger yield equal PIES. b) When increasing I_R (R1 to R2), the proportion of scrounger in the group should decrease until both tactics yield equal PIES again at R2.

Figure 7   Feeding schedule of the birds. The day preceding tests, the birds were given either 100% (dashed) or 50% (speckled) of their normal intake for the last 6h of the day. They were then food deprived 12h overnight and 2h in the morning before testing. A 2h period of ad libitum feeding followed tests.

Figure 8   The mean hopping rate of 8 birds was higher in low (blank) than in the

high (filled) energy reserve level treatment (p=0.013). Hopping rates are shown for a)

producer search, b) producer pursuit, c) scrounger search, and d) scrounger pursuit.


Figure 9   Mean intake rate of producer and scrounger tactics in the low (blank) and

high (dashed) energy reserve level treatments. The payoff of scrounger decreased with

increasing energy reserve levels, but not significantly so.

Figure 10   Cumulative probability distribution of intake rates for intervals of 10s.

Each point represents the average proportion of intervals (n=8), in which the intake rate

for producer (filled triangles and solid line) and scrounger (open squares and dashed line)

was below a given intake rate. In the high energy reserve level treatment (a), curves

crossed below an intake rate of 0.3 seed/s. In the low energy reserve level treatment (b),

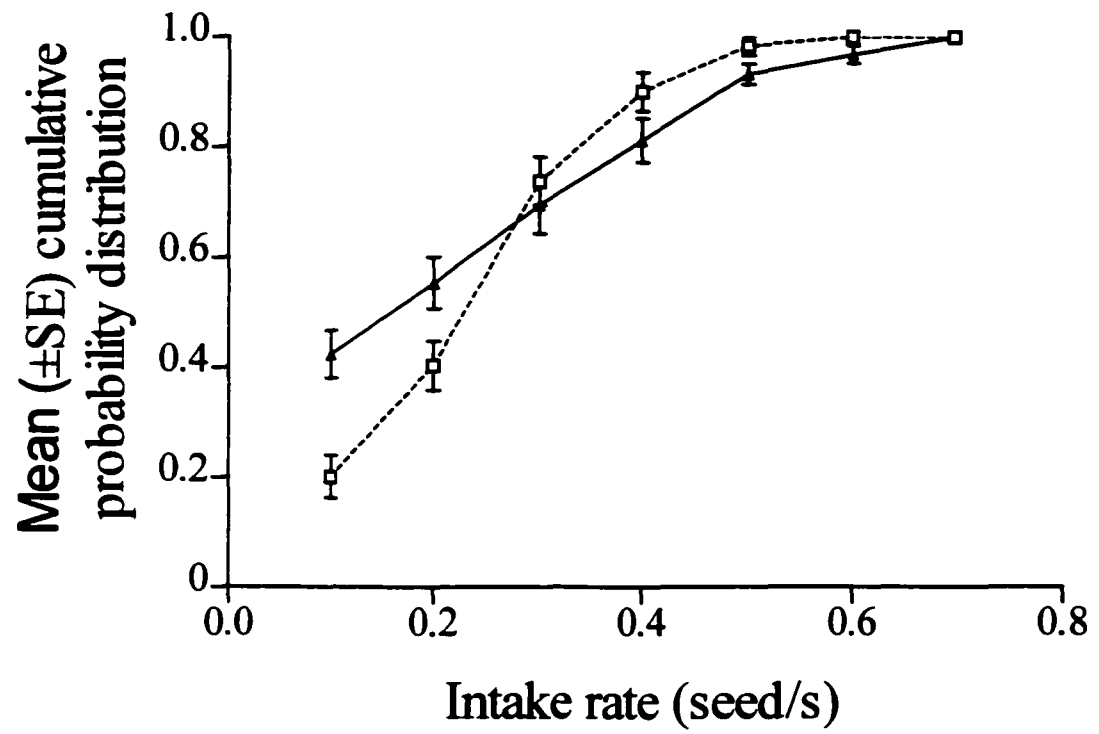the crossing point occurred above an intake rate of 0.3 seed/s.

a. **Concave-down**

Fitness

Reward size

b. **Concave-up**

Fitness

Reward size
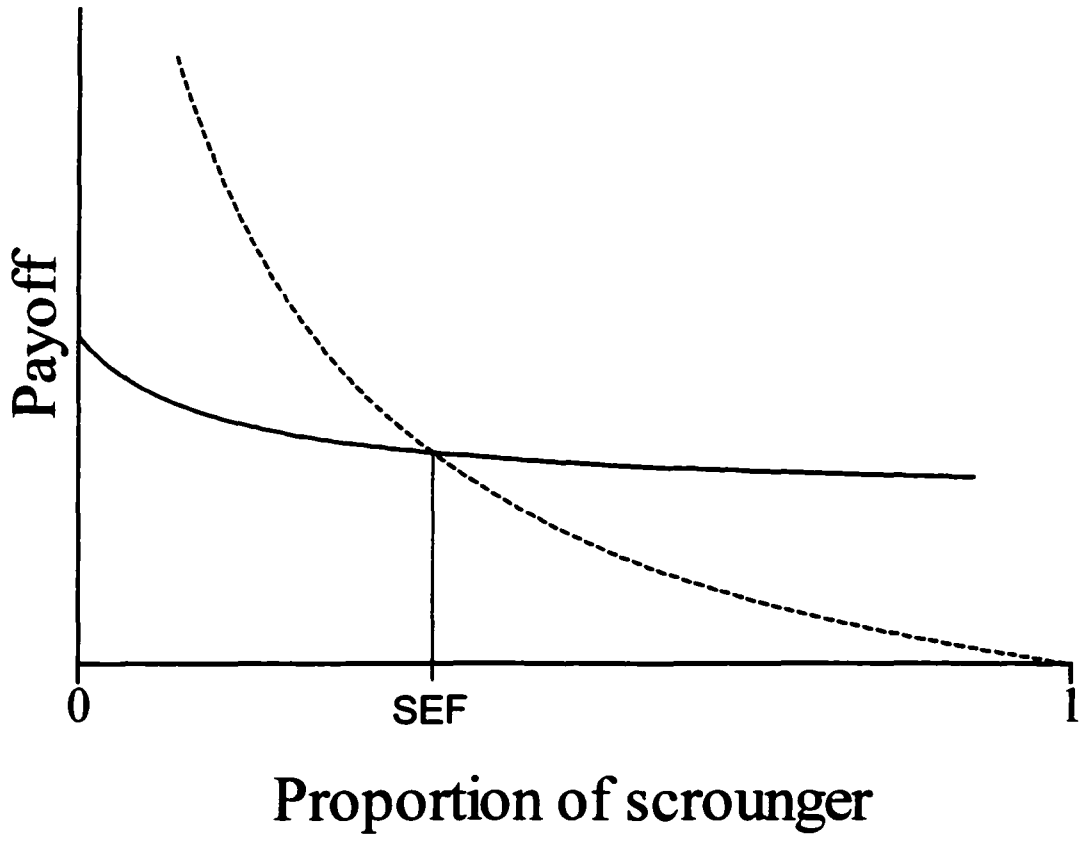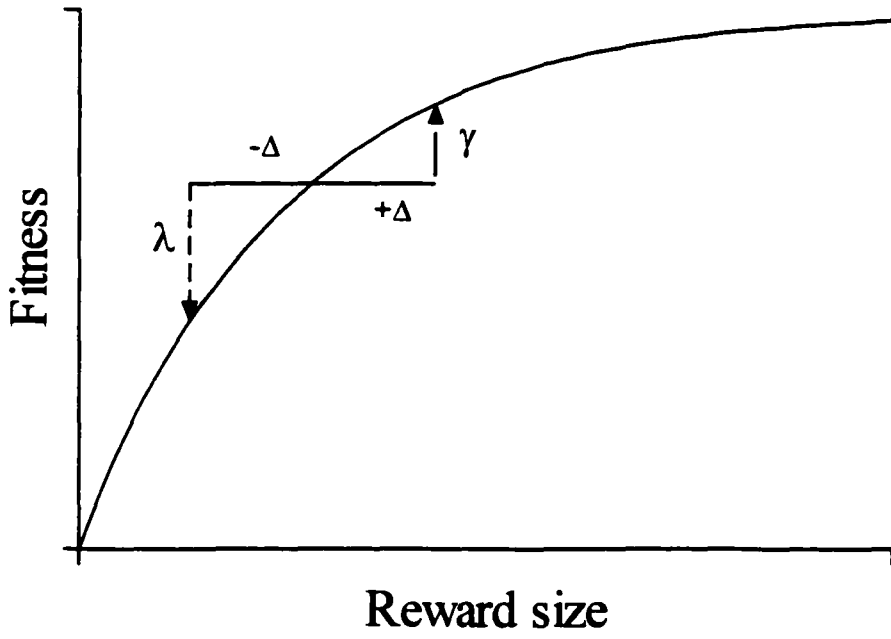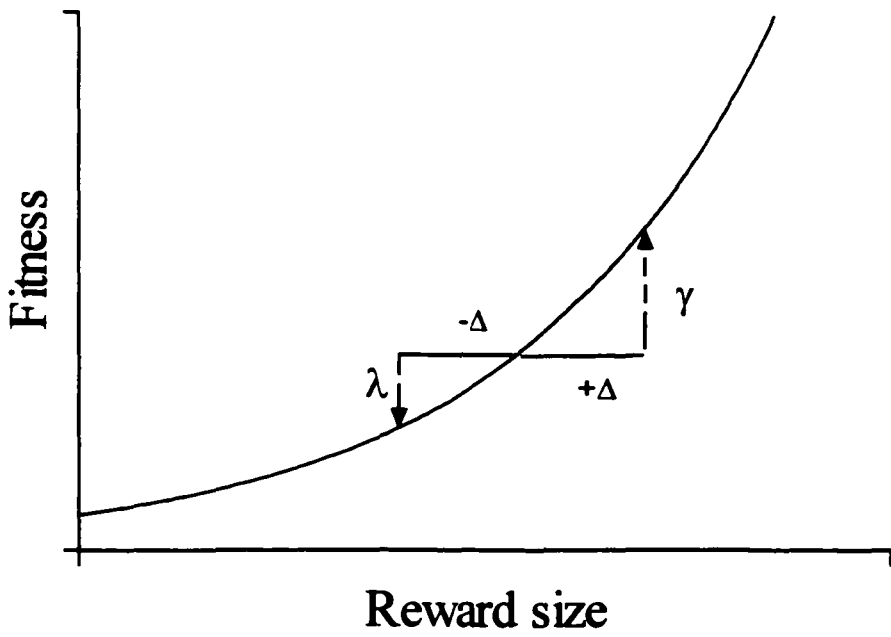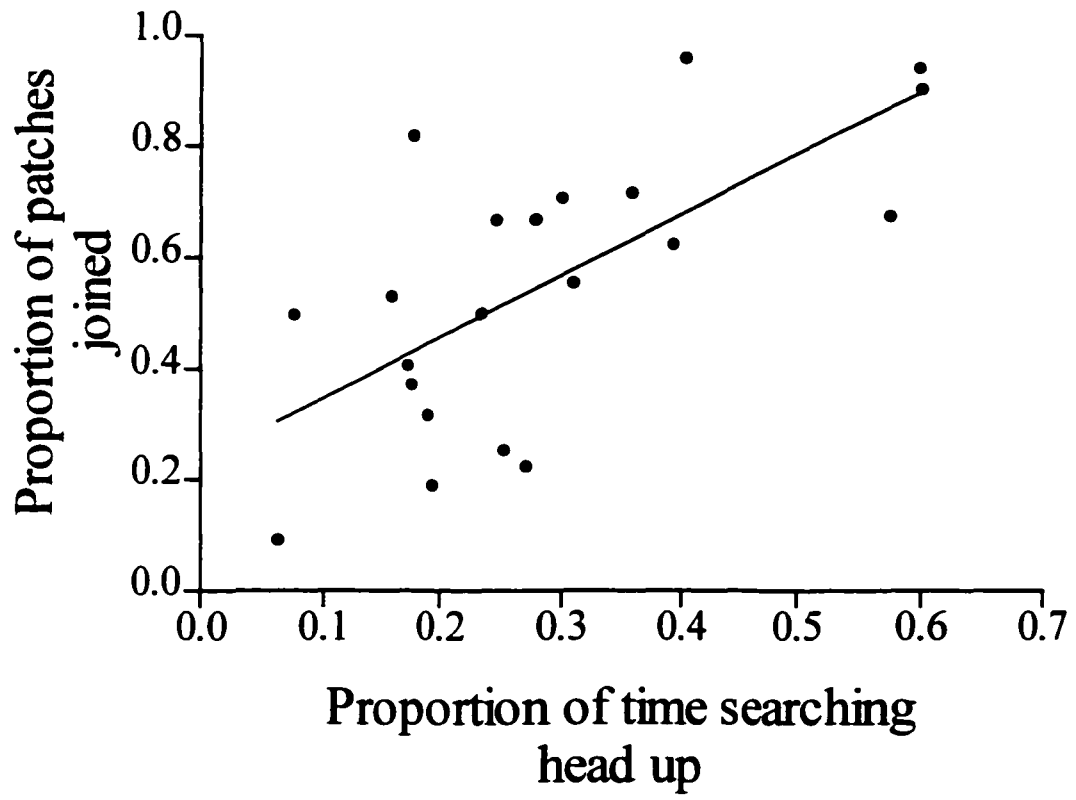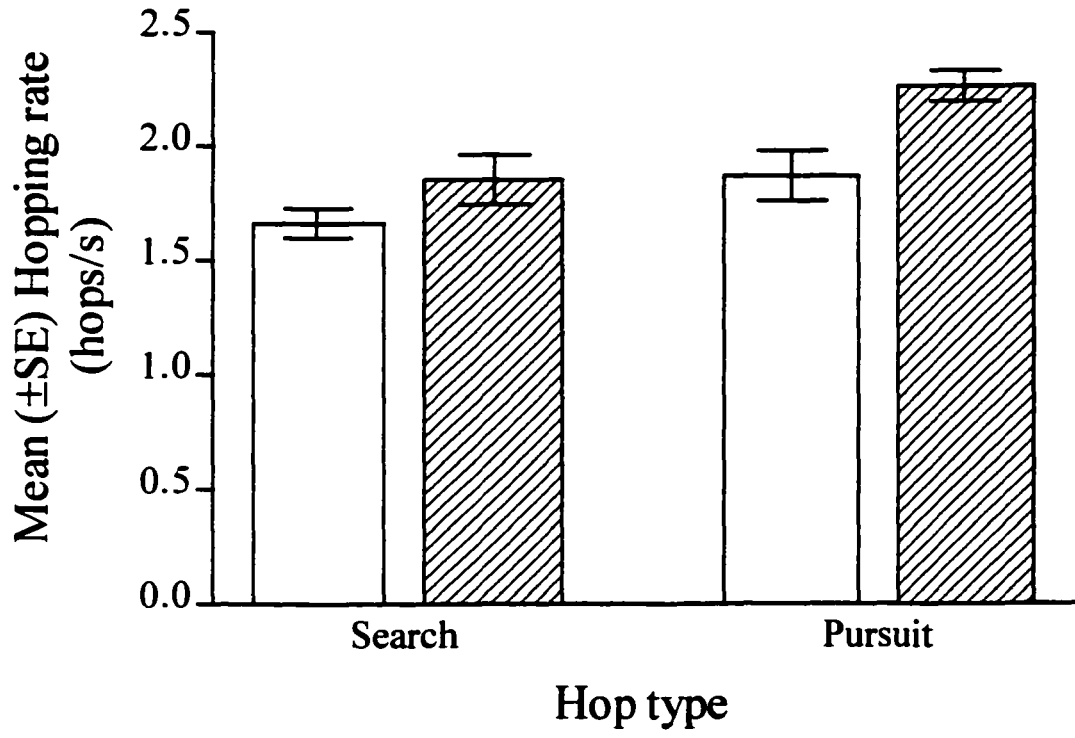
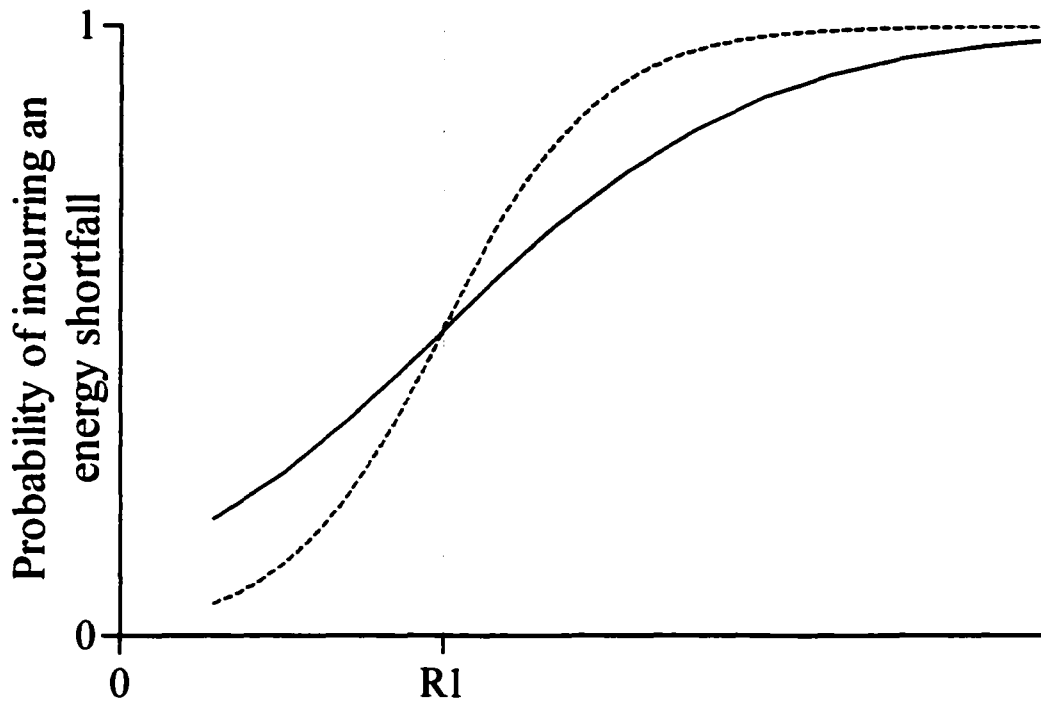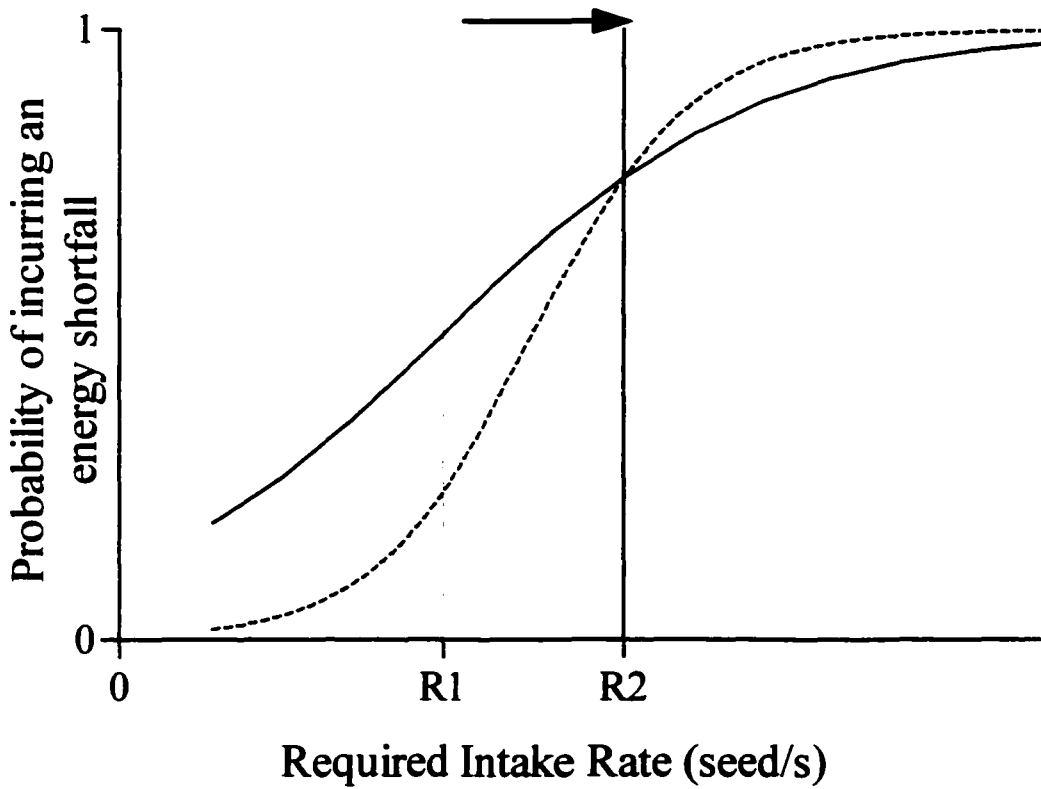a) Low required intake rate

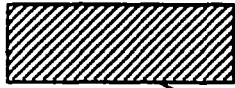b) High required intake rate

Required Intake Rate (seed/s)

High energy reserve level
1.85g seeds / bird
(100% normal intake)
6h

Night (0g)   0g   **Test**   ad lib

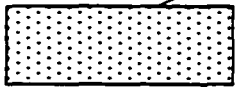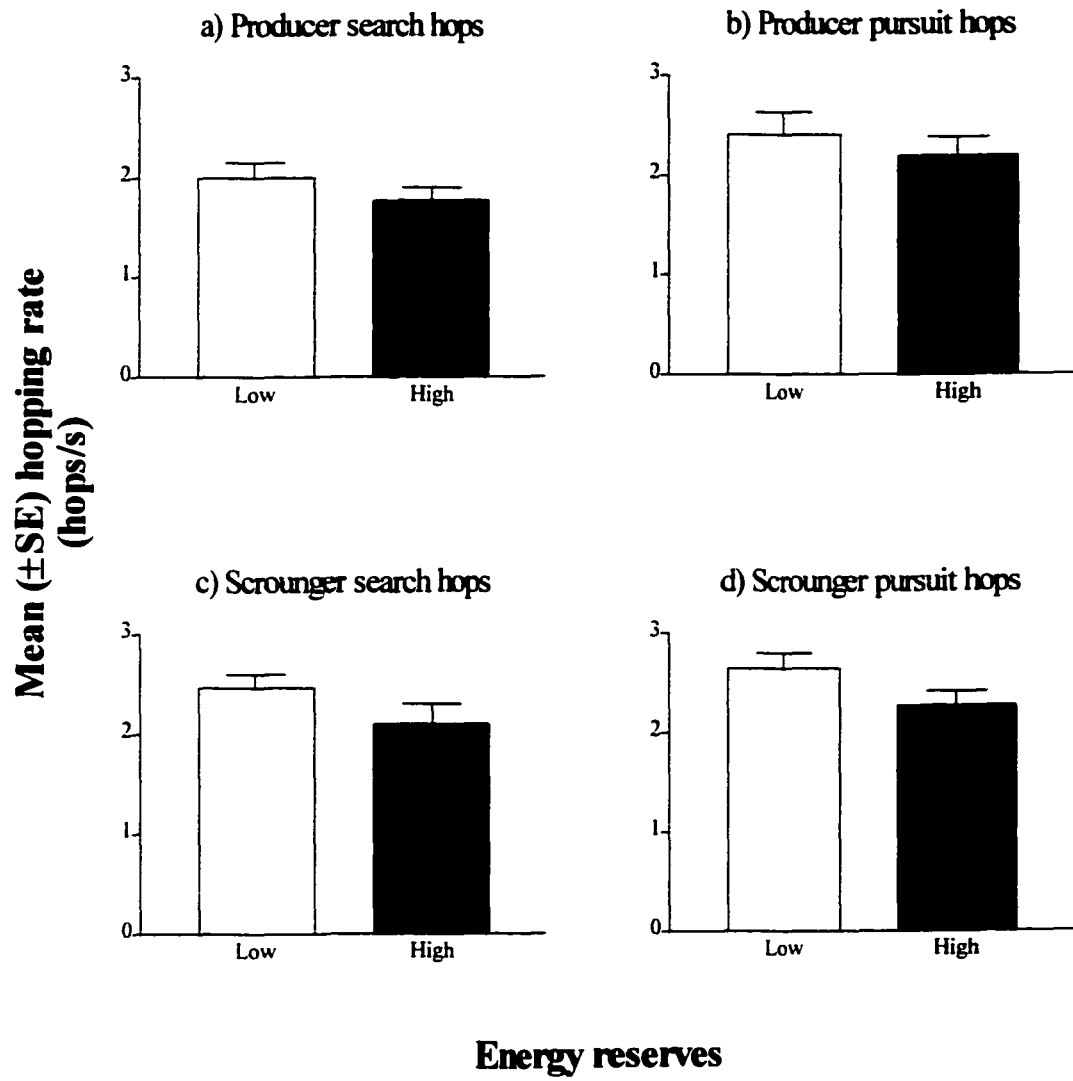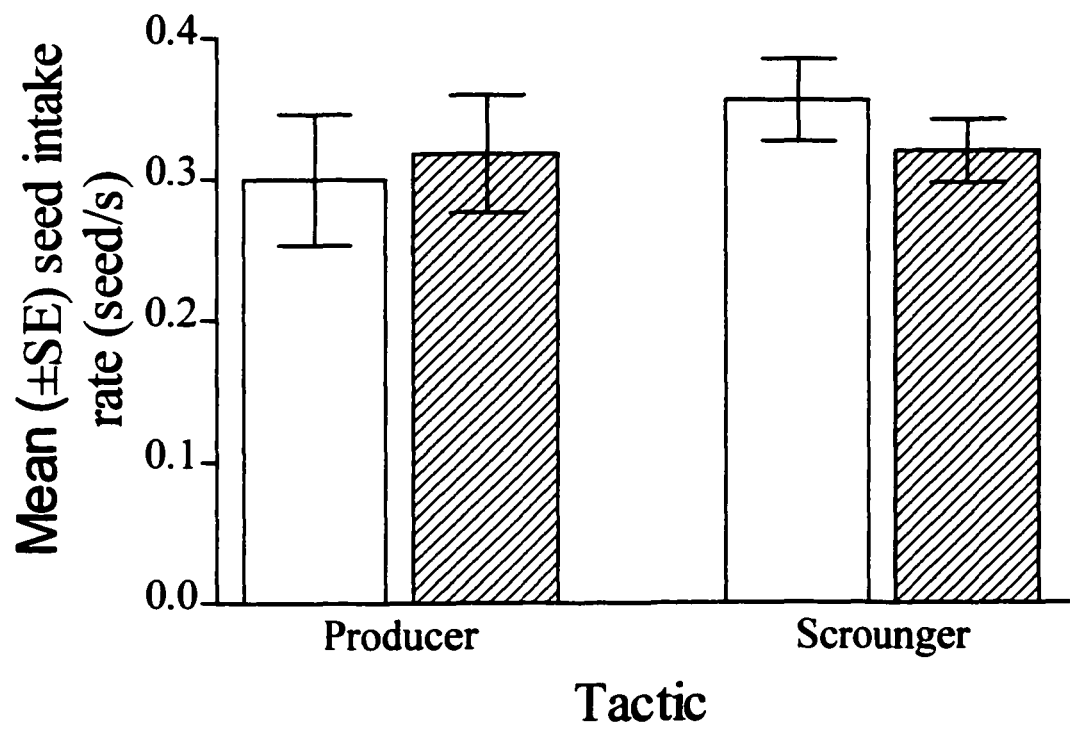12h   2h   2h   2h
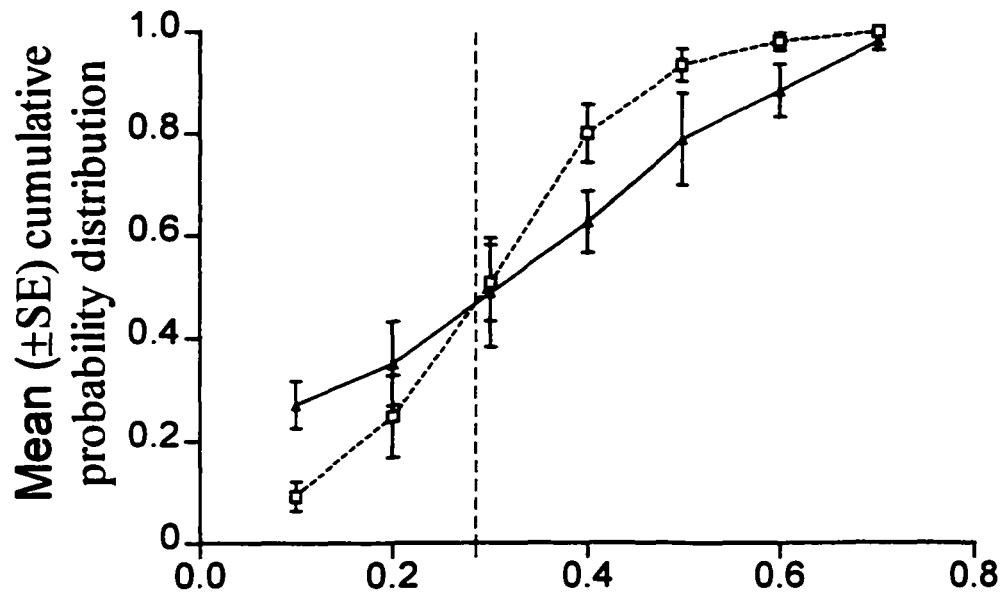
6h
0.93g seeds / bird
(50% normal intake)
Low energy reserve level

a) Producer search hops

b) Producer pursuit hops

c) Scrounger search hops

d) Scrounger pursuit hops

Mean (±SE) hopping rate (hops/s)

Energy reserves

a) High energy reserves

b) Low energy reserves

Intake Rate (seed/s)