

Original Article

Zebra finches in poor condition produce more and consume more food in a producer–scrounger game

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When they forage in groups, animals can search for their own food (producer tactic) or exploit the discoveries of others (scrounger tactic). Previous experimental inquiries have demonstrated that individuals vary in their tendency to play either tactic but the extent to which individual factors influence variation in foraging behavior are little studied. In the present study, we have assessed the influence of natural variation in body condition on the differential use of social foraging tactics and their resulting payoffs in zebra finches (*Taeniopygia guttata*). The producer tactic was found to yield more consistent and predictable rewards across trials than the scrounger tactic. The use of producer was related to reduced variation in food intake and an increased amount of food consumed. We found that poor-condition birds were more likely to produce and so consumed more seeds than good-condition birds. The results are consistent with theoretical models of variance-sensitive social foraging but suggest that scrounging may not represent a variance-averse option in all situations. We propose that in a producer–scrounger context, the variance-averse option may depend on group size and food clumping. Finally, we discuss our results in relation to interindividual differences in metabolism and behavior. *Key words*: bootstrap, decision rules, food intake, residual body mass, scramble competition, variance-sensitive foraging. [*Behav Ecol* 23:174–180 (2012)]

INTRODUCTION

Animals often differ in the behavioral tactics they use to acquire resources, such as mates (Gross 1996) or food (Giraldeau and Caraco 2000). Social foraging offers an opportunity to investigate the causes and consequences of such behavioral diversity within species. When they forage in groups, animals may either actively search for their own food, independently of group mates' behavior (producer tactic), or search for opportunities to join the discoveries of others and feed from them (scrounger tactic) (Barnard and Sibly 1981). Theoretical and experimental results have demonstrated that producer–scrounger foraging tactics have frequency-dependent payoffs (Vickery et al. 1991; Mottley and Giraldeau 2000). Individuals are expected to maximize their food intake through the differential use of these tactics (Bateson 2002), which generally translates into a stable equilibrium frequency of producer and scrounger alternatives within foraging groups (Giraldeau and Caraco 2000; Mottley and Giraldeau 2000). Natural selection is thus expected to have shaped the adaptive decision mechanisms leading organisms to adopt either tactic optimally, at least until a stable equilibrium is reached (Maynard Smith 1982).

Several studies have identified environmental factors that affect the stable equilibrium frequency of producers and scroungers within groups. Among them, predation risk (Barta et al. 2004), group size, and feeding patch size (Coolen 2002) all positively affect the frequency of scrounging in a group at equilibrium. These “group-level studies” have given way to “individual-based studies,” which have pointed out that individuals differ in their tendency to adopt either tactic (Beauchamp 2001; Katsnelson et al. 2011; Morand-Ferron et al. 2011). This suggests that individual phenotype differences must be taken into account when predicting the stable equilibrium frequency within foraging groups. Several characteristics, such as social dominance status (Liker and Barta 2002; Lendvai et al. 2006) and foraging efficiency (Beauchamp 2006), have been found to influence scrounger tactic use. Also, in house sparrows (*Passer domesticus*), individuals with experimentally reduced energy reserves rely more on scrounging (Lendvai et al. 2006). In such small ground-feeding birds with relatively high metabolic rates, nocturnal energetic shortfalls represent an important threat of starvation especially in cold climes (Dall and Witter 1998; Bateson 2002), and so selection is expected to have favored decision mechanisms that take this threat into account (Caraco 1980).

In a social foraging context, Barta and Giraldeau (2000) determined through a state-dependent producer–scrounger model that birds should be more likely to scrounge early in the day when their energy reserves fall below the requirement to survive a nonforaging period. The optimal differential use of producer and scrounger tactics then is likely to vary as a function of individual's state. Scrounging is commonly

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assumed to be the variance-averse tactic in a producer–scrounger game because it is less likely to go without food over any given interval (Barta and Giraldeau 2000). Indeed, Although each producer can either obtain much food when it finds or no food at all when it does not, scroungers are more certain to obtain some food from the pooled search effort of all producers (Barta and Giraldeau 2000). However, this assumption is strongly dependent on the importance of finder's share (Barta and Giraldeau 2000). An increase in finder's share should be linked to a reduction of overall scrounger tactic use (Vickery et al. 1991). Experimental evidence of the influence of the finder's share on the variance-sensitive properties of producer and scrounger tactics are still lacking so far. At least 2 studies to date provided some experimental tests for these assumptions and concluded that scrounging was the variance-averse tactic (Lendvai et al. 2004; Wu and Giraldeau 2005). Although studies that experimentally alter an individual's energetic status are common (Lendvai et al. 2004, 2006), little is known about whether natural variation in individual body condition, a common correlate of energetic status, affects the differential use of scrounger and producer tactics (but see Mathot and Giraldeau 2010). Yet, natural variation in condition may more readily allow individuals to express an adaptive response to variance-sensitive foraging than experimentally induced differences (Kacelnik and Bateson 1996).

In the present study, we test whether natural variation in body condition, estimated as residual body mass (Schamber et al. 2009), is related to foraging tactic use in a producer–scrounger game using the zebra finch (*Taeniopygia guttata*), a domesticated ground-feeding passerine bird (Dall and Witter 1998; Mathot and Giraldeau 2010). Following theoretical predictions (Barta and Giraldeau 2000) and previous experimental evidence (Mathot and Giraldeau 2010), we expect birds in lower body condition to be more likely to adopt the variance-averse scrounger tactic.

MATERIALS AND METHODS

Study subjects

Twelve male and 12 female zebra finches were purchased from a local supplier (L'oisellerie de l'Estrie, Québec, Canada). Before the experiments, birds were kept in 3 adjacent rooms in same-sex groups of 2–3 individuals in small home cages (29 × 52 × 38 cm) containing 4 feeders and 4 perches. Room temperature was maintained at 24 ± 1 °C on a 12:12 h light:dark cycle (0800–2000 h Eastern Daylight Savings Time [EDST]). Millet seeds, water, and cuttlebones were provided ad libitum while vegetables and an egg mixture were occasionally offered. Each individual wore an orange plastic leg ring (AC Hughes, Hampton Hill, UK, size XF) allowing individual identification. Eight days before the experiments, tarsus length was measured twice with a digital caliper to the nearest 0.1 mm, and each individual was weighed twice to the nearest 0.01 g with an electronic balance. All measures were performed by M.D. within a 1-h interval from 0900 h (EDST) to minimize any interindividual differences due to time of day (Mathot and Giraldeau 2010). Measurements of tarsus length (Pearson's $r_{23} = 0.79$, $P < 0.0001$) and weight ($r_{23} = 0.98$, $P < 0.0001$) were significantly repeatable. For each variable, the repeated measurements were averaged and the individual means used thereafter. After the experiment, birds were kept in groups of 2 to be used in subsequent studies.

Producer–scrounger trials

Foraging experiments were conducted with 3 male flocks and 3 female flocks of 4 birds each. Individuals within flocks had been sorted for the purpose of another study based on their exploration tendencies (for more details about this procedure,

see David, Cézilly, et al. 2011). We used same-sex foraging flocks to avoid any interference from behavior related to reproduction. We did not associate birds that had previously been housed together to avoid any potential effect of familiarity.

Experiments were conducted over 3 consecutive days. On the first day, birds were given a unique combination of blue and light blue leg rings for identification from the video footage. Thus, in addition to their orange identification ring, the 4 birds in each flock wore one of the following color combinations: light blue–light blue, light blue–blue, blue–light blue, and blue–blue. Blue and light blue rings are presumed to have little effect on sexual or agonistic interindividual interactions (David, Auclair, et al. 2011). Once ringed, each bird was placed with its new flock mates inside a large aviary (1.5 × 3.8 × 2.3 m) containing 2 tables (1.4 × 0.7 m), one supporting a foraging grid with 64 wells (1.6 cm in diameter and 1 cm deep) spaced every 8.1 cm and the other 2 perches and 2 water containers (David, Cézilly, et al. 2011). The aviaries were kept on the same light cycle and temperature as the holding rooms. To familiarize the birds with the aviary and the foraging grid, each and every well was filled with millet seeds on the first day.

On the second day, the grid and the aviary floor were cleaned in the morning to prevent birds from feeding on seeds that had spilled onto the floor. Birds were then deprived of food for 1 h. Thereafter, each flock was given 50 white millet seeds distributed 5 per well in 10 randomly selected wells every hour for 7 h (training phase). This procedure allows them to forage in flocks in conditions similar to test conditions for 7 consecutive training trials, after which they were given ad libitum access to seeds spread in all grid wells. The same procedure was performed again on the third day (testing phase) but for 5 consecutive trials starting at 0900 h that were video recorded for a maximum time of 10 min each. Ten randomly selected wells were replenished with 5 seeds each before each trial. Following the final trial, the birds were returned to their home cages in groups of 2–3 individuals per cage and provided with ad libitum access to seeds.

During video analysis, we noted each bird's landing order on the grid and counted the individual number of seeds produced, defined as the number of seeds taken from a previously unexploited well. Note that we did not record the investment into the producer tactic per se, which would have required us to measure the number of individual hops with the head up (Coolen et al. 2001). Here, we recorded the actual number of seeds produced, which is correlated to the behavioral investment into the producer tactic (Coolen et al. 2001; Wu and Giraldeau 2005). We never observed a bird attempting to forage from an empty well. However, the possibility remains that the variance in the number of seeds obtained through producing may be underestimated as failed producing attempts could not be recorded. We also counted the number of seeds scrounged, defined as the number of seeds eaten from a well on which other birds were already feeding or had just left (within the last 2 s). Only for one trial in one flock was a full well not discovered. For all the other trials, we stopped the analyses after the last full well had been exploited and seeds inside eaten. The number of seeds eaten by a given individual can easily be recorded as zebra finches perform highly stereotypic beak movements when separating the seed from the husk (Zann 1996). In most cases, the husk can be seen falling from the beak indicating that a seed has been ingested.

Data analyses

Body condition was assessed from the residuals of the linear regression of \log_{10} (weight) on \log_{10} (tarsus length) (Schamber et al. 2009). Residual body mass is a widely used index of

body condition in avian studies (Schamber et al. 2009). It indicates individual mass departure from the value predicted on the basis of its tarsus length. Tarsus length reliably reflects structural body size in zebra finches (Mathot and Giraldeau 2010). As both muscle and fat can provide energy sources for birds (Swain 1992), we feel confident that our residual body mass is an adequate measure of condition (Schulte-Hostedde et al. 2005).

We defined “total number of seeds ingested” as the sum of the number of seeds produced and scrounged across the 5 experimental trials for a given individual. The individual’s mean number of seeds ingested per trial was estimated from the number of seeds produced and scrounged calculated for each trial, then averaged across the 5 trials for each bird. We computed an individual’s average proportion of seeds scrounged as the number of seeds it scrounged in a given trial divided by the sum of the number of seeds it both scrounged and produced during this trial, averaged over the 5 trials. We calculated the average number of seeds that producers actually ingested per producing event by dividing the total number of seeds produced during a trial by the number of producing events during the same trial and calculated the average for the 5 trials. A producing event occurs when a bird finds a previously unexploited well and eats seeds from it. We defined the “finder’s share” as the average number of seeds eaten per producing event less the average obtained by scrounging divided by the total number of seeds in a well. To obtain this value, we assumed that producers stay in a patch until the end and that all scroungers arrive simultaneously at the patch. Given those assumptions, we can estimate the amount of food eaten by a producer before the arrival of scroungers as the difference between the total seeds eaten at a patch when an animal produced it and the total number of seeds eaten when an animal scrounged. Knowing the total number of seeds in each patch, the finder’s share is then estimated as this difference divided by number of seeds in a well. Individual values were averaged across the 5 trials. We calculated an individual’s standard deviation for each variable in a similar way, across the 5 trials for that individual.

We calculated an individual’s coefficient of variation (CV) for each variable as the individual’s standard deviation for that variable across the 5 trials, divided by the mean value of the same variable across the same 5 trials. Interindividual differences in “proportion of seeds scrounged” and “number of seeds ingested per producing event” were assessed through analyses of variance with the 5 individual measures recorded in the 5 trials as the dependent variable and “individual identity” as the predictive variable (Lessells and Boag 1987).

To control for the nonindependence of foraging data within flocks, we performed linear mixed models with “flock” as a random factor using the function “lme” from the “nlme” library of R software (R Development Core Team 2008). Degrees of freedom (df) equaled 17 for these analyses. Sample size was 24 for each analysis except when CVs or the variable proportion of seeds scrounged were involved. In these cases, sample size was 23 because a bird ingested no seeds over the whole experiment, making it impossible to compute a value for it. We did not assess the effect of sex in our analyses due to the small number of same-sex flocks. The effect of leg-ring combination types on foraging behavior was assessed through Friedman tests to control for the nonindependence of data within flocks.

Variables were log, root, or arcsine square root transformed to reach normality when needed. All tests were two tailed. Statistical analyses were carried out using JMP 5.0.1, Statview statistical software (SAS Institute, Cary, NC), and R 2.11.0 (R Development Core Team 2008).

RESULTS

Foraging tactic use and variance in food intake

The birds ate significantly more seeds within each trial by producing (mean per trial \pm 95% confidence interval [CI]: 8.90 ± 2.59) than by scrounging (2.12 ± 0.92 ; paired *t*-test using individual averages: $t_{23} = -5.34$, $P < 0.0001$), and the mean number of seeds produced predicted the total number of seeds ingested over the 5 trials ($R^2 = 0.72$, bootstrap 95% CI [0.52–0.86], $F_{1,18} = 60.5$, estimate $b = 81.5 \pm 10.5$, $P < 0.0001$; Figure 1). Neither the number of seeds scrounged ($R^2 = 0.07$, 95% CI [$<0.01 - 0.33$], $F_{1,18} = 0.58$, $b = 5.8 \pm 7.6$, $P = 0.46$) nor the proportion of seeds scrounged ($R^2 = 0.08$, 95% CI [$<0.01 - 0.31$], $F_{1,17} = 0.96$, $b = -23.4 \pm 23.9$, $P = 0.34$) were predictive of the total number of seeds ingested. The mean proportion of seeds scrounged per bird per trial was $21.7 \pm 9.5\%$, and this proportion varies significantly among individuals, indicating that birds varied in their tendency to use either tactic ($F_{22,105} = 4.72$, $P < 0.0001$). The mean number of seeds ingested per producing event was 2.23 ± 0.26 seeds, and the number of seeds ingested per scrounging event was 1.06 ± 0.19 seeds, which represents an overall finder’s share of 0.23 ($= [2.23 - 1.06]/5$). Furthermore, the mean number of seeds ingested per producing event differed significantly between individuals ($F_{22,99} = 3.29$, $P < 0.0001$), whereas the mean number of seeds ingested per scrounging event did not (Kruskal–Wallis: $H_{20} = 26.26$, $P = 0.16$).

The CVs of both the number of seeds produced (0.46 ± 0.10) and the number of seeds scrounged (0.46 ± 0.13) were not significantly different ($t_{23} = 0.01$, $P = 0.99$). The CV of the number of seeds ingested per trial was negatively affected by the number of seeds produced ($R^2 = 0.22$, 95% CI [0.01–0.53], $F_{1,17} = 9.71$, $b = -0.4 \pm 0.2$, $P = 0.007$; Figure 2), suggesting that the more a bird produced the more consistent was the number of seeds it ingested across trials. Neither the number of seeds scrounged ($R^2 = 0.13$, 95% CI [$<0.01 - 0.43$], $F_{1,17} = 2.07$, $b = -0.1 \pm 0.1$, $P = 0.17$) nor the proportion of seeds scrounged ($R^2 = 0.05$, 95% CI [$<0.01 - 0.23$], $F_{1,17} = 0.03$, $b = -0.1 \pm 0.2$, $P = 0.86$) influenced the CV of the number of seeds ingested per trial. The CV of number of seeds produced significantly predicted the CV of the number of seeds ingested per trial ($R^2 = 0.61$, 95% CI [0.29–0.89], $F_{1,17} = 33.0$, $b = 0.9 \pm 0.2$, $P < 0.0001$; Figure 3). However, the

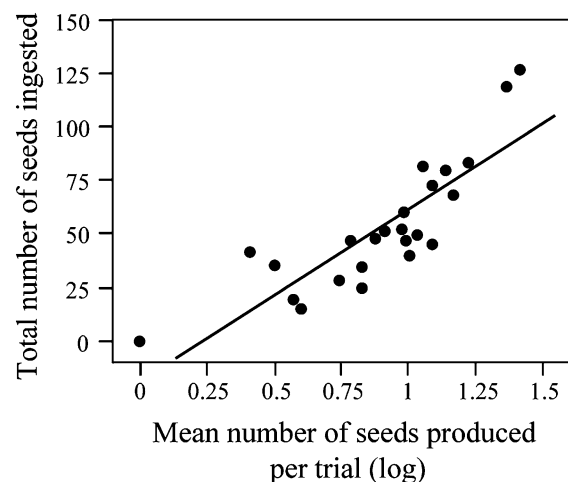


Figure 1
Relationship between the total number of seeds ingested over the 5 producer–scrounger trials and the mean number of seeds produced per trial.

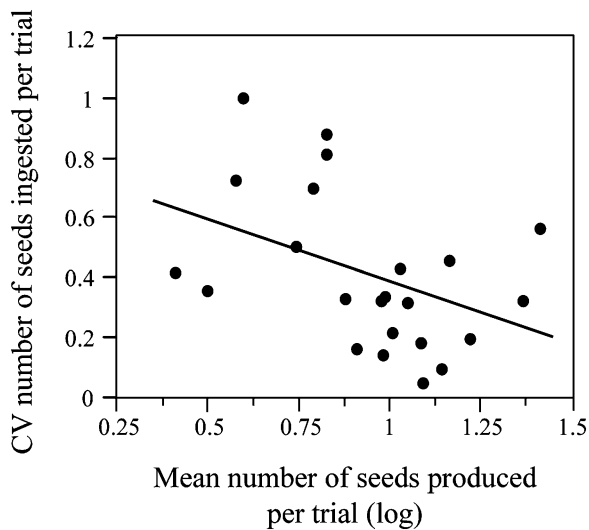


Figure 2
Relationship between the CV of the number of seeds ingested per trial and the mean number of seeds produced per trial. x axis values have been log transformed to reach normality.

CV of number of seeds scrounged ($R^2 = 0.07$, 95% CI [$<0.01 - 0.32$], $F_{1,17} = 0.03$, $b = -0.1 \pm 0.2$, $P = 0.87$) and the CV of proportion of seeds scrounged ($R^2 = 0.14$, 95% CI [$<0.01 - 0.50$], $F_{1,17} = 1.47$, $b = 0.6 \pm 0.5$, $P = 0.24$) did not affect the CV of total number of seeds ingested. Thus, a more consistent amount of seeds produced resulted in a more consistent number of seeds ingested across trials.

Effect of body condition on foraging tactic use

Leg-ring combination type was not related to body condition measured 8 days before the experiments (Kruskal-Wallis: $H = 3.75$, $df = 3$, $P = 0.29$). Leg-ring combination types had no effect on arrival rank order ($\chi^2 = 6.2$, $df = 3$, $P = 0.10$), total number of seeds ingested ($\chi^2 = 3.2$, $df = 3$, $P = 0.36$), nor proportion of seeds scrounged ($\chi^2 = 5.1$, $df = 3$, $P = 0.16$).

Body condition measured 8 days before the experiments did not differ between males and females ($t_{22} = -0.14$,

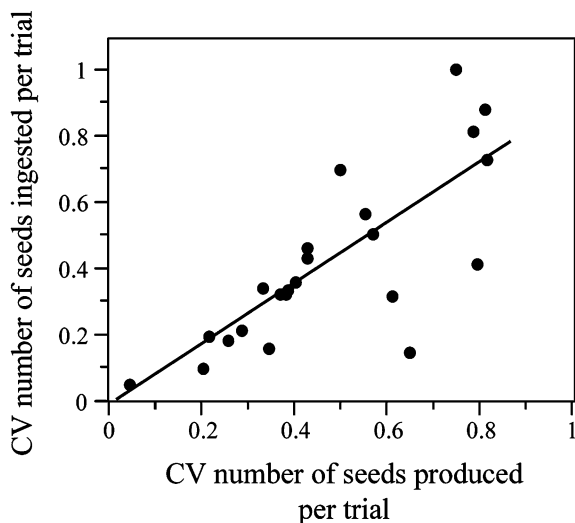


Figure 3
Relationship between the CV of the number of seeds ingested per trial and the CV of the number of seeds produced per trial.

$P = 0.89$). Arrival order on the grid was not significantly influenced by body condition ($R^2 = 0.15$, 95% CI [$<0.01 - 0.43$], $F_{1,18} = 2.99$, $b = 9.3 \pm 5.4$, $P = 0.10$). Body condition predicted the total number of seeds ingested over the 5 trials ($R^2 = 0.19$, 95% CI [$<0.01 - 0.46$], $F_{1,18} = 4.51$, $b = -412.1 \pm 5.4$, $P = 0.05$; Figure 4a), the proportion of seeds scrounged ($R^2 = 0.22$, 95% CI [$<0.01 - 0.51$], $F_{1,17} = 11.64$, $b = 5.3 \pm 1.5$, $P = 0.004$; Figure 4b), the number of seeds produced ($R^2 = 0.23$, 95% CI [$<0.01 - 0.50$], $F_{1,18} = 6.18$, $b = -5.0 \pm 2.0$, $P = 0.02$; Figure 4c), but not the number of seeds scrounged ($R^2 = 0.08$, 95% CI [$<0.01 - 0.33$], $F_{1,18} = 0.95$, $b = 5.6 \pm 5.8$, $P = 0.34$) nor the number of seeds ingested per producing event ($R^2 = 0.10$, 95% CI [$<0.01 - 0.30$], $F_{1,22} = 1.87$, $b = -6.1 \pm 4.4$, $P = 0.19$). Thus, birds in poor condition ate more and were more likely to produce than individuals in good condition.

Body condition significantly predicted the CV of proportion of seeds scrounged ($R^2 = 0.26$, 95% CI [0.02–0.57], $F_{1,17} = 6.75$, $b = 1.9 \pm 0.7$, $P = 0.02$; Figure 5). Birds in poor condition were more consistent in their favoring of a tactic, whereas individuals in good condition showed a greater variation in tactic use across the 5 trials.

DISCUSSION

Our study shows that zebra finches that consumed more seeds from producing had a higher and less variable total food intake, whereas there was no such effect for scrounging. Moreover, individuals in poorer condition consistently favored the producer tactic, whereas individuals in better condition showed a more variable use of alternative foraging tactics. Taken together, these results suggest that zebra finches in poorer condition tend to produce more, obtain more food per trial, and less variable amounts among trials. We discuss the implications of these results in light of variance-sensitive foraging in a producer–scrounger context.

It is commonly assumed in a producer–scrounger game that scrounger is the option that provides a variance-averse foraging alternative (Barta and Giraldeau 2000), an assumption supported experimentally by Wu and Giraldeau (2005). In the present study, on the other hand, we found that the more an individual obtained seeds using the producer tactic, the less variable the number of seeds (producer plus scrounger) it ingested per trial. The number of seeds obtained from scrounging, however, had no effect on variation in total number of seeds ingested. The lower variance associated with the producer alternative may appear at odds with commonly accepted assumptions of stochastic producer–scrounger games (Barta and Giraldeau 2000) and in total contrast with Stephens's (1981) prediction. However, Stephens's (1981) static model predicted the behavior of individuals foraging alone, making it different from Barta and Giraldeau's (2000) stochastic dynamic social foraging model. However, it is important to understand that in the present study, unlike Wu and Giraldeau (2005), we did not measure the variance between successive producing attempts but rather the variance of the amount of food ingested among trials. Our estimate of variation does not correspond to the actual uncertainty of the producer tactic because we do not take into account failed producing attempts that would normally contribute to its uncertainty. Indeed, in the present design, there was no possibility to record failures to acquire seeds through producing and no observation of an individual actually attempting to feed from an empty well. Here, the birds could see from a distance whether wells contained food. However, it is entirely possible that another type of foraging patch involving, for instance, the need to probe actively within wells to determine whether it contains food or not would generate an entirely different level of uncertainty for the producer

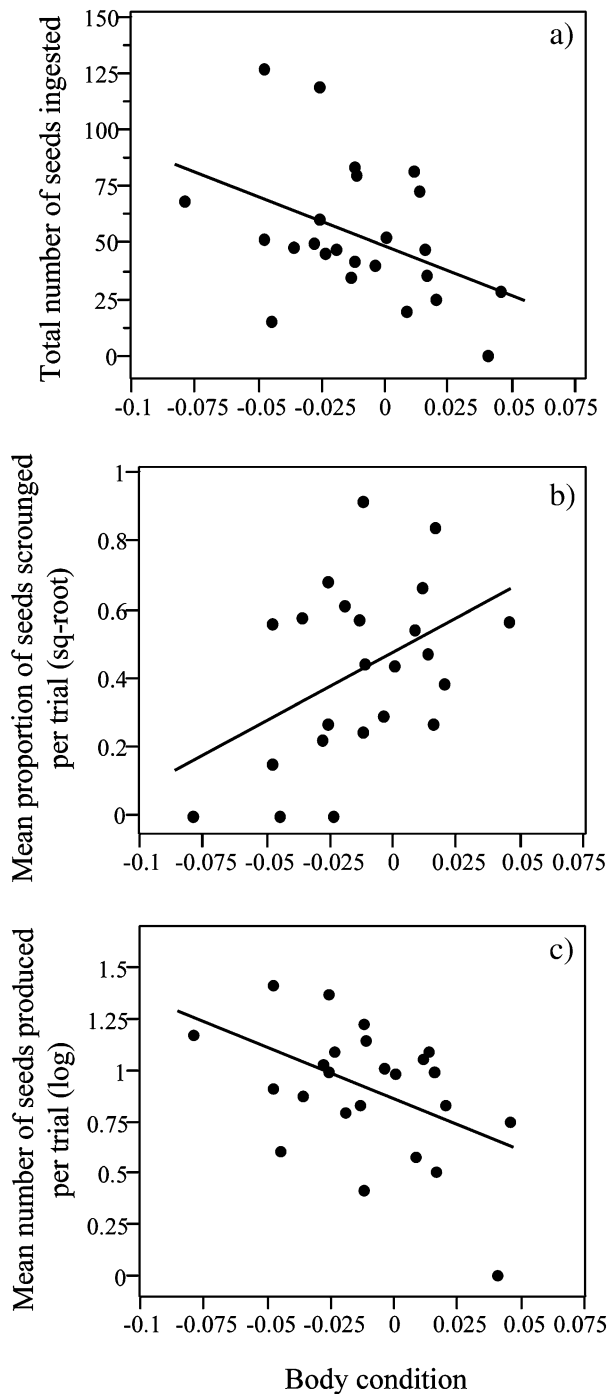


Figure 4
 (a) Relationship between the total number of seeds ingested and body condition. (b) Relationship between the mean proportion of seeds scrounged per trial and body condition. y axis values were square root transformed to reach normality. (c) Relationship between the mean number of seeds produced per trial and body condition. y axis values were log transformed to reach normality. Body condition was defined as the residuals of the regression of body mass on tarsus length (see MATERIALS AND METHODS).

alternative. It would be interesting to explore how different types of prey clumping affect the economics of the producer–scrounger game, and the question still remains why exactly in our situation an increased return from the producer alternative was significantly associated with a less variable total intake between trials.

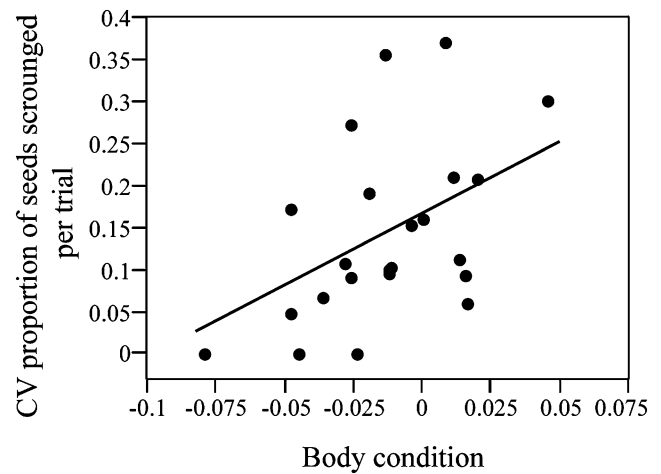


Figure 5
 Relationship between the CV of the mean proportion of seeds scrounged by a given individual per trial and body condition. Body condition was defined as the residuals of the regression of body mass on tarsus length (see MATERIALS AND METHODS).

A number of factors could have contributed to reducing the variability of the producer option in our study. For instance, food patches may be so common or easy to find on our foraging grids that producing is a more certain option than scrounging. This may be especially true when, in addition, the finder's share is so large such that scroungers are left with little to expect and perhaps even no food if they happen to arrive too late. The influence of the finder's share, number of competitors, and food clumping on the predictability of rewards acquired through both tactics deserves further theoretical as well as experimental investigations.

We also found that body condition exerted an effect on an individual's preference for producer. At least individuals in poor condition obtained more food using producer. If residual body mass is a measure of an individual's condition, then poor-condition individuals should have a higher risk of energy shortfall during a food-deprivation period such as nighttime. In support of such an assumption, poor-condition zebra finches were reported to be faster at resuming feeding after a food-deprivation period than good-condition birds (M. David, Y. Auclair, L.-A. Giraldeau, F. Cézilly, submitted). So food deprivation may bring poor-condition birds closer to a significant energetic shortfall.

We found that poor-condition individuals produced more seeds in a social foraging context and were more consistent in their foraging tactic use than good-condition individuals in the present study. These findings are in contrast with a previous experimental study conducted with house sparrows (Lendvai et al. 2004) where scrounger was the less variable tactic preferentially adopted by poor-condition birds. Knowing that producer is associated with a lower intake variance among trials in the present study, and considering predictions from Barta and Giraldeau's (2000), it is possible here that the function of tactic choice is to reduce uncertainty between foraging bouts when in poor condition. Our results are thus consistent with the minimization of uncertainty among trials or foraging bouts.

The observation that poor-condition birds produce while others tend to scrounge is reminiscent of phenotype-limited producer–scrounger games where subordinates are limited to the producer tactic given that scrounging from more socially dominant individuals is simply not an option (Barta and Giraldeau 1998). A recent study conducted in zebra finches

provides evidence that scrounging requires some form of tolerance from producers (Mathot et al. 2009). Scrounging, for instance, was recorded to occur at higher frequencies within flocks of genetically related individuals, whereas agonistic interactions were less frequent than within flocks of unrelated birds (Mathot et al. 2009). Zebra finches, therefore, vary in their tolerance to the scrounging of flock mates, and so differences in scrounging efficiency and reward variance could have been modulated by the producers' tolerance to scrounging and/or their ability to defend access to their discovery. However, few agonistic interactions were observed in our experiment, which could be due to the few scrounging opportunities, and scrounging is not related to dominance in zebra finches (Giraldeau et al. 1990; Beauchamp 2006). Moreover, in a recent paper, David, Auclair, et al. (2011) have shown that body condition does not influence feeding success in an interference competition feeding contest in zebra finches. These findings suggest that body condition is not likely to play an important role in the ability to secure a food patch or to scrounge, at least in our experiment. Thus, the relationship between dominance, condition, and scrounging tactic use should be tested across experimental designs varying in food distribution, producer's payoffs, or number of competitors.

Several studies report that individual success in a competitive context is positively related to body condition (Bercovitch and Numberg 1996; Pärt and Qvarnström 1997; Martínez-Lendech et al. 2007). Our results are in contrast with these findings as we here have highlighted that poor-condition individuals overall consumed more seeds than good-condition individuals. Although this result may seem counterintuitive at first glance, it could make sense in the context of interindividual behavioral differences. Different preferences for the foraging tactic offering the less variable payoffs between individuals differing in condition might reflect variation in life-history strategies (Biro and Stamps 2010). Thus, poor-condition individuals may have a higher metabolic rate and lower energy reserves in the morning forcing them to adopt either variance-sensitive foraging tactic to avoid starvation. Alternatively, good-condition individuals may have higher morning energy reserves resulting from a lower metabolic rate and lower losses during the night. Assessing the metabolic rate of poor- and good-condition individuals would prove useful to determine whether the higher amount of food consumed by poor-condition individuals really translates into an extra relative energetic gain. Further studies should therefore investigate whether preference for the tactic offering the less variable payoffs is related to interindividual differences in metabolism (Mathot et al. 2009) and possibly to risk-taking behavior, or more generally, personality (Dall et al. 2004; Biro and Stamps 2010). Moreover, individuals may suffer from a conflicting demand between playing producer to avoid starvation and playing scrounger to sustain a high level of vigilance (Barta et al. 2004).

In closing, our study suggests that individuals in poorer condition tend to use the social foraging tactic offering the less variable payoffs which, in the present study, turns out to be producer. Further studies should investigate the role of tactics' payoffs and interindividual interactions on the variance-averse qualities of a given foraging tactic to provide a full understanding of the social and individual factors generating behavioral diversity at the group level.

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