RESEARCH PAPER

Learning to Choose Among Social Foraging Strategies in Adult House Sparrows (*Passer domesticus*)

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Abstract

Social foragers may be regarded as being engaged in a producer–scrounger game in which they can search for food independently or join others who have discovered food. Research on the producer–scrounger game has focused mainly on the different factors influencing its evolutionarily stable strategy (ESS) solution, but very little is known about the actual mechanisms that shape players' decisions. Recent work has shown that early experience can affect producer–scrounger foraging tendencies in young house sparrows and that in nutmeg mannikins learning is involved in reaching the ESS. Here, we show that direct manipulation of the success rate experienced by adult sparrows when following others can change their strategy choice on the following day. We presented to live sparrows an experimental regime, where stuffed adult house sparrows in a feeding position were positioned on a foraging grid that included two reward regimes: a positive one, in which the stuffed models were placed near food, and a negative one, in which the models were placed away from food. There was a significant increase in joining behavior after the positive treatment (exhibited by 84% of the birds), but no change after the negative treatment. Further analysis demonstrated that sparrows more frequently used the strategy with which they were more successful (usually joining) and that differences in strategy use were correlated with differences in success. These results suggest that adult birds can monitor their success and learn to choose among social foraging strategies in the producer–scrounger game.

Introduction

Living in a group allows exploitation of resources found by other individuals in addition to one's own discoveries. Inspired by a group of foraging house sparrows, *Passer domesticus*, Barnard & Sibly (1981) developed the general producer–scrounger model to describe this exploitation behavior. They described it as a game with two frequency-dependent strategies: The producer (searcher) looks for the resource by itself, and the scrounger (joiner) exploits the resource findings of the searcher. Subsequent research on the producer–scrounger game has focused mainly on the factors influencing the game equilibrium or evolutionarily stable strategy (ESS) and has demonstrated the importance of group size (Vickery et al. 1991; Giraldeau & Caraco 2000; Coolen 2002), finder's share (Caraco & Giraldeau 1991; Giraldeau & Livoreil 1998; Giraldeau & Caraco 2000; Coolen et al. 2001; Coolen 2002), dominance rank (Barta & Giraldeau 1998; Giraldeau & Beauchamp 1999; Liker & Barta 2002), physiological state (Caraco & Giraldeau 1991; Koops & Giraldeau 1996; Barta & Giraldeau 2000; Lendvai et al. 2004, 2006) and predation risk (Ranta et al. 1998; Barta et al. 2004; Mathot & Giraldeau 2008). Yet surprisingly, little is known about the behavioral mechanisms that shape players' decisions and allow their behavior to appear to be consistent with an ESS.

In its simplest form, the ESS model of the producer–scrounger game may be based on a genetic dimorphism of pure producers and pure scroungers, or on a population of individuals with an innate tendency to play a mixed strategy (Barnard & Sibly 1981; Giraldeau & Caraco 2000). However, complete genetic control over strategy choice is unlikely given the rich evidence for flexible adjustment of the producer–scrounger tendencies under different environmental or physiological states (Giraldeau et al. 1994; Mottley & Giraldeau 2000; Lendvai et al. 2004; Giraldeau & Dubois 2008). A more realistic view of equilibrium structure in the producer–scrounger game may therefore involve a combination of genetic components and a process in which individuals use environmental cues or personal experience to choose among strategies. The genetic basis of producer–scrounger tendencies has been studied only recently (Mathot & Giraldeau 2010), and some role for genetic effects seems plausible in light of evidence for a heritable component of traits that are related to social foraging, such as exploratory behavior and risk taking (Drent et al. 2003; van Oers et al. 2004). The behavioral mechanisms that permit flexible adjustment of the producer–scrounger strategy choice are also not well studied. Some may be based on conditional responses to environmental or physiological cues, such as a greater tendency to join when hungry (Lendvai et al. 2004) and to scrounge more when predation risk is high (Ranta et al. 1998; Barta et al. 2004) or when observing that other individuals have found a good food patch (Templeton & Giraldeau 1995, 1996). Another possible mechanism for choosing among strategies may be based on reinforcement learning (Beauchamp 2000), which entails that instead of trying to read cues in the environment that favor one strategy over the other (which might be difficult to do, or not sufficiently informative), individuals can try both strategies and learn to prefer the strategy that gives them greater success.

The idea that strategy choice in the producer–scrounger game can be based on learning has been suggested and analyzed theoretically by Beauchamp (2000) and more recently by Hamblin & Giraldeau (2009), Dubois et al. (2010), and Katsnelson et al. (2012). Experimental evidence for the effect of learning on strategy choice in the producer–scrounger game was first provided by Katsnelson et al. (2008) and more recently by Morand-Ferron & Giraldeau (2010). The former study showed that young house sparrows that were allowed to follow a mother model that always led them to food were subsequently more likely to use scrounging than those provided with a non-productive mother that led them to empty feeding spots

(Katsnelson et al. 2008). The latter study showed that the proportion of scrounging by adult nutmeg mannikins was affected by whether their past experience with scrounging was under favorable or unfavorable conditions for scrounging (Morand-Ferron & Giraldeau 2010). This latter study manipulated the success rate of each strategy by changing the distribution of food; scrounging was beneficial only when food patches were sufficiently large. Here, we use a complementary method that directly manipulates the success of individuals that follow others without changing the patch size. This may be important because changes in patch size can also change the number of opportunities for learning to scrounge regardless of scrounging success (see Methods). Thus, the effect of learning tested by our method can only be attributed to changes in the relative success experienced while searching and scrounging rather than to changes in the observed number of scrounging opportunities. We use the technique employed by Katsnelson et al. (2008), with taxidermically prepared specimens of adult house sparrows as models that can be joined (scrounged) by live sparrows during social foraging. By placing the stuffed sparrow models near or away from food, we manipulate the experience gained by our live adult sparrows as a result of joining. After removing the stuffed birds and monitoring the sparrows' behavior on the following day, we determine whether strategy choice has indeed been affected by experience. We also analyze and examine the extent to which differences in strategy choice were related to differences in the success rate experienced while using each strategy.

Methods

The Study System

During the winter of 2006/2007, we collected 40 adult house sparrows, 20 males and 20 females. Thirty were collected from a captive colony and ten were wild caught. Captive-origin sparrows were first-year adults and were not used for any other study involving foraging behavior. Wild-caught individuals may be captured because house sparrows in Israel are extremely abundant and legally unprotected. The sparrows were divided into four flocks of five males and five females each. Each individual was marked by a unique combination of colored leg bands. Each flock was housed in a different outdoor aviary at the I. Meier Segals Garden of Zoological Research, Tel-Aviv University. All aviaries were of similar size [flock 1 and 4: 5 × 6.5 × 3 m (LWH), flock 2: 3.5 × 3.5 × 3.5 m, and flock 3: 4 × 5.5 × 3 m] with ample room for a

flock of ten sparrows. Two birds died of unknown causes in two different aviaries, and their bodies were never recovered. The remaining 38 individuals survived in good condition and were released upon termination of the experiment within the I. Meier Segals Zoological Garden area [see Katsnelson et al. (2008) for a detailed description of the release procedure]. Each aviary was equipped with ten nest boxes (40 × 30 × 25 cm), branches and twigs for perching and a sand box. When not participating in an experiment, the sparrows were given food (a mixture of commercial bird feed and grated boiled egg, supplemented by fly larvae) and water *ad libitum*. On the center floor of the cage, a 120 × 120 cm plywood foraging grid was placed. The grid contained 100 evenly spaced wells (30 mm diameter and 13 mm depth) made of water bottle tops spaced 12 cm from well center to well center. The use of a grid in the study of the producer–scrounger game was first introduced by Barnard & Sibly (1981). It permits the control of the amount and distribution of food given. This grid was similar to that used by Katsnelson et al. (2008, 2011). The food dish was always placed on this grid to allow the sparrows to become accustomed to the experimental setup, and a few days before the experiments, the birds were trained to search for food in the grid's wells. A hideout tent, where the experimenter (A.B.) sat, was placed inside the aviary (for all flocks except flock 2 where the size of the aviary did not permit this placement) three meters from the foraging grid. The experiments were filmed by a combination of two cameras: a color micro-CCD camera positioned directly above the foraging grid and connected to the top of the cage (top camera), and a focal camera (Sony DCR-HC32E, Tokyo, Japan) operated by the experimenter. These two cameras allowed us to recognize the sparrows individually by comparing the image in the focal camera to the one in the top camera. Only the top camera image was analyzed. The study was carried out under an animal care permit (Permit # L-04-035) from the Tel-Aviv University Animal Care Committee.

Experimental Design

Each of the four flocks went through an experimental procedure that lasted 15 consecutive days (Table 1),
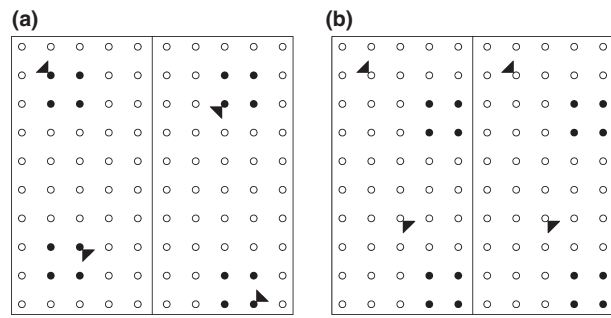

Fig. 1: The arrangement of the foraging grid in the positive (a) and negative (b) treatments. Dark triangles represent the models, and circles represent wells that either contain food (dark circles) or do not contain food (empty circles). Models were placed facing the center of each patch.

which were divided into five phases of 3 d each: alternating control phases, in which the aforementioned taxidermically prepared models were not present on the grid, and treatment phases, during which models were placed on the grid (i.e., control, treatment, control, treatment, and control). The two treatment phases were either a 'positive' treatment during which the models were placed near food or a 'negative' treatment during which the models were placed away from food (Fig. 1, and see below). The order of treatments varied between flocks (Table 1). Each experimental day started at 07:00 (sunrise was between 06:10 and 06:42 and did not vary by more than 15 min for each flock) by removing the food dish from the aviary and cleaning any food remains from the cage floor. The sparrows were then deprived of food for 2 h to encourage foraging, during which time the cameras were set up, and food and stuffed models (if needed) were placed on the grid. Food was given in four patches of four wells each arranged in a square, giving 16 wells in total, each containing 1.50 ml of millet seed. The four food patches were separated by a distance of at least two wells but otherwise were located at random. In order to ensure that food location was not visible to the sparrows, and that they were forced to search actively, food was covered by 2.25 ml of fine sea sand, and food and models were placed under an opaque fabric. Wells not containing food were filled with 3.75 ml of sand to match overall level of filling but preventing the sand from becoming a cue for the presence of food.

Table 1: Order of phases for each flock

Flock/day	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15
Flocks 1 and 3	0	0	0	+	+	+	0	0	0	−	−	−	0	0	0
Flocks 2 and 4	0	0	0	−	−	−	0	0	0	+	+	+	0	0	0

Each flock went through 3 control phases (0), a positive treatment (+) and a negative treatment (−). See text for further details.

The removal of the fabric signaled the start of the experiment. The sparrow's foraging behavior was videotaped for an hour (first filming) followed by an additional hour (second filming) with the food and models placed at a different location during each filming. After the second hour, the cameras were taken down and the sparrows were given food *ad libitum* until the next morning. Because some sparrows hesitated to forage on the grid in the presence of the models during the first day of the treatment phase, on the second day of all treatments, we added another two filling cycles to provide an additional 2 h during which the sparrows could become accustomed to the presence of the models on the grid (either near or away from food). This protocol proved to be effective, and by the third day, all the sparrows readily came to feed on the grid in the presence of the models (see Discussion).

Reinforcement Regime During Experimental Treatments

As explained earlier, each flock received two treatments, positive and negative, in different orders (Table 1). In the positive treatment, four stuffed models of adult house sparrows, two males and two females, were placed on the foraging grid near the location of food, one model per patch (Fig. 1a). The models were placed using metal wire that fitted into a small hole drilled next to each well. They were prepared by a professional taxidermist and mounted in a typical foraging posture of a sparrow searching for food on the ground. In the negative treatment, the same models were placed in the same position away from food at sufficient distance that all of the wells surrounding the model did not contain food (Fig. 1b). The positive treatment was designed to reward joining and to reduce to zero the benefit of searching: A sparrow feeding in close proximity to a model, essentially joining the model, would be rewarded in at least 4/9 cases (Fig. 1a), while a sparrow that searched away from the models (i.e., not in the same well or in one of the eight adjacent wells) would not find food. The negative treatment was meant to reduce the reward probability of joining; a sparrow joining a model would not be rewarded. It is important to note, however, that the actual experience gained by the sparrows during a treatment was a combined result of their experience with the models and their experience with other live sparrows on the grid. The latter could not be controlled by the experimenter. In the case of the positive treatment, although food was always associated with joining (either joining a model or a

model together with a live sparrow), not all cases of joining a model were rewarded with food (see above), and joining a live sparrow that foraged away from the models was also not rewarded with food. Nevertheless, although the positive treatment did not increase the reward probability of joining to 100%, it effectively reduced the reward probability of searching to zero, making joining relatively much more successful. The negative treatment allowed a sparrow joining a live one to still be rewarded with food, and both joining and searching had a positive probability of finding food (see further analysis and discussion below).

The effect of the experimental manipulation was tested by comparing the sparrows' behavior before and after the treatment phase, rather than during the treatment when the model sparrows were present on the grid. This was important for two reasons: first, to control for the immediate effect of the models on the sparrows' behavior owing to factors that are not related to learning, such as fear or an increase in the density of sparrows on the grid, and second, in order to demonstrate learning of strategy choice, it is critical to verify that the experience gained with the models could be generalized to live sparrows and affect strategy choice in the producer–scrounger game setting after the models were removed. We also considered the possibility that the stuffed models would be treated by the sparrows as arbitrary signals for the location of food rather than as real sparrows. In this case, the positive treatment could still facilitate high success when joining live sparrows (and no success when searching) because all birds quickly aggregate near the food that is highlighted by the presence of the models, and a significant treatment effect could still provide evidence for learning. Our results suggest, however, that this was not the case (see Discussion).

Behavioral Data Analysis

We analyzed the videos taken on the days before and after each treatment, as well as those taken during the third day of the treatment (to verify treatment integrity). For each individual, the first 30 foraging steps of each filling cycle (that lasted an hour) were analyzed to give a total of 60 steps per day. All videos were transferred to a PC desktop computer and analyzed blindly. After identifying the focal bird in the top video (through synchronization with the focal camera), the movie was rewound to find the first step of the bird's sequence of steps on the grid. The bird was then followed and every foraging step was classified as one of the options described in the following

paragraph until 30 steps had accumulated for each bird for a filling cycle. If the bird left the grid, the process was iterated when it entered the grid again until 30 steps were completed.

A feeding step was readily identified in the video as any peck inside the perimeter of the well and repeated pecks in the same well were not considered different steps. Each step was classified as either 'direct joining' – feeding at the same well as a model or conspecific – 'area copying' – feeding at one of the eight wells surrounding a model or foraging conspecific – or 'searching' – feeding further away than the eight surrounding wells. A step was also classified as direct joining or area copying if the other sparrow left the target well <1 s before the focal individual approached it. Because 'direct joining' and 'area copying' are two forms of joining (Barnard & Sibly 1981; Giraldeau & Caraco 2000), we pooled them into one category of 'joining', but retained the possibility of analyzing them separately if needed. Unless otherwise specified, the term 'joining' is referred to the pooled data of direct joining and area copying.

In addition to classifying step type, for each step we also recorded the number of other birds on the grid, which determines the potential number of birds that could be joined (see below), and whether the well contained food prior to the start of the trial. We could then calculate the success rate for each sparrow as the proportion of food-containing wells initially visited by the focal sparrow. Our measure of success was based on our prior knowledge of food location. Pecking in a well that was known to contain food entails that the probability of receiving a reward is greater than zero. Because each sparrow visited many wells during the entire experiment, and depletion was rare, it is logical to conclude that, on average, wells that contained food at the beginning of the experiment actually provided reward throughout its duration. We could not, however, measure whether a sparrow actually received a reward when pecking in a well containing food, and how large that reward was. Nevertheless, we feel that our measure of success is valid for the case of positive findings (i.e., it may fail to detect some differences or trends, but it cannot create differences or trends that are absent).

We also recorded any aggressive interactions of the focal individual with other birds. Aggression was defined as any sudden peck at another sparrow that displaced the latter from its location. Both attacks initiated and attacks received were recorded, and individual level of aggression was calculated as the number of attacks initiated divided by the number of

attacks received. In no case was the number of attacks received zero. Using the proportion of attacks instead of this measure gives exactly the same results.

Statistical Data Analysis

We used nonparametric statistics to analyze the behavioral data (using the R software version 2.10.1 for statistical computing, The Free Software Foundation (FSF), Boston, MA, USA). The analysis of the main effect of the experiment compared individual behavior 'before' and 'after' treatments and used Wilcoxon's matched-pairs signed-ranks test. Because the experiment was designed to give a directional prediction for the results, we used one-tailed tests whenever appropriate. As mentioned earlier, the number of other birds on the grid determined the potential number of birds that could be joined, and it could therefore be a confounding variable of strategy choice. Indeed, joining proportion (direct joining plus area copying, averaged for the three control phases) was positively correlated with the mean number of birds on the grid (Spearman's rank correlation: $R_s = 0.34$, N = 38, p = 0.037). We therefore corrected for this covariate by using the residuals from a regression of joining proportion on the mean number of birds on the grid. These corrected values were analyzed using nonparametric statistics because rank statistics better suit the within-flock dependency of joining behavior (a dependency that can magnify the differences in joining proportion within a group, but not their relative rank, see also Katsnelson et al. 2008, 2011). Data on individual behavior that were not connected directly to the experimental treatment (such as aggression and success rate) were averaged for each individual across the three control phases and were not corrected. Although our main analysis was based on within-individual differences, we pooled the data from the four flocks only after confirming that there were no significant differences in joining proportion between flocks and that our main effect was clearly indicated in all four flocks (see Results). Treating individuals (rather than flocks) as the statistical unit for analysis is a common procedure in social foraging studies (e.g., Mottley & Giraldeau 2000; Liker & Barta 2002; Morand-Ferron & Giraldeau 2010). The only within-group statistical dependency that could possibly create a pseudo-replication effect in our analysis is the existence of social learning (copying) of social foraging strategy choice, which is a much more advanced form of learning than the simple reinforcement learning suggested in this study (see Discussion).

Results

General Behavior

Analysis of their behavior during the control phases shows that on average sparrows used each strategy about a third of the time (direct joining: 0.29 ± 0.15 SD; area copying: 0.37 ± 0.12 SD; and searching: 0.33 ± 0.14 SD). With copying as a form of joining, it follows that sparrows joined about two-thirds of the time, which is consistent with the joining proportion found for house sparrows by Katsnelson et al. (2008), and within the range found by Barnard & Sibly (1981). There was no difference in joining proportion between males and females (Mann–Whitney U-test: $U = 165$, $n_1 = 18$, $n_2 = 20$, $p = 0.67$), and therefore, the data for males and females were pooled.

Checking Treatment Integrity

In order to check whether our experimental treatment manipulated individual experience as intended, we analyzed the videos taken during the third day of the treatment phase.

As explained earlier (see Methods), even though the models in the negative treatment were placed near empty wells, joining a live sparrow could still be rewarded with food, so that both joining and searching could have a positive probability of finding food. Our analysis of the third day of the negative treatment showed that this problem was even more severe than anticipated. The success rate for the sparrows when searching was 0.45 ± 0.26 SD, while the success rate while joining a live sparrow was 0.70 ± 0.17. Including the cases where sparrows joined a model (and got no reward) reduces the success rate of joining (either live or model sparrows) to 0.66 ± 0.17. This still implies that the high success rate while joining live sparrows could effectively cancel the intended effect of our negative treatment (the success rates of producing and scrounging were similar in this case to those experienced by the sparrows during the control phase – see below). The positive treatment, on the other hand, worked as expected: Our analysis showed that the overall success rate of joining a model or a live sparrow was 0.54 ± 0.19, while searching independently gave zero success (no food was placed away from the models). Thus, if adult sparrows learn to choose among strategies based on experience, we should expect an increase in joining behavior following the positive treatment (searching/joining success = 0/0.54), but no change in behavior after the negative treatment (searching/joining success = 0.45/

0.66). It is also important to note that while the relative success of joining was higher in the positive treatment, the positive treatment did not allow more scrounging opportunities than the negative treatment.

The Effect of Learning

The response to the treatment is illustrated by the change (i.e., 'after' minus 'before') in joining proportion. Only the days immediately before and after the treatments were used for this calculation. The results – summarized in Fig. 2 – show a clear and a highly significant response to the positive treatment when it occurred first in the order of treatments (one-tailed Wilcoxon test for paired data: $T = 174$, n = 19, p = 0.0003), but no response to the positive treatment when it was applied second (one-tailed Wilcoxon test for paired data: $T = 67$, n = 19, p = 0.87), or to the negative treatments when applied either first or second (one-tailed Wilcoxon test for paired data: $T = 96$, n = 19, p = 0.52 and $T = 85$, n = 19, p = 0.35, respectively). This effect of the positive treatment was similar in the two flocks that experienced the positive treatment first (one-tailed Wilcoxon test for paired data: $T = 52$, n = 10, p = 0.005 for one flock and $T = 39$, n = 9, p = 0.027 for the other). It is also important that of the 19 birds that composed the positive-first group, 16 (84%) increased their joining proportion after the positive treatment.

Success Rate and Strategy Use

In addition to our experimental results, the three control phases offer a large data set that can be explored.
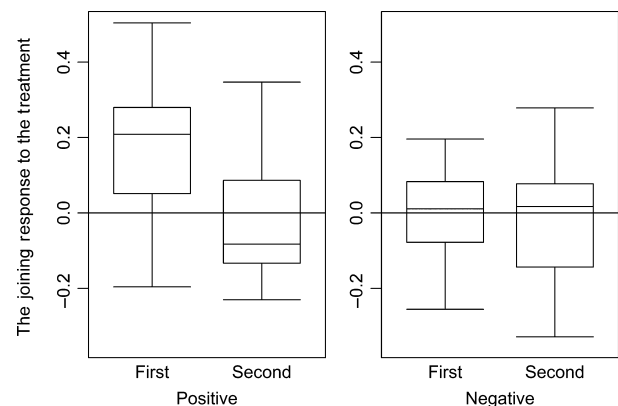

Fig. 2: The joining response (after minus before), corrected for the number of birds on the grid, in the different treatment-order groups (positive-first, positive-second, negative-first, negative-second). The line at 0 signifies no response, while positive or negative numbers indicate an increase or decrease in joining, respectively.

Models of reinforcement learning predict that if strategy choice is learned, an individual will use the more rewarding strategy more frequently, often in proportion to its relative success (Herrnstein 1970; Estes 1994; Sugrue et al. 2004). Our analysis confirmed this prediction: Joining success was on average higher than searching success (Fig. 3a, vertical dashed lines; Wilcoxon test for paired data: $T = 1340.5$, n = 38, p < 0.001), and was also used more often (Fig. 3a, horizontal dashed lines; Wilcoxon test for paired data: $T = 1352$, n = 38, p < 0.001). In addition, and as confirmed by Fig. 3a, the mean success rate of joining and searching in the population (66 ± 16% SD, and 32 ± 16% SD, respectively) almost exactly matched the mean proportion of using joining and searching (66 ± 14% and 33 ± 14%, respectively). Second, most individuals (32/38 = 84%) used the strategy that was more rewarding for them much more often (Fig. 3b). Third, the differences in strategy use calculated for each individual (proportion of joining minus proportion of searching) were positively correlated with the differences in the success rate experienced by each individual when applying each strategy (Fig. 4, Spearman's rank correlation: $R_s = 0.38$, n = 38, p = 0.018).

The Effect of Aggression

Analysis of strategy usage and aggressive behavior during the control phases showed no significant correlation between joining rate and individual level of aggression (Spearman's rank correlation: $R_s = 0.23$, n = 37, p = 0.18 – one particularly aggressive individual was taken out of the analysis, but its inclusion does not fundamentally change the results). However, when splitting joining into direct joining and area copying, we find an interesting result: Direct joining is positively correlated with aggression (Spearman's rank correlation: $R_s = 0.46$, n = 37, p = 0.004), whereas area copying is negatively correlated with aggression (Spearman's rank correlation: $R_s = -0.37$, n = 37, p = 0.023). This implies that the relative use of area copying as a joining strategy [i.e., area copying/ (area copying + direct joining)] is correlated with a low level of aggression (Spearman's rank correlation: $R_s = -0.50$, n = 37, p = 0.002).

Discussion

Experimental Evidence for Learning

Our experimental results show a highly significant increase in joining proportion after the positive
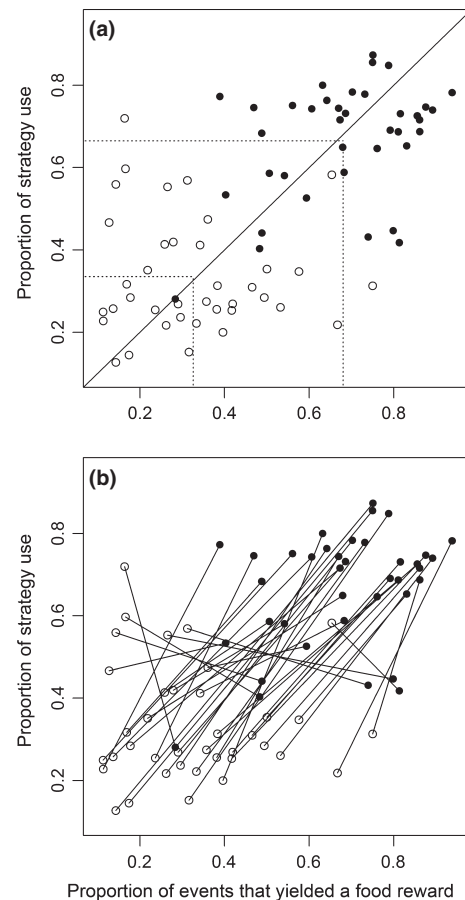

Fig. 3: (a) The proportion of use of searching (open circles) and joining (dark circles) plotted against the success rate while using each strategy. The solid line graphs $y = x$. The vertical and horizontal dashed lines represent the average values for success and use, respectively. (b) Same data as in 'a' but with lines connecting the two data points of each individual, illustrating that most individuals use the more successful strategy more frequently.

treatment when it is given first, but no change in joining frequency in any of the other treatment-order combinations (positive-second, negative-first, and negative-second). The experimental design that was based on testing changes in behavior after the treatment, when conditions returned to be exactly as they were before, precluded the observed change in behavior being a result of a fixed response rule (Morand-Ferron & Giraldeau 2010). The lack of change in behavior following the negative treatment is consistent with our analysis of treatment integrity, showing that the high success rate when joining live sparrows (0.7) may effectively cancel the intended effect of placing the models near empty wells. After the positive treatment, on the other hand, an increase in joining rate was still expected because this treatment reduced searching success to zero while maintaining moderate joining
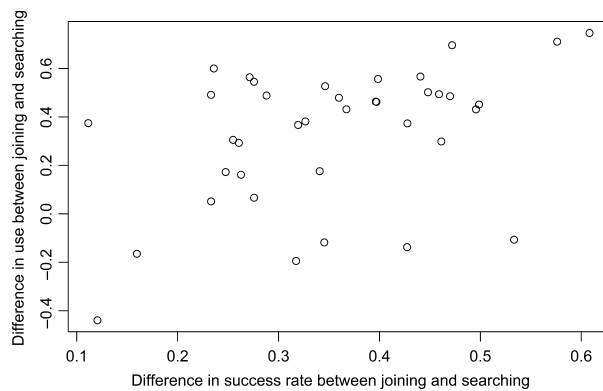
Fig. 4: The difference in use between the two strategies (joining-searching) plotted against the difference in success between the two strategies (joining success-searching success).

success (0.54). It is therefore less clear why the positive treatment gave highly significant results only when applied first. The response to the positive-first treatment was exhibited independently by two different flocks housed in two separate aviaries. Any factor besides learning that could have affected the sparrows' response had to have been present in these two cages independently – an option we find highly unlikely. In addition, if the increase in joining was merely an order effect of experiencing the models first, regardless of learning, we would have expected the negative-first group to respond in a similar way, that is, increase its joining frequency, which did not happen. Only a treatment-order interaction can explain our results; thus, for some reason, placing the models near food in the first treatment allowed the sparrows to learn to prefer joining but doing the same after a previous exposure to the models did not work.

We believe that the most likely explanation for this result is that sparrows that were first exposed to the models during the negative treatment (the negative-first group) learned that the stuffed models are not as reliable predictors of food as real sparrows and gradually started to ignore them. It was quite apparent that the sparrow's reaction to these models was not the same as their response to a live conspecific. This was mainly indicated by the long latency to come down to the feeding grid after the first time that the models were introduced (see Methods). When the positive treatment was applied first, joining the models that were mounted in a foraging posture near food might have slowed down the discrimination process and possibly 'convinced' the sparrows to classify the models as real sparrows. On the other hand, when the negative treatment was applied first, the sparrows had three extra days to experience the static models and

to learn to ignore them before experiencing the positive treatment. Moreover, during the negative treatment, following the models was not as rewarding as following live sparrows, which might even have helped to speed up the discrimination process. The success of our learning protocol was critically dependent on the sparrows' ability to generalize from their positive experience with the models to their attitude toward live sparrows. For this, they should have been sufficiently naive to interpret the models as real sparrows. In fact, it is reasonable to expect that this naive stage would not last too long. Many birds can quickly habituate to taxidermically prepared models of predators or conspecifics, and this is a well-known practical problem in bird control or experimental design (Curio 1975). In this light, our experimental results are very consistent with what is known about learning, demonstrating that, as in previous experiments (Katsnelson et al. 2008; Morand-Ferron & Giraldeau 2010), learning may be an important factor in strategy choice in the producer–scrounger game.

Three alternative interpretations of our results may be considered. First, from the beginning of the experiment, the sparrows might have treated the models as merely arbitrary signals for the location of food, facilitating higher success when joining live sparrows (see Methods). This is still consistent with learning – learning from a live conspecific is still learning – but cannot explain the treatment-order interaction discussed above (i.e., the positive treatment should be effective in this case regardless of treatment order). A second alternative interpretation is that the increase in joining after the positive treatment was not a result of learning but rather of foraging in a more compact flock because of fear of the models. We find this highly unlikely because (1) the increase in joining was measured during the next day, in the absence of the models; (2) such an effect of fear, had it existed, should have been apparent, or even stronger, in the negative treatment where the sparrows had fewer opportunities to habituate to the models in their very close vicinity; and (3) while the sparrows initially feared the models, after the second day of training (see Methods), they readily came down to feed even before the experimenter entered the observation post (Amos Belmaker, pers. obs.) and were seen to be interacting physically with the models with no apparent fear. Finally, one can also suggest that sparrows may copy their producer/scrounger strategy choice from each other. Accordingly, the experimental results could have been a by-product of a situation in which only two individuals responded to the positive treatment, perhaps by chance, and all other birds copied their strategy choice. This explanation requires, however, the existence of an advanced form of

learning, never observed or even anticipated in the field of social foraging, and one which is far more sophisticated than the simple reinforcement learning mechanisms tested here and proposed by previous studies for choosing among social foraging strategies (Beauchamp 2000; Katsnelson et al. 2008, 2012; Morand-Ferron & Giraldeau 2010).

Do All Sparrows Learn?

From previous work, it has been difficult to determine what proportion of individuals actually learned and contributed to the apparent effect of learning. A recent theoretical analysis (Dubois et al. 2010) suggests that a gene for learned strategy choice in the producer–scrounger game can evolve successfully but would not exceed a frequency of 40% in the population. In this case, previous evidence for learning (Katsnelson et al. 2008; Morand-Ferron & Giraldeau 2010) may be interpreted as learning by only a relatively small fraction of the birds (see discussion by Dubois et al. 2010). Yet, a more recent theoretical analysis, in which the learning process was modeled explicitly, suggests that when learning is adaptive, it can easily evolve in the whole population (Katsnelson et al. 2012). Our results show that 84% of the individuals responded to the experimental treatment as expected, and exactly the same proportion exhibited a tendency to use the strategy with which they were more successful (Fig. 3b). This suggests that learned strategy choice may not be restricted to only a small fraction of the population as predicted by Dubois et al. (2010) but may spread in the whole population as predicted by Katsnelson et al. (2012). Whether learned strategy choice can evolve to fixation is an important question which warrants further theoretical and empirical investigation.

Success Rate Analysis

In addition to our main experimental results, the analysis of the success rate of each strategy during the control phases provides results that are consistent with learning; most individuals used the strategy with which they were more successful more frequently, and the differences in success were correlated with differences in strategy use. While such correlations alone may not be conclusive (i.e., cannot disentangle cause and effect), we may view this finding as further evidence in support of our experimental results. The alternative interpretation, according to which frequency of use affected success rate, is less plausible because food was well hidden and was found mainly

by chance (i.e., it was very difficult to learn how to find food even after many searching steps). In addition, a higher proportion of searching steps was, in fact, not correlated with a higher absolute number of searching steps (Spearman's rank correlation: $R_s = 0.06$, n = 37, p = 0.7), making the causality from searching rate to success rate even less likely. Moreover, the remarkable match between the population mean values of success rate and strategy use (illustrated by Fig. 3a) is intriguing. Probability matching is a well-known property of many learning models (Herrnstein 1970; Harley 1981; Sugrue et al. 2004), and matching was proposed as a property of the evolutionary stable learning rule (Harley 1981; Tracy & Seaman 1995; Hamblin & Giraldeau 2009; but see Houston & Sumida 1987 for a different view). Nevertheless, while this result is very appealing, the fact that clear matching is only apparent at the level of the population means suggests that many more factors may be involved in shaping strategy choice at the individual level, and these warrant further study. We should also recall that our measurement of success rate was not very accurate and was insensitive to differences in the amount of reward (see Methods). Thus, while our success rate data were sufficiently informative to reveal a significant relationship with strategy use (Figs 3 and 4), they are not able to tell us how strong this relationship might be or what is the nature of the learning mechanism involved.

One possibility is that the mean payoffs of joining and searching were equal (i.e., searching had lower success rate but greater rewards) and that the sparrows learned to prefer joining according to a learning rule that generates a preference for the option that is better most of the time (Shafir et al. 2008). Alternatively, the mean payoff to searching was lower than that to joining (similar to the differences in the success rate of the two strategies) and the sparrows matched their strategy choice to the differences in payoffs. It is also possible that the sparrows attempted to join only searchers that had already found food (Templeton & Giraldeau 1995, 1996), and therefore, some of the cases where they used searching were simply because of the lack of such joining opportunities at that moment.

The Effect of Aggression

Our results did not show a correlation between aggression level and joining tendency in house sparrows, a finding that seems to contradict the results of Liker & Barta (2002). However, we combined direct joining and area copying into one measure of joining. In their study of house sparrows, Liker & Barta (2002) only

used direct joining. Separate analyses of direct joining and area copying in our data clarify this apparent contradiction. Our results show that the more aggressive the sparrow, the more it uses direct joining [which is consistent with the study by Liker & Barta (2002)], but the less it uses area copying. The definition of area copying was initially suggested because we felt there is an inherent difference between area copying and direct joining, and these results corroborate our intuition. The two types of joining incur different costs and benefits. Direct joining will provide a reward with a high probability, but also incurs the risk of injury because of aggressive interactions with others. Area copying provides an increase in reward as well – food is likely to be found in the vicinity of where food was found before – but the increase is not as high as with direct joining. The benefit received by area copying, in relation to direct joining, is a reduced risk of injury. This reasoning may explain why aggressive individuals prefer to join directly and weaker individuals prefer to area copy: Weak individuals who prefer scrounging may only be able to area copy because direct joining will be too risky. The effect of aggression may create a phenotype-limited producer–scrounger game (Barta & Giraldeau 1998) where more aggressive individuals use joining more frequently and receive a higher payoff. It is quite possible that the risk involved in aggressive interactions affects the sparrows' strategy choice in addition to the payoffs they obtain. Alternatively, models of the producer–scrounger games may be refined by considering three social foraging strategies (i.e., searching, direct joining and area copying) and their interaction with social dominance.

Acknowledgements

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