



Early experience affects producer–scrounger foraging tendencies in the house sparrow

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Group foragers can use a ‘producer’ tactic which involves searching for food or a ‘scrounger’ tactic which involves joining others who have discovered food. While these alternative behaviours are well documented, it is not clear to what extent an individual’s tendency to forage independently or to follow others is under genetic control or rather is affected by experience. To examine whether hand-reared juveniles can learn to prefer using a producer or a scrounger tactic, we hand-reared house sparrow, *Passer domesticus*, nestlings that upon fledging were assigned to one of two training groups; the first was expected to enhance joining (scrounging) behaviour and the second to enhance searching (producing) behaviour. In the first group, fledglings were imprinted on a parent model (stuffed female sparrow) that visited locations containing food. In the second group, fledglings were imprinted on a parent model that visited locations containing no food, while food was available in different locations. At the end of a 5-day training phase, all fledglings were released into a shared aviary, and their social foraging tendencies were measured. We found that fledglings from the first group used significantly more joining behaviour than fledglings from the second group, suggesting that an individual whose early experience positively reinforced joining behaviour is more likely to later become a joiner. To our knowledge, this is the first experimental evidence for the effect of learning on the choice between social foraging strategies in the context of the producer–scrounger game.

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Living in groups creates complex interactions between individuals. In many cases, the consequences of an individual’s actions depend not only on that individual and its environment but also on the behaviour of others. Inspired by observations on house sparrow, *Passer domesticus*, flocks that forage socially, Barnard & Sibly (1981) proposed a model of animal interactions known as the producer–scrounger game. According to this model, group–living animals can use one of two alternative tactics while

foraging. The ‘producer’ tactic involves independent search for resources whereas the ‘scrounger’ tactic involves taking advantage of resources discovered or obtained by others (using public information). The equilibrium levels of producing and scrounging change according to several variables including group size and patchiness of resources (reviewed by Giraldeau & Caraco 2000).

During the past decade the dynamics of the producer–scrounger game have been examined both theoretically (e.g. Barta & Giraldeau 1998, 2000; Ranta et al. 1998; Dubois et al. 2003) and empirically (e.g. Beauchamp & Giraldeau 1997; Coolen 2002; Ha & Ha 2003; Wu & Giraldeau 2005; Lendvai et al. 2006). These studies showed that social foragers tend to follow the predictions of the producer–scrounger game under a variety of conditions. However, the mechanisms that result in an individual forager acting

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as a producer or a scrounger remain unknown. In particular, it is not clear to what extent an individual's tendency to forage independently or to follow others is under genetic or environmental control. The genetic basis of the producer–scrounger tendencies has never been investigated directly. There is evidence, however, from great tits, *Parus major*, that traits related to social foraging may have a strong genetic component (Drent et al. 2003; van Oers et al. 2004). On the other hand, a considerable degree of phenotypic plasticity is suggested by studies showing the effects of environmental factors, such as group size, dominance and predation risk, on the producer–scrounger frequencies (Bugnyar & Kotschal 2002; Coolen 2002; Liker & Barta 2002; Barta et al. 2004).

Phenotypic plasticity in the producer–scrounger game can be expressed only when individuals adopt a mixed strategy (i.e. play producer with a probability p and scrounger with a probability $1 - p$). It has been suggested that changes in p may emerge as a result of a learning process, in which an individual learns from its experience which foraging tactic is more profitable (Beauchamp 2000). Such learning can facilitate individual flexibility as a response to a changing environment. However, it can also result in consistent behaviour if the relative reinforcement values of the two strategies do not change much over time. Thus, the ability to learn to choose among foraging tactics can be consistent with the entire observed spectrum of consistency and flexibility in producer–scrounger behaviours (Barnard & Sibly 1981; Giraldeau & Lefebvre 1986; Beauchamp 2001; Thibaudeau & Giraldeau 2004).

To date, no experiment has been carried out to test whether animals' tendencies to use producing or scrounging behaviour are affected by previous experience. In this study we tested whether house sparrows are capable of such learning. We hand-reared house sparrow nestlings that upon fledging were assigned to one of two training groups: a 'productive parent' group, in which fledglings were imprinted on a parent model (stuffed female house sparrow) that visited locations containing available food, and a 'nonproductive parent' group, in which the parent model visited locations containing no food while food was available in different locations. At the end of the training phase, all fledglings were released into a shared aviary and their social foraging tendencies were monitored. We examined whether individuals trained with the productive parent developed a greater tendency to join others and whether those trained with the nonproductive parent learned to rely more on independent search.

METHODS

Hand Rearing of Sparrow Nestlings

During the breeding season of spring 2005, nestlings at the age of 3–4 days were taken from nests of a captive sparrow breeding colony (five nestlings) and of free-living sparrows at the I. Meier Segals Garden of Zoological Research, Tel-Aviv University (13 nestlings). Nestlings were allowed to be taken from wild nests because house sparrows in Israel are extremely abundant and legally unprotected (nevertheless we acted under an animal care

permit; see below). Hand rearing from an early age ensured that subsequent behaviour of the nestlings was not affected by fear of humans or by early social experience with their biological parents or siblings, and it allowed the nestlings to become imprinted on a stuffed female sparrow as a parent model (see below). We hand reared two cohorts of 13 and 12 nestlings (collected on 13–15 April 2005 and 26 May 2005, respectively). Two of the nestlings of the second cohort were initially passive and died on the first and second days of hand rearing. All other nestlings survived to independence in good condition. The birds were taken from nine nests (six in the first cohort and three in the second). No more than three nestlings were taken from a single nest and at least two nestlings were left at each nest to maintain parental breeding activity. Until the age of 13–14 days, nestlings were kept in two large incubators; each nestling was kept in a private rearing box (10 × 8 × 10 cm). The nestlings were fed from a syringe with a commercial blend for hand-reared birds supplemented by fly larvae. To facilitate imprinting on the correct parental image, starting from 5 days of age food was offered to the nestlings next to the beak of a stuffed house sparrow female oriented towards the young. The stuffed bird was positioned on a pole held by the experimenter. While in the incubators, the nestlings were weighed every morning (± 0.5 g). The nestlings were individually marked with a numbered aluminium ring and three colour rings at the age of 10 days.

Fledgling Stage

When most nestlings in a cohort reached the age of 14 days (fledgling age), nine were chosen for the experiment and transferred to outdoor individual cages (45 × 45 × 75 cm) that were visually isolated from one another. The remaining fledglings were reared to independence and released into a garden that contained a bird feeding station. The birds were later identified among flocks of house sparrows that visit the station (E. Bar-Shay, personal observations). The individual cages, which allowed comfortable movement and flight practice, included branches and artificial foliage for shelter and environmental enrichment at the rear and a wooden foraging grid (47 × 38.5 cm) in the front (to be used in the training period; see below). A water plate for drinking and bathing and a food plate containing ad libitum supply of a mixture of a commercial bird food and grated cooked eggs were placed on the wooden grid. Following the transfer to the individual cages, the young fledglings were hand fed next to the beak of a stuffed house sparrow female to mimic the natural situation in which young fledglings continue to be fed by their parents outside the nest. At this stage, it was clear from the fledglings' behaviour that they were indeed imprinted on the stuffed mother model (they chased it while begging vigorously, flapping their wings and gaping towards its beak). To facilitate the transition to self foraging, food offered in this manner was gradually restricted and the stuffed mother model was made to simulate pecking movements at the food plate, mimicking a feeding bird. Gradually the fledglings joined the stuffed bird in feeding and eventually

ate independently. Since the whole process took place on the surface of the wooden grid, the fledglings were also accustomed to picking up food items dropped on the grid surface and to treating the grid as a foraging place. Upon independence, the bond with the stuffed mother model was maintained by regular visits in which fly larvae were offered next to its beak (fly larvae are desirable food items, absent from the food offered on the feeding plate).

Training Stage

The training period started when all fledglings in a cohort were capable of independent feeding but were still attached to the stuffed mother model (26–27 days old in the first cohort and 24 days old in the second cohort). Each fledgling was assigned to one of two training programmes: the first was the productive parent programme that simulated a scenario in which the parent allowed its offspring to share food discoveries even after the young were capable of self feeding; the second was the nonproductive parent programme that simulated a scenario in which the parent did not allow its offspring to share food discoveries (or did not have enough food to share). In this latter case, the young could find food only by searching for it independently. To minimize coincidental bias in group composition when assigning the fledglings to the treatment groups (which may occur in small samples), we used a procedure similar to a randomized block design: we first subdivided the nestlings of each cohort based on their nest of origin and general observed temperament (passive versus active) and second selected nestlings randomly from each subgroup for the two treatment groups. Altogether, five and four fledglings were assigned to the productive parent programme (in the first and second cohorts, respectively) and four and five fledglings were assigned to the nonproductive parent programme (in the first and second cohorts, respectively). The means of the nestlings' body masses (according to the last measurement at the age of 13 days) did not differ between the treatment groups to which the nestlings were assigned ($\bar{X} \pm \text{SE}$; 25.900 ± 0.517 g versus 25.644 ± 0.420 g) or between the cohorts (25.467 ± 0.423 g versus 26.078 ± 0.496 g), and there was no interaction between the two factors (two-way ANOVA: treatment: $F_{1,14} = 0.222$, $P = 0.645$; cohort: $F_{1,14} = 0.867$, $P = 0.367$; interaction: $F_{1,14} = 0.001$, $P = 0.980$).

Training Procedure

The training period continued for 5 days, during which each fledgling had three training sessions per day (morning, noon and afternoon) and a last morning session on the sixth day (16 training sessions in total). Each training session lasted 3 min. The food plate was removed from the cage 1 h before each training session. During the rest of the day, food was available ad libitum on the food plate. Considering the short duration of the training sessions, possible differences in feeding success during training were unlikely to affect overall food availability. For the training we used the wooden grid mentioned above

(hereafter, the grid). The grid contained 30 wells (2.5 cm in diameter, 1.8 cm in depth, and 8.5 cm centre to centre) but only three adjacent wells were filled with food (fly larvae, a desirable food used only for training).

During the training session, the stuffed mother model, controlled by the experimenter, was made to peck in certain wells. In the productive parent group, the mother model was made to peck continuously and exclusively in the three adjacent wells that were filled with food. In the nonproductive parent group, it pecked continuously and exclusively in three adjacent wells that contained no food; fly larvae were available in three other adjacent wells. In this manner, the young of the first group were rewarded with food when following the mother model, whereas those of the second group were rewarded with food only when they searched independently. (A short video describing the training sessions for each group can be viewed at: http://www.tau.ac.il/~lotem/pdf/movies_link.htm to video.) In both training groups, the locations of the three adjacent wells filled with food or pecked by the model were changed between training sessions. In the productive parent group, to prevent coupling of the removal of the mother model with the return of the feeding plate, leftover larvae were removed from the grid at the end of the training, and only 10 min later the food plate was returned to the cage. Likewise, in the nonproductive parent group, to decouple the presence of food on the grid from the presence of the stuffed mother model (i.e. to minimize the risk that the fledglings would learn to associate the presence of food with the presence of other individuals), a small amount of fly larvae was placed in four discrete wells 1 h before the training (when the food plate was removed). In addition, after the training, the food plate was returned to the cage only after the fledgling ate some larvae from the grid, which ensured a positive experience from independent search.

Behavioural Observations in Social Foraging

Following the last training session, all nine fledglings in a cohort were released into a shared outdoor aviary where they formed a flock of young sparrows for the first time in their lives and their emerging social foraging behaviour could be observed. The aviary ($4 \times 3.6 \times 4$ m) included branches, nestboxes (for shelter), a water plate (for drinking and bathing), a sand tray (for sand-bathing) and a food plate (with ad libitum supply of a commercial bird food and grated cooked eggs). Behavioural observations were conducted from a hidden location adjacent to the aviary. We followed methodologies applied in previous work on producer–scrounger behaviours in sparrows and other seed-eating birds (e.g. Barnard & Sibly 1981; Beauchamp 2001; Coolen et al. 2001; Liker & Barta 2002; Lendvai et al. 2004). The birds were observed while foraging on a wooden grid (130×130 cm) that contained 144 wells (2.5 cm in diameter, 1.8 cm depth, and 10 cm centre to centre). A video camera was located above the grid, providing a top view of its entire surface. To allow individual identification of each bird from this top view during an observation, the observer with binoculars recorded the

colour bands and location of each bird (well number) into a microphone connected to the video camera. This method allowed the verbal identification to be matched with the bird's image (during video analysis) which could then be followed throughout its movement on the grid.

Behavioural observations (1.5 h each) were carried out in the morning and afternoon of the first 3 days after the release into the aviary, and additional observations were carried out in the morning of the fifth and seventh days after the release (eight observations in total). Before each observation the birds were deprived of food for 1.5 h. Each observation started with filling four patches of four adjacent wells with fly larvae (thus, providing food in only 16 of 144 wells). According to the birds' feeding rate (viewed from the hidden location), additional fillings were provided up to three times per observation. For each filling, different patches were selected to prevent learning of food location.

Birds' Release

After the observations of the first cohort were completed, the fledglings were transferred temporarily to three cages (45 × 100 × 155 cm, three birds in a cage) to make the aviary available for the second cohort. When the observations of the second cohort were completed, the two cohorts were unified in the shared aviary. During the summer of 2005 five of the birds died (probably due to pox disease which is common in young wild birds during the summer in Israel and which was clearly diagnosed as the cause of death in two of them).

Four and a half months after the death of the last bird, and ensuring that all birds were healthy and behaved normally in the aviary, the birds were released within the Meier Segals Zoological Garden area (mean body weight at the day of release was 28.862 ± 0.472 g). Food and water for free-living birds are provided year round at the garden and numerous flocks of house sparrows live in its area. The released birds most probably mingled among local flocks of house sparrows because they were occasionally identified for several months after release (E. Katsnelson, personal observations). The study was carried out under an animal care permit from the Tel-Aviv University Animal Care Committee (No. L-04-035).

Behavioural Data Analysis

To describe the birds' foraging tactics we used the terms searching and joining instead of producing and scrounging, respectively. We felt that these terms describe more accurately and objectively the behavioural variables that were measured. To score each individual's joining/searching tendency, we analysed the videos on a computer screen. A foraging session started at the moment the first individual landed on the grid (when it was empty of birds) and ended when the last individual left the grid (sessions that were shorter than 45 s or included less than three foraging birds were not analysed). Each individual that was identified at a specific time and location on the grid was followed backwards until its entrance to the grid. From

this moment on we analysed the foraging behaviour of that individual, which we term the focal bird, until it left the grid or until the data quota for this individual was achieved (see below). Each visit to a well was classified as either a searching or a joining event. A searching event was a visit to a well that was not occupied by another individual. Moreover, if a well adjacent to this well was occupied by another individual, the visit was classified as searching only if the focal bird was not oriented towards this individual. A joining event included a visit to a well occupied by another individual on the moment of arrival or just before arrival or a visit to a well adjacent to a well occupied by another individual if the approaching focal bird was oriented towards the other individual. We also used a more conservative classification where searching was based only on visits to an unoccupied well whose adjacent wells were also unoccupied and joining was based only on visits to a well occupied by another individual at the moment of arrival or just before arrival (hereafter 'clear-cut' searching or joining). This classification was based on fewer foraging events but gave qualitatively similar results (available at http://www.tau.ac.il/~lotem/pdf/supplementary_data.pdf). For each foraging event, the number of other foraging individuals on the grid was indicated. Data collection for each individual continued until it accumulated 20 clear-cut events during the behavioural observation or until the observation was ended. For each behavioural observation, individual behaviour was represented by the individual's joining proportion (number of joining events divided by the sum of searching and joining events).

Statistical Analysis

We used a nonparametric approach to analyse the main data. For each fledgling we averaged its joining proportion over the entire period of eight observations and then ranked these averages and compared the rankings between the two treatment groups using the Mann–Whitney *U* test. This was done for each cohort. The overall *P* value for testing whether the joining proportion was higher for the productive parent treatment group was then calculated using the method for combining data from several experiments suggested by Lehman (1975, pp. 132–141). A similar approach, but using a two-tailed test, was used for comparing between the two treatments with respect to the mean number of other foragers on the grid. The consistency of each individual's ranking (with respect to joining proportion) over the entire period of eight observations was checked by Kendall coefficient of concordance. The mean joining proportion for each individual was calculated by first calculating the joining proportion in each observation and second averaging these means over all observations. For all results $\bar{X} \pm SE$ are given.

RESULTS

We tested whether the mean joining proportion was higher in the productive parent group than in the non-productive parent group. For both cohorts, the mean

joining proportion of the productive parent group was higher than that of the nonproductive parent group over each of the eight observations (Fig. 1). These differences were especially pronounced in the second cohort (Fig. 1b). Interestingly, the effect of the training programme on the joining proportion of the fledglings did not diminish during the 7 days of observations. The results shown in Fig. 1 represent repeated measurements of the same individuals and are therefore informative but not statistically independent. To obtain statistically independent data points from each individual, we averaged its repeated measurements across observations. Averaging over the eight observations of each individual, the joining proportion of the productive parent group was not significantly higher than that of the nonproductive parent group for the first cohort (Fig. 2a; 0.655 ± 0.053 versus 0.528 ± 0.092 , respectively; one-tailed Mann–Whitney U test: $U = 6$, $N_1 = 5$, $N_2 = 4$, $P = 0.206$) but was significantly higher for the second cohort (Fig. 2b; 0.766 ± 0.026 versus 0.483 ± 0.049 , respectively; one-tailed Mann–Whitney U test: $U = 0$, $N_1 = 4$, $N_2 = 5$, $P = 0.008$). The overall one-tailed P value, for the two cohorts combined (using Lehmann’s method), was 0.008.

Individuals from both cohorts were consistent in their relative tendencies to use joining. That is, ranking the nine fledglings in a cohort for each of the eight observations

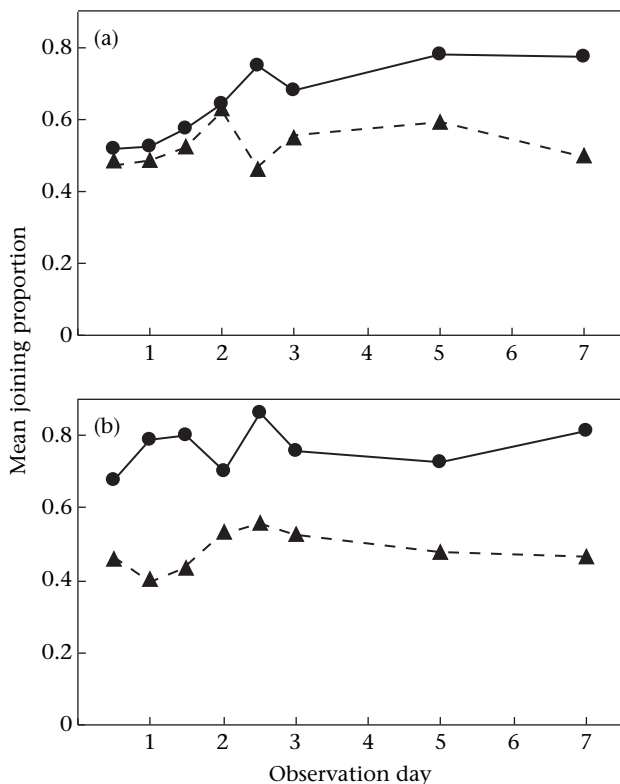


Figure 1. Mean joining proportion for the productive parent (●) and nonproductive parent (▲) treatment groups throughout the eight observations. (a) First cohort: five and four fledglings in the productive parent and nonproductive parent groups, respectively. (b) Second cohort: four and five fledglings in the productive parent and nonproductive parent groups, respectively.

according to their joining proportion results in statistical agreement between ranks of each fledgling throughout the observations (Kendall coefficient of concordance: first cohort: $W = 0.573$, $\chi_8^2 = 36.7$, $P < 0.001$; second cohort: $W = 0.642$, $\chi_8^2 = 41.1$, $P < 0.001$). The highest average joining proportion of a fledgling (averaged for the eight observations) was 0.832 ± 0.054 and the lowest was 0.347 ± 0.052 . As illustrated in Fig. 3, considerable variation among individuals was apparent within each treatment group.

Finally, because the ability of an individual to forage as a joiner depends on the presence of others, we had to ensure that differences between groups were not confounded by the number of individuals that were present on the grid at the moment of each foraging event. Based on our video analysis (see Methods) we calculated for each individual the mean number of other foragers that were present on the grid during its foraging events. This analysis showed no differences in the mean number of ‘other foragers on the grid’ in training groups in both the first and the second cohorts (5.988 ± 0.165 versus 5.624 ± 0.219 and 5.255 ± 0.092 versus 5.012 ± 0.171 for the productive and nonproductive parent groups in the first and second cohort, respectively; two-tailed Mann–Whitney

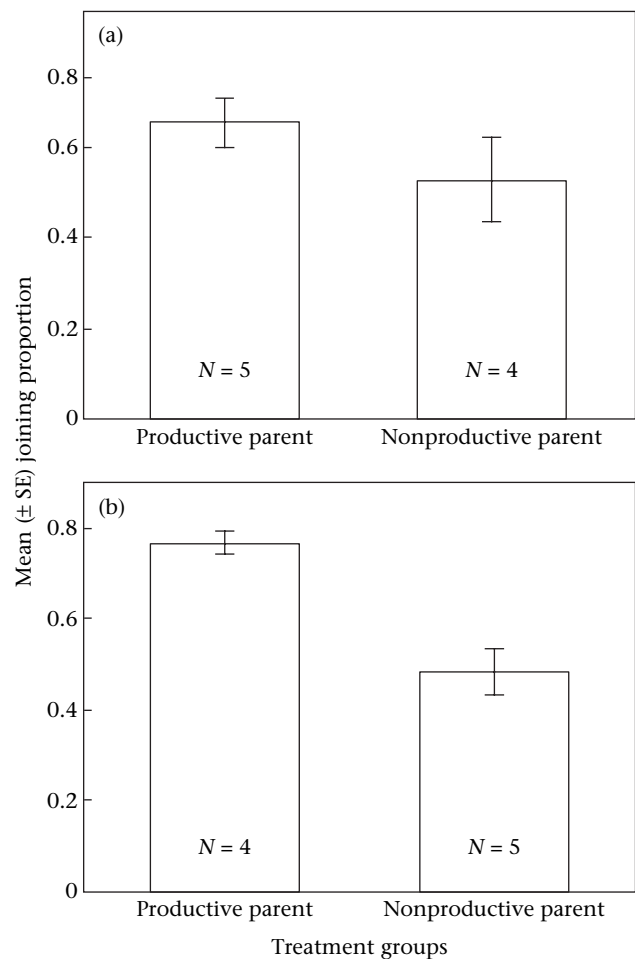


Figure 2. Mean \pm SE joining proportion for both treatment groups. (a) First cohort. (b) Second cohort.

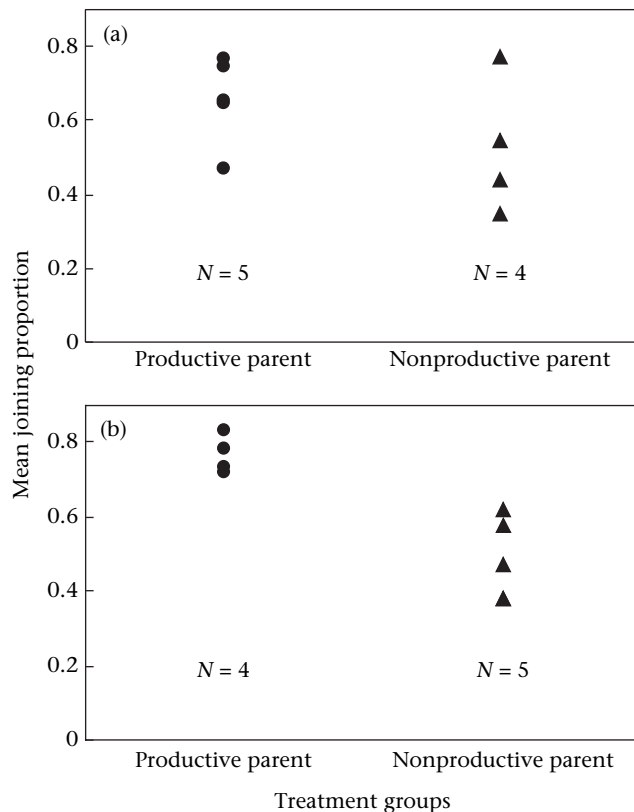


Figure 3. Mean joining proportion of each fledgling over all eight observations (● and ▲ represent the productive parent and nonproductive parent treatment groups, respectively). (a) First cohort. (b) Second cohort.

U test: first cohort: $U = 5$, $N_1 = 5$, $N_2 = 4$, $P = 0.286$; second cohort: $U = 8$, $N_1 = 4$, $N_2 = 5$, $P = 0.730$). These results remained insignificant also when the data from the two cohorts were combined: the overall two-tailed P value for the combined two cohorts was 0.235.

DISCUSSION

Our results show that, when foraging in a group, young sparrows that were previously rewarded for following a parent model (the productive parent group) were more likely to join others than those rewarded for independent searching (the nonproductive parent group). To our knowledge, this is the first experimental evidence for the effect of learning on the choice between social foraging strategies in the producer–scrounger game. It was previously suggested that learning may enable individuals to choose between alternative tactics because learning could offer a possible explanation for the results of several earlier studies (Mottley & Giraldeau 2000; Beauchamp 2001; Thibaut & Giraldeau 2004). Furthermore, in a simulation model, Beauchamp (2000) has shown that learning can account for the emergent equilibrium in the producer–scrounger game. Consistent with these suggestions, our results confirm that learning is indeed involved in shaping whether an individual becomes a producer or a scrounger.

Despite the effect of learning shown, there were still large differences in behaviour within each treatment group (Fig. 3). This variation may be explained by (a) coincidental differences in individual experiences that were not intended by the experimenter (such as some individuals finding more food by chance or having different experiences during the period that preceded the training), (b) phenotypic differences unrelated to learning that might still influence social behaviour (such as differences in hunger or fear; Barta et al. 2004; Lendvai et al. 2004) and/or (c) heritable genetic differences in behavioural tendencies. In fact it is quite possible that all the above worked together. Individuals might have an innate predisposition to use a certain level of scrounging behaviour that can then be shaped by learning (for a similar view of behavioural tendencies see Nelson & Marler 1993; Lachlan & Feldman 2003; Laland & Janik 2006).

Similar to previous studies of social foraging in birds (Giraldeau & Lefebvre 1986; Beauchamp 2001; Thibaut & Giraldeau 2004), our results show consistency in the individuals' relative tendencies to use joining in repeated observations, together with flexible use of searching and joining by each individual. When learning is involved, the mixed use of both tactics allows continuous sampling and more frequent use of the currently more rewarding tactic (see learning modelling by Beauchamp 2000). However, consistent individual behaviour is expected when permanent phenotypic constraints make one tactic consistently more rewarding than the other. Such constraints might include fighting ability (Liker & Barta 2002), foraging efficiency (Beauchamp 2006), and possibly behavioural syndromes that can influence foraging success (Marchetti & Drent 2000; Dingemanse et al. 2002; van Oers et al. 2004).

It is interesting to note that the effect of the training lasted throughout the 7 days in the aviary without further reinforcement. One explanation for this is that weaning acts as a sensitive period (see Bateson 1979) during which early experience shapes social foraging tendencies for life. Such a time window during which learning takes place can vary. According to this explanation, early experience may lead to high levels of consistency and specialization. Alternatively, animals may continue to monitor their relative success with each strategy throughout life and change their behaviour accordingly, but, during the 7 days in the aviary, each individual continued to be reinforced by the behaviour used more frequently and the effect of the training period was not eradicated by any significant new experience. Further work will be needed to assess whether the learning shown by our experiment is limited to a young age or continues through life.

In recent years, there has been increasing interest in viewing the producer–scrounger game as an example of a more general game between 'information-producers' and 'information-scroungers'. Thus, producing and scrounging may be viewed as two cognitive modes: one in which the individual interacts directly with the environment and uses personally acquired information based on its own experience and another which is based on being attentive to the behaviour of others (Giraldeau et al. 2002; Kameda & Nakanishi 2002; Laland 2004; Bicca-Marques & Garber

2005). From this perspective, producing and scrounging may be viewed as precursors to individual and social learning, which may suggest that, by learning to choose between searching and joining, our sparrows actually learned how to learn. At this stage, however, we cannot make such an assertion because sparrows in our study could not learn anything more than the reward probability of searching and joining. There was no cue on the grid that could help to predict where the food was and thus could be learned through individual or social learning. However, such cues may be present under natural conditions and might then be learned through individual learning (when searching) or through social learning (when joining others). This may lead to an interesting interaction between the producer–scrounger game and the prospect for individual and social learning. Although simple forms of social learning may be viewed as extensions of individual learning (Laland et al. 1993; Galef 1995), their prevalence determines the transmission of information among individuals (Feldman et al. 1996) and the potential evolution of more advanced forms of social learning (reviewed by Zentall 2004). The circumstances under which individuals learn to prefer joining over searching may therefore be relevant for the evolution of different social learning mechanisms across different taxa. An intriguing possibility for future exploration is that the initial fate of different social learning mechanisms may be determined by their contribution to the player's success in the producer–scrounger game.

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