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Individual-learning ability predicts social-foraging strategy in house sparrows

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Social foragers can use either a ‘producer’ strategy, which involves searching for food, or a ‘scrounger’ strategy, which involves joining others’ food discoveries. While producers rely on personal information and past experience, we may ask whether the tendency to forage as a producer is related to being a better learner. To answer this question, we hand-raised house sparrow (*Passer domesticus*) nestlings that upon independence were given an individual-learning task that required them to associate colour signal and food presence. Following the testing phase, all fledglings were released into a shared aviary, and their social-foraging tendencies were measured. We found a significant positive correlation between individual’s performance in the individual-learning task and subsequent tendency to use searching (producing) behaviour. Individual-learning score was negatively correlated with initial fear of the test apparatus and with body weight. However, the correlation between individual learning and searching remained significant after controlling for these variables. Since it was measured before the birds entered a social group, individual-learning ability could not be the outcome of being a producer. However, the two traits may be initially associated, or individual learning could facilitate producing behaviour. To our knowledge, this is the first evidence that associates individual-learning abilities with social-foraging strategies in animal groups.

Keywords: associative learning; social behaviour; individual variation in behaviour; house sparrow

1. INTRODUCTION

Consistent variation in behaviour among individuals has long been a well-recognized phenomenon in animals [1–5]. A growing body of evidence suggests that this variation may include consistent individual differences in sets of correlated behavioural traits, creating different ‘personalities’ (also referred to as ‘temperament’ or ‘behavioural syndromes’) [6–9]. While the existence of animal personalities is currently supported by extensive empirical research, theoretical explanations for their evolution are just starting to emerge [10–13], and relatively little is known about their genetic basis or ontogenetic development [9]. Since behaviour may be shaped by both innate and learned factors [14–16], it is reasonable to suggest that behavioural differences among individuals may be related to different learning abilities or learning strategies [9,17–20]. However, clear evidence relating inter-individual behavioural differences to learning is rare: in *Drosophila*, a recent study found that a genetic variant associated with foraging behaviour affects some key parameters of learning and memory [21]. In laboratory mice, learning ability was shown to be correlated with exploration behaviour [22] and some association was found between lighter body weight and better learning [23]. Other studies have demonstrated relationships

between problem-solving ability and competitive rank and certain measures of neophobia or novelty seeking [18]. Interestingly, the intuitive prediction associating fear and neophobia with poor learning goes back to Hillel the Elder (a first century BC Talmudic scholar) who said: ‘...nor can the shy man learn, or the impatient man teach’ (*Mishna*, Ethics of the Fathers 2:6). However, explicit and ecologically relevant research on learning abilities in relation to different personalities or social-foraging strategies is still lacking.

The producer–scrounger game [24] may provide a specific framework in which to study the evolution and development of animal personalities. Based on a relatively simple frequency-dependent game between a tendency to search for food independently (producing) and a tendency to join other individuals’ food discoveries (scrounging), it offers both the frequency-dependent component, and the potential trade-offs between coexisting behavioural traits, which are necessary to explain the evolution of animal personalities [10–13,25]. The producer–scrounger game has been studied thoroughly under a wide range of ecological and social conditions (reviewed in [26] and [27]). Most relevant to the study of animal personalities is evidence associating producing behaviour with boldness [28] and foraging efficiency [29]; and scrounging behaviour with aggressiveness [30] and fast movement [31]. There is also evidence for both individual consistency in the use of the producer/scrounger strategies and flexible expression of these strategies [24,32–35]. However, the idea that a tendency

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to search independently (while foraging socially) is related to individual-learning ability (i.e. to individual ability to learn to find food in the environment) has never been tested.

Producers are expected to have better individual-learning abilities than scroungers because in order to survive they must rely on their own experience and acquire personal information based on interacting directly with the environment [17,27,36–39]. The possible association between individual-learning ability and producing may emerge by three, not mutually exclusive, mechanisms: (i) individuals that have an innate or acquired preference for the producer strategy become specialized in individual learning, (ii) individuals that have an innate or acquired advantage in individual-learning ability learn to prefer the producer strategy, and (iii) individual-learning ability and a tendency to behave as a producer are initially associated through shared mechanisms, genetic or non-genetic. In the last case, this association can be further enhanced during life by mechanisms (i) and/or (ii). Alternatively, there might be no association between individual-learning ability and producer/scrounger tendencies.

In this study, we tested for the first time whether individuals' tendency to forage as producers or scroungers is related to their individual-learning abilities. We hand-raised house sparrow (*Passer domesticus*) nestlings that upon independence were given an individual-learning task that requires associating a colour signal with food presence. Following the testing phase, all fledglings were released into a shared aviary, and their social-foraging tendencies were measured. We were thus able to assess whether the sparrows' producer/scrounger tendencies developed in the flock could be attributed to their previously exhibited individual-learning ability.

2. MATERIAL AND METHODS

(a) *Hand-rearing of sparrow nestlings*

During the breeding season of spring 2007, nestlings at the age of 4 days were taken from house sparrow nests at the I. Meier Segals Garden of Zoological Research, Tel Aviv University. Hand-rearing ensured that subsequent behaviour of nestlings was not affected by fear of humans or by early social experience with their biological parents or siblings. We collected two cohorts of 12 nestlings each, on 23–25 April and 3–4 June, respectively. Not all individuals survived or participated in the experiment, and we were left with 10 and 8 individuals in the first and second cohort, respectively. Only two nestlings that took part in the experiments were from the same brood, and removing each one of them from the data did not change the results.

The hand-rearing procedure followed methodologies described in detail by Katsnelson *et al.* [40]. Until the age of 13–15 days, nestlings were kept in two large incubators (each nestling in a separate box) and were imprinted on a stuffed house sparrow female oriented towards the young during hand-feeding. On reaching their fledging age (13–15 days), the nestlings were weighed for the last time and transferred to individual cages (45 × 45 × 75 cm) located within an outdoor aviary and visually isolated from one another (see [40] for more details). A wooden foraging grid (47 × 38.5 cm) was placed on the floor of the cage, and a wooden rectangle (38 × 5 cm) containing two wells at each

of its two edges (2.5 cm in diameter, 1.8 cm in depth) was placed in front of that grid (both are used in the individual testing stage; see below). After developing their ability to eat independently from a food plate and to pick food from the surface of the foraging grid, the fledglings were also accustomed to feed on peeled millet seeds, and from the wooden rectangle in which peeled millet seeds were placed. Though we could not determine nestlings' sex at an early age, nestlings from the second cohort were kept longer in captivity to allow reliable sexing. The cohort was composed of four individuals from each sex. No sex differences were found in the measured behavioural traits in agreement with the producer/scrounger literature [30,41].

(b) *The individual stage*

The individual stage started when all individuals in a cohort fed without any apparent hesitation from the wells of the wooden rectangle. Altogether, it took 11 and 10 days from leaving the incubators until the individual testing stage started, for the first and second cohort, respectively. Our goal was to explore the correlation between individual-learning ability and social-foraging tendency. For this purpose, the fledglings were given an individual-learning test in which they had to associate a colour signal with the presence of food (described in the next paragraph). We also used the individual stage to expose the fledglings to foraging techniques that they would use during the social-foraging stage (described below). These techniques included finding seeds hidden in sand and finding seeds distributed in the wells of the entire foraging grid (both abilities, tested after the individual-learning test of the first day, were required later during the social-foraging stage). Thus, we could measure the number of seeds retrieved by the fledglings and correlate this with their social-foraging behaviour measured later during the social-foraging stage. No correlation was found, indicating that our measurements of social-foraging behaviour (see below) were not confounded by variation in nestling ability to forage on the grid.

(i) *The individual-learning test*

An hour prior to the test, the food plate was removed from the cage. The test included 20 trials in each of which the fledgling was presented with the 'test apparatus': a wooden rectangle, identical to the one from which it was accustomed to feed (see above), with the exception that each of the two wells was surrounded with a coloured frame, one well with a blue frame and the other with a red frame (hereafter: blue and red wells, respectively). The sides of the blue and the red wells (left versus right) were randomized with the constraint that each colour had to be presented 10 times on each side and no more than two consecutive times on the same side. The same sequence was applied for all fledglings, ensuring that differences in learning performances could not emerge from differences in the sequence of presentation. In each trial, food (three millet seeds) was placed in the blue well only. The fledglings were thus expected to learn to prefer the blue well over the red well. We used blue and red colours based on preliminary work and because these colours differ from house sparrows' natural food colour, and have been shown to be relatively unattractive to house sparrows [42]. At each trial, the test apparatus was inserted into the cage covered with cardboard and was exposed when the fledgling retreated to the back of the cage. At the beginning of each trial, if the fledgling did not

approach the test apparatus soon after it was exposed, the experimenter encouraged the fledgling to approach it by finger-tapping on the middle section of the cage front and by soft verbal vocalization (an activity used to encourage the nestlings to approach their human care givers during the earlier hand-rearing process). This procedure did not include a hint as to the location of food prior to the fledgling's initial choice. In trials in which the fledglings initially chose the red well, or chose the blue well but did not consume all or part of the seeds following their initial choice, the trial continued until we ensured that all seeds were eventually eaten (so that the fledglings were rewarded the same number of times regardless of the well they visited first).

Video recording allowed us to classify each fledgling's initial choice in each trial as 'correct' or 'incorrect' based on the well visited first (i.e. blue first = correct). Video clips of two representative trials with correct and incorrect choices are provided in the electronic supplementary material (see electronic supplementary material). We first confirmed that the proportion of correct choices increased significantly across the trials as expected from associative learning (§3). Then, a fledgling's individual-learning score was calculated as the proportion of correct choices made throughout the test's trials, excluding, of course, the first trial, which was uninformative—the fledgling could only choose at random at this stage, and its behaviour could not be attributed to learning. This simple individual-learning score method was found to represent learning ability more accurately than using the slope of a logistic regression (a detailed analysis of this aspect and results of a simulation are available upon request).

(c) Social-foraging stage

Following the learning test, all fledglings in a cohort were released into a shared outdoor aviary ($4 \times 3.6 \times 4$ m) where they formed a flock of young sparrows for the first time in their lives. The birds were monitored (using video cameras) 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). Full details regarding housing conditions and video monitoring are described in Katsnelson *et al.* [40]. Observations (1.5 h each) were carried out in the morning, during the 5 days that followed the release into the aviary. Before each observation, the birds were deprived of food for 1.5 h. Each session started with filling four patches of four adjacent wells (i.e. 16 wells in total out of 144) with 0.4 ml of millet seeds, covering the seeds with a layer of sand and placing four exposed seeds on top of the sand. According to the birds' feeding rate (viewed from the hidden location), two additional fillings were provided. For each filling, different patches were selected to prevent learning of food location.

(i) Video analysis of social-foraging behaviour

To describe the producer and scrounger social-foraging strategies, we use the terms searching and joining, respectively, as these terms describe more accurately and objectively the behavioural variables that were measured [40]. To score each individual's joining/searching tendency, we analysed the videos on a computer screen, following the methods described in detail in Katsnelson *et al.* [40], with appropriate modifications. Each visit to a well (foraging event) was classified as either a searching or a joining event. For analysis, we used a conservative classification of searching and joining events: 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. Data collection for each individual continued until it accumulated 30 such searching/joining events during the behavioural observation or until the observation was ended. For each foraging event, the number of other foraging individuals on the grid was noted. For each session, the social-foraging strategy of each individual was measured as the proportion of searching events (number of searching events divided by the sum of searching and joining events), and the individual's overall score for its social-foraging strategy was then calculated as its mean searching proportion in the five sessions. We then ranked the individuals from each cohort according to their overall score for social foraging (with higher values meaning higher searching proportion), and used these ranks in subsequent analyses.

(d) Birds' release

After the observations of each cohort were completed, the fledglings were kept in the aviary for an additional three weeks for the first cohort and 15.5 weeks for the second cohort. Ensuring the birds were healthy and behaved normally in the aviary, they were released within the I. Meier Segals Zoological Garden area (mean body weight \pm s.e. at the day of release was 27.020 ± 0.370 and 28.088 ± 0.708 g in the first and the second cohort, respectively); for further details, see [40].

3. RESULTS

(a) Individual testing stage

The mean proportion of fledglings that chose the correct well during each of the 20 trials of the individual-learning test is shown in figure 1. This proportion increased significantly across the trials during the first day, as expected under associative learning (figure 1*a*; $t_{15,55} = 5.30$, $p < 0.001$; SAS generalized linear mixed model with correct versus incorrect as a binomial distribution and individual as a random variable; data from the two cohorts were pooled for this analysis after no difference in individual-learning slopes was found ($t_{15,26} = 1.12$, $p = 0.28$, see also figure 1*a*). In the test conducted on the second day, the fledglings showed a preference for the correct well from the beginning and throughout the test (figure 1*b*). Hence, the fledglings indeed learned to prefer the blue-framed well and they did not forget their learned preference from the day before. Considering the learning curve indicated by figure 1, we calculated each fledgling's individual-learning score based on its performance in the first testing day when learning clearly occurred. Thus, the scores (the proportion of correct choices in all but the first trial—§2) were 0.695 ± 0.144 and 0.618 ± 0.104 (mean \pm s.d., in the first and second cohorts, respectively).

To check whether individual differences in initial preference for blue could explain our results, we compared the individual-learning score and the searching proportion of fledglings that choose blue versus red on the first trial of the individual-learning test. The results show no significant differences between those groups, which could explain our main results (Mann–Whitney U test: first cohort: $U = 9.5$, $N_1 = 6$, $N_2 = 4$, $p = 0.610$; second cohort: $U = 4.0$, $N_1 = 5$, $N_2 = 3$, $p = 0.393$).

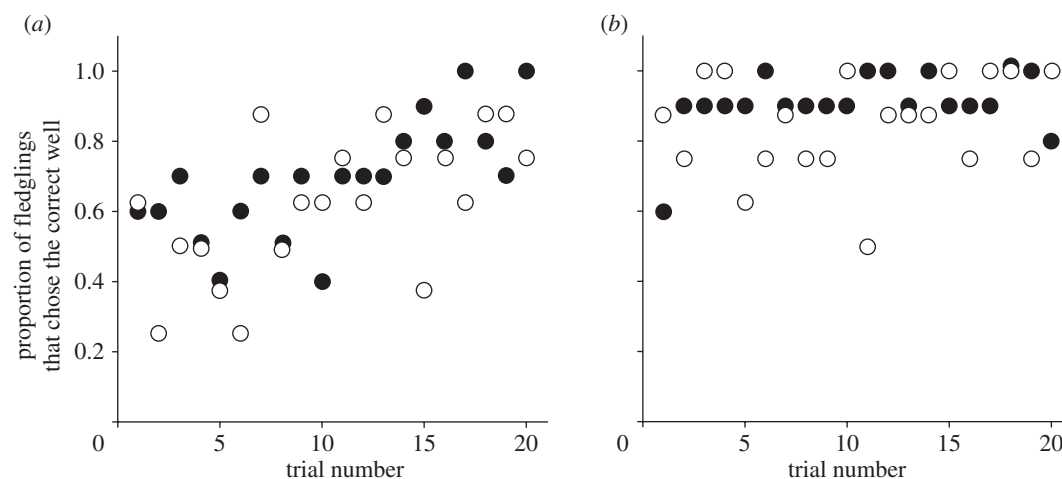


Figure 1. The proportion of fledglings that chose the correct well on each of the 20 trials in the individual-learning test (filled and open circles represent the first ($n = 10$) and second ($n = 8$) cohorts, respectively). (a) First testing day. (b) Second testing day.

Our primary goal was to correlate the individual's learning score with its social-foraging tendency. We noticed, however, that the time it took the fledglings to complete the first trial of the individual-learning test was longer and more variable than those of the remaining 19 trials. Accordingly, we used the duration of the first trial as an individual score of initial fear from the testing apparatus. The average time it took the fledglings to complete the first trial was 169.60 ± 55.62 and 267 ± 168.67 s for the first and second cohorts, respectively (mean \pm s.e.). Since these time durations had a skewed distribution (with a few individuals exhibiting especially long delays), the 'initial fear score' was expressed and analysed as $\log_{10}(\text{seconds})$.

We found no significant differences in either the learning scores or in the initial fear scores between the two cohorts, and consequently, we pooled the data from the two cohorts.

(b) *Social-foraging strategies*

Individuals from both cohorts were consistent in their relative use of the searching strategy (measured by searching proportion) during the five daily sessions in the shared aviary. That is, ranking the fledglings in a cohort for each of the five sessions according to their searching proportion resulted in statistical agreement between ranks of each fledgling throughout the observations (Kendall coefficient of concordance; first cohort: $W = 0.559$, $\chi^2_9 = 25.161$, $p = 0.003$; second cohort: $W = 0.679$, $\chi^2_7 = 23.780$, $p = 0.001$). This result allowed us to use the mean searching proportion from all five sessions as an individual's overall score for social-foraging strategy. This mean searching proportion ranged from 0.211 to 0.832 (average 0.439, $n = 10$) and from 0.238 to 0.830 (average 0.537, $n = 8$) in the first and second cohorts, respectively. We further confirmed that this foraging strategy score was not biased by the presence of other individuals on the grid [43] by verifying that this number (7.046 ± 0.123 and 4.922 ± 0.156 , mean \pm s.e. for the first and second cohorts, respectively) was not correlated with the individual's mean searching proportion ($r_s = -0.176$, $n = 10$, $p = 0.627$; $r_s = -0.095$, $n = 8$, $p = 0.823$, for the first and second cohorts, respectively).

We then pooled the ranks of both cohorts (taking into consideration the different sizes of the cohorts) to obtain a single ranking scale for the entire group of 18 fledglings (with rank 18 implying the highest searching proportion).

(c) *Social-foraging strategies and individual-learning score*

Figure 2a presents the relation between the individual's learning score and its subsequent social-foraging tendency (note that high y -axis ranks are related to high searching tendencies while foraging). We expected this to be positive, and to test whether this positive correlation is significant, we used Spearman's rank correlation coefficient: $r_s = 0.582$ ($p_{\text{one-tailed}} = 0.006$).

We also checked the relation between the fear score and the learning score (figure 2b). *A priori*, we expected a negative correlation between timidity and the learning achievements (§1). Indeed, Spearman's rank correlation coefficient was negative: $r_s = -0.440$ ($p_{\text{one-tailed}} = 0.034$).

Closing the circular argument is the fact that the correlation between initial fear and searching tendency was also negative: $r_s = -0.405$ ($p_{\text{one-tailed}} = 0.048$), figure 2c.

Since our primary interest was the correlation between the learning score and the foraging tendency, we further checked that this correlation is still significant when the fear score is held constant, that is, we calculated the partial correlation between the learning score and the foraging tendency [44,45] and obtained $r_s = 0.492$ ($p_{\text{one-tailed}} = 0.023$).

Finally, since in mice Matzel *et al.* [23] found a trend according to which lighter individuals learned better, we checked the relation between our measurements of nestling body weight (taken for the last time on day 13) and their learning score (tested 10–11 days later; §2). We found that also in our study lighter individuals had a higher learning score, though this correlation was not statistically significant ($r_s = -0.408$, $N = 18$, $p_{\text{two-tailed}} = 0.093$). A stronger and significant correlation was found, however, between body weight and initial fear ($r_s = 0.617$, $N = 18$, $p_{\text{two-tailed}} = 0.006$), suggesting that lighter nestlings are less fearful and this may affect their learning score or foraging tendency. Recalling that our

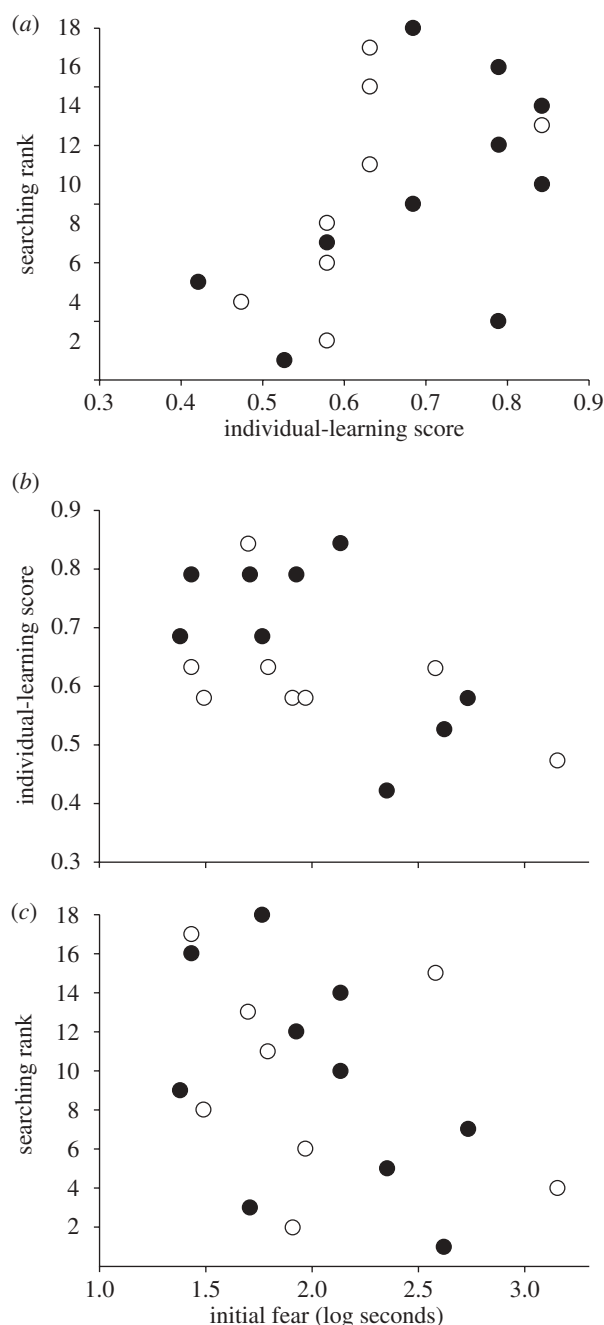


Figure 2. (a) The relationship between individual's score in the individual-learning test (a high score means better learning ability) and its searching rank (a high rank means higher searching proportion). (b) The relationship between individual's initial fear (log seconds) and its score in the individual-learning test. (c) The relationship between individual's initial fear and its searching rank.

primary interest was the correlation between the learning score and the foraging tendency, we checked and verified that this correlation remains significant when both the fear score and the body weight are held constant. (The partial correlation between the learning score and the social-foraging tendency when both fear and weight are held constant was $r_s = 0.475$, $n = 18$, $p_{\text{one-tailed}} = 0.031$).

4. DISCUSSION

Our results show a positive correlation between the performance of young house sparrows in an

individual-learning task, measured prior to any social experience, and their tendency to forage as producers later, while foraging in a group. This correlation also remains significant after controlling for the effects of fear and body weight on the fledglings' performance in the individual-learning test.

The negative relation between fear and individual-learning is consistent with previous studies that examined the relation between learning and neophobia (e.g. [18,46,47]). An effect of fear on learning performance is almost inevitable since learning requires attention and active exploration that are usually inhibited by fear [48]. Indeed, humans' scores in exams are known to be affected by their level of worry or stress [49]. The association found between low body weight and learning ability appears to be inconsistent with studies on song-learning in birds ([50], or on learning in humans, e.g. [51,52]), which show that poor condition or low weight early in life is correlated with poor learning performance later on. Yet, this association is consistent with the trend Matzel *et al.* [23] found in laboratory mice. It is important to note that in our experiment we only measured nestlings' weight. As this is not a direct measure of body condition (as it varies with body size), we cannot determine the relationship between body condition, individual-learning ability and social foraging. We suggest that in our study, the relationship between low body weight and high learning score was mediated by the much stronger correlation observed between body weight and fear (§3). Accordingly, nestlings with a low body weight had less food reserves and were therefore more likely to take risks in order to find food. This could suppress their level of fear and facilitate faster learning. It should be noted, however, that this possible scenario cannot fully explain the correlation between learning ability and searching behaviour that also remained significant after fear and body weight were held constant (§3). Thus, the picture emerging from our results is that in young sparrows, the tendency to forage as a producer is associated with better individual-learning abilities and also with low body weight and low level of fear of a novel setting.

We cannot determine whether the individual-learning scores measured in our tests represent innate or acquired abilities. Despite being tested at an early age and under the same experimental conditions, nestlings may differ in their phenotypic or physiological conditions, and the experience they had during the fledging period may not be identical (allowing dynamic interaction between fear and reward, for example, to amplify small initial differences in learning ability). While learning abilities are known to vary between individuals and to be heritable to some degree [53–56], further work would be necessary to determine the heritability and the exact nature of the sparrows' individual-learning ability that was measured in our study.

Although the mechanisms underlying the emergence of animal personalities are not clear [9,25], our results can nevertheless shed some light on the particular association between individual-learning ability and social-foraging strategy. As described in §1, this association may emerge from three not mutually exclusive mechanisms: (i) individuals that have an innate or acquired preference for the producer strategy become

specialized in individual learning, (ii) individuals that have an innate or acquired advantage in individual-learning ability learn to prefer the producer strategy, and (iii) individual-learning ability and a tendency to behave as a producer are initially associated through shared innate, genetic (genetic linkage or conditional expression) or non-genetic mechanisms. Since it was measured before entering a social group, the high individual-learning score in our study could not be the outcome of being a 'producer', which allows us to eliminate explanation (i) in our case.

The possibility that individuals with innate or acquired advantage in individual-learning ability learned to prefer to be searchers (explanation ii) is especially relevant in light of recent work on passerines' ability to learn to choose between the producer and scrounger strategies [35,40]. However, the case for learned strategy choice in the present study is much less clear because foraging on the grid in the shared aviary did not require associative learning of the kind tested in the individual-learning test (the presence of food on the foraging grid was not indicated by any sign or colour). In other words, the probability of being rewarded for searching behaviour on the grid was not assumed to be higher for individuals that are better in associative learning. Learned strategy choice can nevertheless explain our results if it developed earlier, and by a more subtle process. For example, the high success rate of fast learners (either during the individual-learning test or during other foraging events that we did not monitor) may increase their 'confidence' in independent searching and reduce the attractiveness of following others. One way to view it is that young sparrows have a default rule of the type: 'follow others when food is hard to find'. This rule is retained from the time they followed their parent (the stuffed model in our experimental setup), but the more successful they become in finding food, the easier they perceive finding food to be, and the relative attractiveness of following others is reduced. Thus, initial advantage in self learning can facilitate experience-based strategy choice of this kind.

The third explanation of our results is that individual-learning ability and a tendency to behave as a producer are initially associated through shared mechanisms (genetic or non-genetic). There is evidence that problem-solving propensities in European starlings (*Sturnus vulgaris*) are relatively consistent across asocial and social contexts [19], suggesting a common mechanism for both behaviours. In a similar manner, it is possible that the same mechanisms that generate exploratory behaviour or improved attention provide a common pathway for both associative learning and searching behaviour. Such pathways might be influenced by both genetic and non-genetic factors [6,9]. Alternatively, the genetic basis of the two traits could be coded by different genes that evolved to be associated as a result of their complementary functionality [6,57].

Finally, the three basic mechanisms discussed above may also interact in creating a positive feedback leading to further specialization and coevolution of individual learning and searching, resulting in the 'individual *status quo*' scenario envisaged by Sih & Bell [9]. This interaction can also lead to a developmental niche construction process in which the individual modifies its own developmental environment and influences its own learning and

searching propensities [58], i.e. strategy choice constructs a niche for learning abilities that may form a niche for further strategic choices. While these exciting ideas require extensive additional work to be tested, the association between individual-learning ability and social-foraging strategy demonstrated in this study may provide a good start and a concrete model system.

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