



# Does Innovation Success Influence Social Interactions? An Experimental Test in House Sparrows

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## Abstract

In group-living animals, individuals may benefit from the presence of an innovative group-mate because new resources made available by innovators can be exploited, for example by scrounging or social learning. As a consequence, it may pay off to take the group-mates' problem-solving abilities into account in social interactions such as aggression or spatial association, for example because dominance over an innovative group-mate can increase scrounging success, while spatial proximity may increase the chance of both direct exploitation and social learning. In this study, we tested whether the individuals' innovation success influences their social interactions with group-mates in small captive flocks of house sparrows (*Passer domesticus*). First, we measured the birds' actual problem-solving success in individual food-extracting tasks. Then, we manipulated their apparent problem-solving success in one task (by allowing or not allowing them to open a feeder repeatedly) while a new, unfamiliar group-member (focal individual) had the opportunity to witness their performance. After this manipulation, we observed the frequency and intensity of aggression and the frequency of spatial associations between the focal individuals and their manipulated flock-mates. Although flock-mates behaved according to their treatments during manipulations, their apparent problem-solving success did not affect significantly the focal individuals' agonistic behaviour or spatial associations. These results do not support that sparrows take flock-mates' problem-solving abilities into account during social interactions. However, focal individuals attacked those flock-mates more frequently that had higher actual problem-solving success (not witnessed directly by the focal individuals), although aggression intensity and spatial association by the focal birds were unrelated to the flock-mates' actual success. If this association between flock-mates' actual innovativeness and focal individuals' aggression is not due to confounding effects, it may imply that house sparrows can use more subtle cues to assess the group-mates' problem-solving ability than direct observation of their performance in simple foraging tasks.

## Introduction

Animal innovation, that is the learning of novel behaviours or modification of existing behavioural patterns (Reader & Laland 2003), is believed to be adaptive by enabling animals to better exploit their environment, for example find novel food resources

(Fisher & Hinde 1949), use novel materials to repel parasites (Suárez-Rodríguez et al. 2013), attain more attractive sexual displays (Elias et al. 2006; Madden 2007) or deceive social companions in order to acquire resources (Byrne 2003). Evidence is accumulating that innovations can increase the individuals' fitness: for example better problem-solving

performance correlates with higher mating success in male satin bowerbirds, *Ptilonorhynchus violaceus* (Keagy et al. 2011) and higher nestling survival in great tits, *Parus major* (Cauchard et al. 2013), although these relationships can vary both between and within species (Cole et al. 2012; Isden et al. 2013).

In group-living species, innovative behaviours may have fitness consequences not only for the innovative individuals but also for their group-mates. For example, in foraging groups innovative members can make novel food sources available for their group-mates (Liker & Bókony 2009; Morand-Ferron & Quinn 2011). First, group-members may obtain food discovered by innovators either by food sharing or non-aggressive scrounging (Giraldeau & Caraco 2000; Boogert et al. 2010), or by aggressively exploiting the innovator's efforts, for example via kleptoparasitism or aggressive scrounging (Lendvai et al. 2006; Iyengar 2008; Tóth et al. 2009a). Second, by observing the innovator, group-members may copy and learn its behavioural techniques and thereby can exploit the new food sources on their own (Giraldeau et al. 1994; Altshuler & Nunn 2001). Social learning has been suggested to explain the spread of some well-known foraging innovations like milk bottle opening by birds or potato washing by macaques (Fisher & Hinde 1949; Kawai 1965; Lefebvre 1995; Reader & Laland 2003).

Given the mechanisms above, the social relationships of group-members may be influenced by their innovativeness in various ways. First, if higher dominance rank facilitates the social exploitation of group-mates, for example through aggressive scrounging (Wiley 1991; Liker & Barta 2002), it may pay off for group-members to attain dominance over the innovators. For example, this can be achieved by more frequent or more intense aggression towards the most innovative group-mates than towards other group-mates. Second, if innovations can be learned or shared, it may be worth to maintain closer spatiotemporal associations with the innovators than with less skilled group-mates, because such associations may promote social learning as in the case of song and other sexual behaviours (Freeberg 1999; Poirier et al. 2004). Furthermore, if affiliative relationships enhance the efficiency of social learning and/or the probability of food sharing (reviewed by Stevens & Gilby 2004; and see De Kort et al. 2006), group-mates may increase affiliative behaviours and/or reduce aggression towards the innovators.

Correlative studies produced mixed results for the above hypotheses. Individual performance in

problem-solving tasks, a proxy for innovativeness, was not related to dominance rank in several birds and mammals (Wiley 1991; Bouchard et al. 2007; Pongrácz et al. 2008; Benson-Amram & Holekamp 2012), whereas subordinates were either less innovative (Boogert et al. 2006, 2008) or more innovative than dominants in others (Laland & Reader 1999a; Reader & Laland 2001; Cole & Quinn 2012; Thornton & Samson 2012). Moreover, the performance of individuals in cognitive tasks may be altered by the presence of group-mates, implying that correlative results might be confounded by the study conditions (Drea & Wallen 1999; Nicol & Pope 1999; Overington et al. 2009a). Similarly, the relationship between innovativeness and social associations is poorly known. For example, in mixed wintering flocks of three Paridae species, more central individuals of the social network were more likely to use novel food sources, suggesting the importance of associations in information transfer (Aplin et al. 2012). On the other hand, the association network did not predict the spread of innovations in another bird species (Boogert et al. 2008). To our knowledge, no study has experimentally tested whether aggressive and affiliative relationships are causally influenced by the innovativeness of group-mates.

In this study, we conducted an experiment to investigate whether individuals behave differently towards their innovative and non-innovative flock-mates in the house sparrow, *Passer domesticus*. This species is one of those with the highest number of foraging innovations reported among wild birds (see supplementary material of Overington et al. 2009b) and also readily solves foraging tasks in the laboratory (Liker & Bókony 2009; Bókony et al. 2014). In the non-breeding season, sparrows live in flocks and often establish close to linear dominance hierarchies with frequent aggressive interactions (Anderson 2006). They typically do not engage in affiliative interactions but maintain spatial associations with preferred flock-mates such as siblings (Tóth et al. 2009b). During social foraging, they often use aggressive scrounging to obtain food from their flock-mates and more dominant birds scrounge more frequently (Liker & Barta 2002), whereas individuals with superior learning ability are more likely to forage as producers (Katsnelson et al. 2011).

Specifically, we tested the following predictions in house sparrows. Firstly, because dominance facilitates scrounging, individuals may attempt to achieve dominance over their innovative flock-mates by behaving more aggressively against them. Thus, individuals perceived as more successful innovators should be

attacked more often and/or more intensively by their flock-mates. Secondly, because spatial association enables social learning and the less frequent non-aggressive scrounging, we expect that sparrows tend to associate more with their more innovative flock-mates. To test these predictions, first we measured the individuals' actual problem-solving success in three foraging tasks, and then manipulated their apparent innovation success in the eyes of an unfamiliar conspecific. Finally, we tested whether the aggressive and non-aggressive social behaviours of these unfamiliar flock-mates differ towards the birds with apparently different innovative ability.

## Methods

This study is part of a more general project that explores the causes and consequences of behavioural flexibility in birds (Bókony et al. 2014; Papp et al. 2015, Vincze et al. 2015). The experiment presented here is built on this previous work and utilizes some of the data used in a previous paper that examined the predictors of individual problem-solving performance (Bókony et al. 2014, Papp et al. 2015). However, the two papers report two entirely different sets of analyses investigating separate research questions, and there is no overlap in the presented results. Methods shared with the previous studies are repeated here to make all relevant details readily available.

During the procedures described here, 13 of 104 birds (12.5%) died for unknown reasons, 7 of them within the first week after capture; this rate of mortality is within the range (3.3–38.5%) reported by other studies of captive sparrows (e.g. Gonzalez et al. 2001; Poston et al. 2005; Liker & Bókony 2009; Bókony et al. 2012a). Although the weight and apparent condition of these birds was normal at capture, our subsequent physiological analyses suggested that at least some of them were already in poor health (see Bókony et al. 2014 for details). All described procedures were in accordance with Hungarian laws and licensed by the Middle Transdanubian Inspectorate for Environmental Protection, Natural Protection and Water Management (permission number: 31559/2011).

## Subjects and Overall Experimental Design

In January–March 2012, we captured 10–14 house sparrows each week over 8 weeks using mist nets (Ecotone, Gdynia, Poland); each week we sampled two capture sites 6.8–69.2 (mean  $\pm$  SE = 32.7  $\pm$  6.8) kilometres apart. As house sparrows are very

sedentary (Anderson 2006; Liker et al. 2009), it is likely that birds from the two capture sites sampled in a given week were not familiar with each other. Upon capture, we measured body mass ( $\pm$ 0.1 g using a Pesola spring balance) and tarsus length ( $\pm$ 0.1 mm using dial callipers). Birds were brought into captivity and housed for 3 weeks.

The outline of the study is illustrated in Figure S1. In short, first we assessed the birds' problem-solving performance in three tasks in which they were tested individually. Then some of the birds were trained to use a novel feeder, while the others were not presented with this task. We used this latter group of birds as focal individuals in the next part of the study, in which we manipulated the information available to the focal individuals about the problem-solving performance of the trained birds (which were unfamiliar to the focal individuals) so that some appeared successful while others appeared unsuccessful. Up to this phase of the experiment, the birds were kept in individual cages. Finally, we observed the focal individuals' aggressive and affiliative behaviours towards the manipulated birds while they were allowed to interact in small flocks. We describe each of these steps in detail below.

## Measuring the Birds' Actual Problem-solving Performance

After 1–2 days of acclimation following capture, we tested the performance of each individual in three food-extracting tasks (Figure S2, panels A–C) over 3 days. These procedures were the same as detailed by Bókony et al. (2014); therefore, here we provide a short description only. Birds were kept in individual cages, and those captured from different localities were visually separated by opaque plastic sheets to prevent them from getting visual information about each other; and during the tests, every bird was visually blocked from the others. Each test took place in the morning after 90 min fasting, and we recorded each bird's latency to solve the task (i.e. time elapsed from the start of test until the bird started to feed) over 90 min per task. As individual performance across the three tasks was weakly but significantly repeatable (ICC = 0.153, 95% confidence interval: 0.033–0.286,  $F_{97,196} = 1.54$ ,  $p = 0.006$ ; for further details see Bókony et al. 2014), from these data, we calculated innovation rank for each individual as the mean of the 3 within-task ranks of problem-solving latencies; higher innovation rank means faster problem-solving performance.

### Training in a New Task

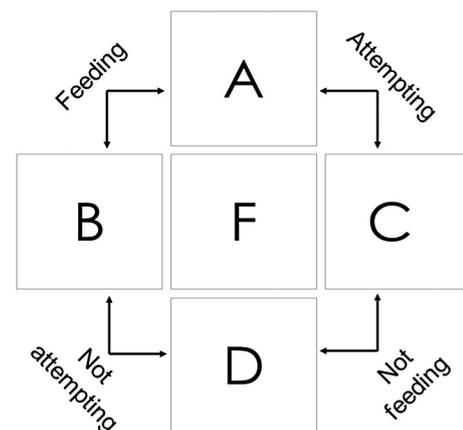
After the third problem-solving test, birds were transferred into another room where they were allowed to acclimate for 2 days in individual cages. On days 8–12, we presented a subset of birds ( $n = 72$ ; hereafter referred to as ‘flock-mates’) with a fourth task repeatedly in a total of 19 training sessions, as detailed by Bókony et al. (2014), to train them to use a special feeder (henceforth ‘training feeder’). This training feeder was an  $8.5 \times 8.5 \times 2.5$  cm white plastic box with one transparent side and a lid on the top (Figure S2, panel D); birds had to insert their beak and head under the lid and push it up to reach the food. The training feeder did not remain open after the bird first fed from it; instead, it had to be opened every time to peck a seed. There were four 30-min training sessions each day (except the last day) between 9:00 and 16:00, each preceded by 60 min fasting, and the behaviour of the birds was observed during each training session from behind a one-way window. Birds that did not open the training feeder by the 10th training session ( $n = 18$ ) were allowed to remain in visual contact with one of their neighbours that could already use the feeder; if then the bird fed from the training feeder successfully in two consecutive training sessions ( $n = 6$ ), we re-inserted the opaque sheet again between the cages. 12 birds did not learn this task by the end of the training period; in the subsequent stage of the experiment, 5 of these birds were allocated to treatment groups where there was no need for the trained skill. Between the training sessions, birds were allowed to feed from the training feeder with the lid fixed in open position by a small transparent cup.

The rest of the birds ( $n = 26$ , hereafter referred to as ‘focal individuals’) were not trained; they were kept visually separated from the trained birds, with *ad libitum* food available in their cages from a transparent plastic dish (7.5 cm diameter, 3.5 cm high; henceforth ‘feeder dish’). After the 19th training session, all birds were individually colour marked on the top of their head using non-toxic marker pens (Decopainter, Marabu Co., Bietigheim-Bissingen, Germany) to facilitate individual recognition by the observer in the subsequent stage of the experiment, and they were placed into new cages as follows.

### Manipulation of Apparent Problem-solving Performance of the Trained Birds

On day 12, ten birds were selected for further procedures randomly with some constraints detailed below.

These birds participated in 7 sessions over 2 days in which we manipulated the information about the trained birds’ (i.e. flock-mates’) innovation success to the untrained birds (i.e. focal individuals). The 10 birds were divided into 2 ‘flocks’, each consisting of five members of the same sex; note that the flock-mates still remained in separate cages during the manipulation. In each flock, the four trained flock-mates had been captured from the same location, whereas the fifth (the focal individual) had been captured from a different site. Due to the visual separation during the earlier innovation tests and training, focal individuals had no previous experience of their assigned flock-mates’ actual problem-solving performance. The flock-mates could have had prior experiences with each other as they were captured at the same sites and they were allowed visual contact with each other during the acclimation and training periods. The cages of each flock were arranged in a way that the focal individual’s cage was surrounded by the four cages of its flock-mates (Fig. 1). Due to test room arrangement, two of the flock-mates’ cages were further from the door through which the experimenters got about (we assumed this was ‘safe’ position for the birds) and two cages were closer to the door (considered as ‘risky’ position); flock-mates’ cages were moved into different, randomly selected positions three times over the seven sessions. The focal individual was visually separated from the four flock-mates except for the duration of manipulation sessions. The two simultaneously manipulated flocks were visually



**Fig. 1:** An example of cage arrangement during the sessions of manipulating apparent problem-solving performance. Letters designate treatment groups as follows: F—focal individual; A—had to ‘problem solve’ repeatedly to get food; B—received an open feeder; C—received a sealed feeder; D—had no feeder (see Methods). Note that cages of treatment groups A–D were relocated randomly 3 times over the 7 manipulation sessions.

separated from each other by opaque sheets. During the manipulation, we used 16 such flocks (i.e. 8 pairs of flocks) in total.

In each flock of 5 birds, each of the 4 flock-mates was assigned to a treatment group (A–D) and during the manipulation sessions the birds of different treatment groups were presented with different feeders as follows. Birds in treatment group A were presented with the familiar training feeder, so they could solve the problem (open up the lid) repeatedly to get food during the manipulation sessions. Birds in treatment group B received an open feeder that was a training feeder with a narrow opening cut into its otherwise sealed lid, so the birds could feed without problem solving. Birds in treatment group C received a sealed training feeder that was impossible to open, whereas birds in treatment group D and the focal individuals had no feeder in their cage during the manipulation sessions. Thus, birds in treatment groups A and B could feed during the manipulation sessions but only the former were actually problem solving, whereas birds in treatment groups C and D were not feeding but only the former were attempting to feed by manipulating the feeder (Fig. 1). We used this  $2 \times 2$  treatment design to separate the possible effect of feeding success from the effect of problem-solving success, as it is yet unclear whether sparrows may judge each other's performance by the act or the result of innovation (i.e. successful problem solving vs. successful feeding). Birds were randomly selected for treatment groups A and C from those individuals that had been successful during training, whereas both successful and unsuccessful birds were randomly allocated to treatment groups B and D, due to the constraint that some flock-mates did not learn to open the feeder. Over the whole experiment, 5 unsuccessful birds were allocated to treatment groups B or D in 3 of 15 flocks; omitting these 3 flocks from the analyses does not change our results qualitatively. Otherwise, the treatment groups did not vary significantly in any investigated trait (Table 1).

Each manipulation session was preceded by a 60-min fasting period, after which the visual separation between the focal individuals and their flock-mates was suspended and birds in treatment groups A, B and C received their respective feeders for a 30-min session. During these sessions, we observed the birds from behind a one-way window, and each minute we recorded whether each flock-mate was feeding (treatment groups A and B) or attempting to feed (i.e. touching the feeder with the beak without eating; treatment groups A and C). We chose to conduct 7 manipulation sessions because our pilot study indicated that trained birds would readily and repeatedly use the feeder, providing ample opportunity for the focal birds to observe their flock-mates' performance over a total of 3.5 h; and our earlier experience with sparrows showed that a winter day allows sufficient time for 4 sessions per day including the fasting periods and resting time (Seress et al. 2011). On the second day, we conducted 3 sessions instead of 4 to leave more time for the birds at the end of the day to accommodate to their new cage for the next stage of the experiment. Apart from the manipulation sessions and the preceding fasting periods, birds had *ad libitum* food available from feeder dishes for focal individuals and from training feeders held open for the flock-mates.

### Observing Social Interactions in Flocks

After the 7th manipulation session, birds were weighed and transported to the location of the social interaction observations, where each flock of those 5 birds that participated in the manipulation sessions together was housed as a flock in one of two outdoors cages ( $100 \times 60 \times 65$  cm), one placed above the other. Each cage contained 3 perches, a plastic bush and 4 roosting boxes. Food, water, sand and sepias were present *ad libitum* except for the fasting periods before observations. Food was available from a large transparent feeder box ( $50 \times 50 \times 5$  cm), filled with seeds that could

**Table 1:** Characteristics of the focal individuals (F) and birds in the treatment groups (A–D)

Dependent variable	Treatment groups					$\chi^2$	p
	F (n = 15)	A (n = 15)	B (n = 14)	C (n = 15)	D (n = 14)		
Innovation rank	48.72 ± 4.68	51.3 ± 5.1	51.1 ± 4.7	51.6 ± 4.4	46.3 ± 3.4	1.32	0.858
Body mass index (g)	24.46 ± 0.45	24.3 ± 0.5	24.8 ± 0.6	25.1 ± 0.4	25.0 ± 0.5	2.21	0.696
Aggressiveness (%)	23.36 ± 2.88	24.5 ± 0.0	15.0 ± 0.0	20.6 ± 0.0	18.8 ± 0.1	3.73	0.444

Mean ± SE,  $\chi^2$  and p-values are shown from analysis of deviance tables of LME models with treatment group as fixed factor and flock ID as random factor (n = 15 flocks).

be obtained through 16 equidistant wells (Liker & Bókony 2009). We observed the focal birds' social interactions with their 4 flock-mates over 3 days through a one-way window as follows.

We investigated aggressive behaviours in 6 sessions (2 each day), each lasting 30 min. Before each session, we removed the large feeder box and all food from the cage, and birds were fasted for 60 min; then, the flock was presented with a small feeder dish containing seeds. The feeder dish was big enough for the whole flock to feed together, and although it could be monopolized by a dominant individual this was rarely observed over the whole time of the experiment. We recorded all aggressive interactions between any two birds, noting the identity of both participants, the attacker and the winner of the dyadic fight; we also scored the intensity of the fight on a scale from 1 to 4 (Tóth et al. 2009c) as 1—supplant: intentional movement without physical contact; 2—threat: wing display or beak gaping without physical contact; 3—peck: short physical contact; 4—fight: prolonged physical contact. Some additional aggressive interactions were recorded during the observations of spatial associations.

Spatial associations of the focal individual with its flock-mates were recorded in 6 sessions (2 each day). Each session lasted for 30 min, during which we recorded the identity of the flock-mate nearest to the focal individual every 30 s, to estimate the proportion of time spent by the focal individual nearest to each flock-mate. This yielded 360 records in total for each focal individual. During the first 4 sessions, birds were not fasted and were allowed to feed freely from the large feeder box, whereas the last 2 sessions were preceded by 60 min fasting and birds could not access the food provided for these sessions; however, we obtained the same results when we analysed these two data sets separately, therefore, we present results from the pooled data set.

### Statistical Analyses

We used three dependent variables to describe the focal individuals' behaviours towards their flock-mates: (i) relative attack frequency, that is percentage of focal individual's attacks against the respective flock-mate out of the focal individual's all attacks; (ii) attack intensity, that is the average intensity of focal individual's attacks against the respective flock-mate; and (iii) relative association frequency, that is the percentage of records in which the respective flock-mate was the nearest individual to

the focal bird (excluding records when more than one bird was closest to the focal individual).

To investigate whether problem-solving success of flock-mates as well as other factors affected the focal individuals' behaviours towards the flock-mates, we used linear mixed-effects (LME) models with the flock ID as random factor throughout the analyses (Pinheiro & Bates 2000). Due to the death of birds B and C in one flock, we could use the data of 15 of 16 flocks. Two of these 15 flocks were incomplete because one bird died in each (birds B and D, respectively), but omitting these flocks from the analyses did not change our results qualitatively. Initial models for each dependent variable included treatment group (i.e. the flock-mate's treatment during the manipulation sessions, A–D) as a fixed factor, and the actual innovation rank of the flock-mate and of the focal individual as covariates. Additionally, we included the following potentially confounding variables: body mass index and aggressiveness of the flock-mates, sex of the flock, date of capture, position of outdoor cages (upper or lower) and colour marking of the head of the birds (see all full models in Table S1, for the calculation of df in mixed-effects models see Pinheiro & Bates 2000). Body mass index was calculated as a measure of body condition following Peig & Green (2009), applying the equation of Bókony et al. (2012b) to the body mass data taken after the last manipulation session. Aggressiveness was calculated as the percentage of fights initiated by the respective individual out of all fights within the flock. Because the variance in mean attack intensity decreased with increasing number of attacks by the focal individual (i.e. birds that were attacked more frequently were less likely to receive extremely low or high mean intensity), we allowed for this heteroscedasticity in all models of attack intensity using fixed variance weights. Non-significant predictors were omitted stepwise, removing the variable associated with the largest p-value in each step. We report the final models with significant effects only ( $p < 0.05$ ) excepting that we always retained actual innovation rank in each final model to estimate its effect even if this was non-significant.

We tested whether the distribution of the focal individuals' spatial associations across its 4 flock-mates differed from random (i.e. from uniform distribution) using  $\chi^2$  tests in each of the 15 flocks. All analyses were carried out in R 2.15.0 (R Development Core Team 2012). Mean values with  $\pm$  SE and two-tailed p-values are reported.

**Results**

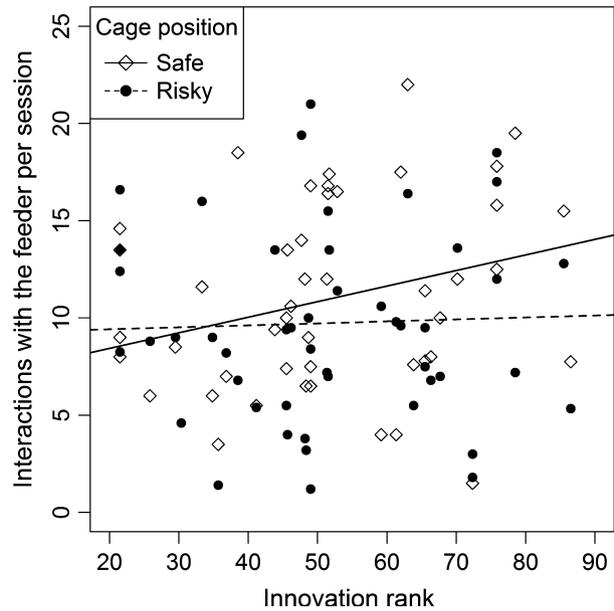
Birds behaved according to their assigned treatment (A–D) during the manipulation sessions: of 210 records over the 7 sessions, birds in treatment group A (who had to open the feeder) were feeding or attempting to feed  $80.9 \pm 6.2$  times, birds in treatment group B (with permanently open feeder) were feeding  $85.9 \pm 6.7$  times, whereas birds in treatment group C (with permanently closed feeder) attempted to feed  $42.3 \pm 6.0$  times. The frequency of interacting with the feeder (i.e. either feeding or attempting) in treatment groups A, B and C tended to increase with the individual’s actual innovation rank, but only in the ‘safer’ cage positions (Table 2, Fig. 2). There was no difference among the 5 groups of birds (treatment groups A–D, and focal individuals) in actual innovation rank, body mass index and aggressiveness (Table 1).

We recorded  $211.1 \pm 19.0$  aggressive interactions per flock ( $n = 15$  flocks). Out of these the focal individuals (who had no prior social interactions with the other 4 flock-mates) participated in  $98.7 \pm 11.9$  interactions ( $46.4 \pm 3.1\%$  of all fights) that tends to be higher than expected by chance (40%, one-sample  $t$ -test:  $t_{14} = 2.07$ ,  $p = 0.058$ ). Out of all aggressions participated in, focal individuals initiated  $48.2 \pm 4.0\%$ . The focal individuals’ relative attack frequency and intensity did not differ between the 4 flock-mates with different problem-solving treatments (Table 3). The focal birds’ associations were non-randomly distributed across the four flock-mates in 87% of the flocks ( $\chi^2$  tests,  $p < 0.05$  in 13 of 15 flocks) indicating that most focal birds expressed flock-mate preferences, but the treatments of flock-mates did not influence the relative association frequencies (Table 3).

However, the relative attack frequency of focal individuals towards their flock-mates was positively correlated with the flock-mates’ actual innovation rank

**Table 2:** The effects of cage position and innovation rank on the frequency of interacting with the feeder (either feeding or attempting to feed) during manipulation sessions in treatment groups A, B and C combined ( $n = 44$  birds, LME with flock ID as random factor,  $n = 15$  flocks)

Predictor variables	b ± SE	t	df	p
Intercept (safe position, lowest rank)	6.84 ± 2.21	3.10	26	0.002
Innovation rank	0.08 ± 0.03	1.85	26	0.071
Cage position (risky compared to safer)	2.38 ± 1.68	1.42	26	0.158
Innovation rank × cage position	-0.07 ± 0.03	-2.30	26	0.022



**Fig. 2:** Birds with higher actual innovation rank interacted with the feeder (i.e. fed or attempted to feed) more frequently when their cage was in safer position, whereas birds with lower actual innovation rank interacted with the feeder relatively infrequently in both safe and risky positions. Only birds in treatment groups A, B and C are shown as birds in treatment group D had no feeder during manipulation sessions.

(Pearson correlation,  $r = 0.36$ ,  $p = 0.005$ ,  $n = 58$  flock-mates), that is birds that had been faster innovators in the individual tests (not seen by the focal birds) were attacked more frequently by the focal individuals (Fig. 3). This relationship was robust, that is it remained significant after controlling for potentially confounding variables and for the non-independence of flock-mates using mixed models (Table 4). The focal individuals’ attack intensity and relative association frequency showed no relationship with the flock-mates’ actual innovation rank (Table 4).

Relative attack frequency by focal individuals increased with the aggressiveness of flock-mates ( $r = 0.41$ ,  $p = 0.001$ ,  $n = 58$  flock-mates; see Table 4 for the results of mixed models), and birds with higher body mass index were also attacked more often ( $r = 0.33$ ,  $p = 0.012$ ,  $n = 58$  flock-mates; Table 4). Attack intensity of focal individuals was higher towards more aggressive flock-mates ( $r = 0.46$ ,  $p < 0.001$ ,  $n = 58$  flock-mates; Table 4). Flock-mates’ actual innovation ranks did not correlate with either their aggressiveness or body mass index (Table S2).

**Discussion**

In this study, we tested experimentally whether birds take their flock-mates’ innovative skills into account

**Table 3:** The focal individuals' behaviour towards the 4 treatment groups (mean ± SE)

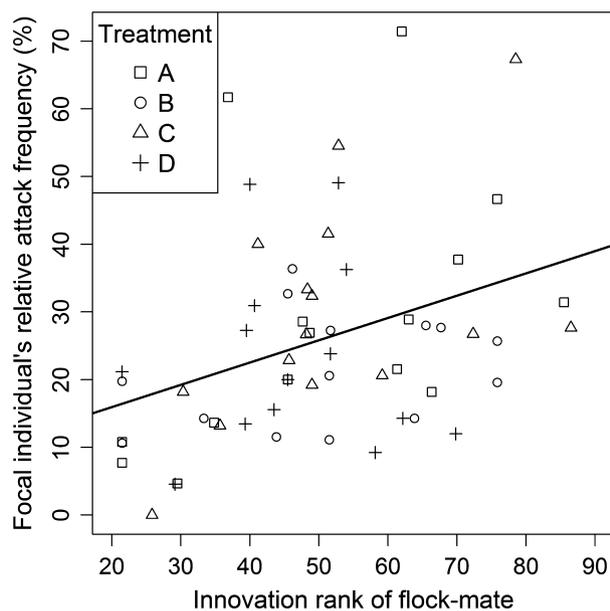
Dependent variable	Treatment groups				$\chi^2$	p
	A (n = 15)	B (n = 14)	C (n = 15)	D (n = 14)		
Relative attack frequency (%)	28.7 ± 5.0	21.4 ± 2.2	29.6 ± 4.3	23.3 ± 3.7	3.05	0.384
Attack intensity	3.3 ± 0.1	3.0 ± 0.1	2.9 ± 0.1	2.8 ± 0.2	6.18	0.103
Relative association frequency (%)	26.3 ± 1.6	24.0 ± 2.5	26.7 ± 2.2	26.4 ± 2.3	1.03	0.795

$\chi^2$  and p-values are shown from analysis of deviance tables of LME models with treatment group as fixed factor and flock ID as random factor (n = 15 flocks).

**Table 4:** The effects of flock-mates' (n = 58) actual innovation rank on focal individuals' (n = 15) behaviours

Focal individual's behaviour (dependent variable)	Flock-mate's traits (predictor variables)	b ± SE	df	t	p
Relative attack frequency (%)	Intercept	-75.23 ± 23.00	40	-3.27	0.002
	Innovation rank	0.43 ± 0.09	40	4.57	<0.001
	Aggressiveness (%)	0.38 ± 0.10	40	3.80	<0.001
	Body mass index	2.91 ± 0.88	40	3.30	0.002
Attack intensity	Intercept	2.17 ± 0.37	40	5.81	<0.001
	Innovation rank	0.005 ± 0.007	40	0.75	0.459
	Aggressiveness (%)	0.025 ± 0.008	40	3.07	0.004
Relative association frequency (%)	Intercept	23.63 ± 3.36	42	7.03	<0.001
	Innovation rank	0.04 ± 0.06	42	0.70	0.490

Other predictors of the focal individuals' behavioural responses are shown only if they were retained in the final LME models (with flock ID as random factor; n = 15 flocks).



**Fig. 3:** Relationship between the focal individual's relative attack frequency and the flock-mates' actual innovation rank (for explanation of treatment groups see Methods and Fig. 1).

when interacting with them. Although the flock-mates' behaviour (e.g. the frequency of feeding or attempting to feed) during the manipulation sessions

was consistent with the aims of the treatments, focal individuals did not show differential behavioural responses towards different treatment groups, for example did not attack or accompany more those birds that were experimentally allowed to perform successful problem solving (treatment A) than those that were experimentally forced to appear completely unsuccessful (treatment C). In contrast, we found that aggressive behaviour was more frequent towards flock-mates with better actual problem-solving performance, although no such relationship was found for other behavioural variables (attack intensity, spatial association). We suggest several potential explanations for these conflicting results.

Firstly, one explanation is that, as suggested by the lack of difference between treatment groups, sparrows do not take the problem-solving ability of flock-mates into account during their social interactions, instead they base their decisions about aggression and association on other kinds of information (such as dominance rank or relatedness of the flock-mates; e.g. Liker & Barta 2001, 2002; Anderson 2006; Tóth et al. 2009b). For example, we found here that flock-mates' aggressiveness and body mass index both predicted the frequency of attacks by the focal individual, and aggressiveness also predicted attack intensity. If sparrows do not take each other's innovativeness into

account, the correlation we found between the focal birds' aggression and the flock-mates' actual problem-solving success may have arisen by some confounding variables that may be related to the flock-mates' problem-solving success and at the same time can influence either the focal individuals' aggressive behaviour or the opportunities for interactions. For example, dominance may be associated with problem-solving behaviour in wild house sparrows like in some other group-living birds (e.g. Boogert et al. 2006, 2008), and the dominance rank of birds before the experiment (i.e. in their wild flocks) also might have had an effect on their aggressive interactions in our experimental flocks (e.g. through winner-loser effects, Rutte et al. 2006), creating a spurious correlation between aggression and problem-solving success. However, this explanation is unlikely as the actual problem-solving success of sparrows in our sample was not associated with their own fighting success in the experimental flocks, body mass and size, bib size and wing bar coloration (Table S2), traits that have been found to predict dominance in house sparrow flocks (Møller 1987; Liker & Barta 2001; Bókony et al. 2006). Similarly, although body mass index and aggressiveness of the flock-mates correlated with the focal individuals' relative attack frequency (Table 4), neither of these two traits was related to actual innovation rank (Table S2). A further possibility is that the stress-sensitivity of flock-mates influenced both their problem-solving success and aggressive interactions. In an earlier study, we showed for these birds that individuals with lower levels of stress hormones were more successful during some individual problem-solving tests (Bókony et al. 2014). If stress tolerance allowed these birds to spend more time at the feeder dish in the flock cages compared to the individuals with higher stress hormone levels, the focal individuals could have had more opportunity to fight with them. However, the focal birds' relative attack frequencies were not related to the stress hormone levels of flock-mates (Table S2). Finally, the flock-mates' activity level may also affect the opportunities for the focal individuals to fight with them, for example less active birds with slower metabolism may spend less time at the feeder (the main site of fights); and these birds might also be less successful in problem solving, for example by attempting less vigorously (Benson-Amram & Holekamp 2012; Sol et al. 2012; Thornton & Samson 2012). Although birds that had higher attempt frequencies were more likely to succeed in our tests (Papp et al. 2015), this kind of activity was not related to the relative attack frequency by focal birds (Table S2).

Secondly, an alternative explanation is that focal individuals assessed their flock-mates' problem-solving ability and used this information at least in their aggressive interactions (causing our correlative result), but this assessment was not based on the manipulated problem-solving performance of flock-mates (causing the lack of treatment effect). For example, there are various behavioural (e.g. neophobia, Boogert et al. 2008) and morphological (e.g. body size, Laland & Reader 1999b; plumage coloration, Mateos-Gonzalez et al. 2011) correlates of problem-solving success, and these traits can potentially be used as cues to assess the flock-mates' abilities. Such cues may even be more reliable than the direct observation of the flock-mates' performance in actual problem-solving situations, because the social context may change the individuals' innovative performance; for example, both primates and birds perform worse in the presence of conspecifics, especially dominants (Drea & Wallen 1999; Nicol & Pope 1999; Overington et al. 2009a; Griffin et al. 2013). In our study, we found no correlation between innovativeness and phenotypic traits that may be used as such cues (Table S2), but the frequency of interacting with the feeder during the manipulation sessions in the 'safe' cages tended to correlate positively with the birds' actual problem-solving success (Fig. 2). Thus, focal birds could potentially use this kind of activity to judge the problem-solving ability of flock-mates and adjust their behaviour accordingly during their interactions later in the experimental flocks. However, if this scenario is true, it is unclear why they did not differentiate between the treatment groups because, for example, birds in treatment group A (successful birds) had twice as many interactions with the feeder during the manipulation sessions as birds in treatment group C (unsuccessful birds; see Results). We might speculate that, instead of overall activity (i.e. interacting with the feeder), the flexibility of the flock-mates' behaviour could have served as a cue for focal individuals, as sparrows with high innovation ranks were the ones that were more active in safety than in risky cages. Interestingly, behavioural flexibility in response to predation risk was found to correlate with explorativeness in great tits (Quinn et al. 2012), and this personality trait may be a major determinant of problem-solving success (Boogert et al. 2008; Cole et al. 2012).

Regardless of the interpretation of the results, the focal individuals' behaviours clearly demonstrated that house sparrows do not discriminate their more innovative flock-mates positively. Even if the birds took their flock-mates' innovative skills into account,

our results suggest that dominating over an innovator would be more important than associating with it. One reason for this can be that aggressive scrounging might be preferred to social learning by foraging house sparrows. As shown for other species, the trade-off between scrounging and social learning may suppress the latter (Giraldeau & Lefebvre 1987).

In addition to the relationship with innovativeness, we found that the agonistic behaviour of the focal individuals was positively related to the flock-mates' aggressiveness and body mass index. Furthermore, flock-mate aggressiveness predicted not only the frequency but also the intensity of attacks by the focal birds. A possible explanation for the high frequency and intensity of agonistic behaviour against aggressive flock-mates is that these birds initiated a high number of fights against the unfamiliar focal individuals (e.g. when they were feeding together on the feeder dish), which in turn might have generated a large number of counterattacks by the focal birds (e.g. if they were to regain their position on the feeder). Alternatively, as both aggressiveness and body condition may indicate resource-holding potential (Hardy & Briffa 2013), our findings may suggest that house sparrows preferentially target the strongest opponents for some reason when they are in an unfamiliar flock. Attacking the most aggressive flock-mates might pay off if the focal individual has disproportionately more to gain by defeating those flock-mates. For example, when male great tits are defeated, more aggressive ('fast') birds show stronger reduction in activity than less aggressive ('slow') birds (Carere et al. 2001). If a similar phenomenon exists in sparrows, attacking the aggressive flock-mates could be a rewarding strategy when competing for limited food sources. Note, however, that we did not quantify the birds' actual aggressiveness in separate assays, so we do not know if our aggressive sparrows had genuinely more aggressive personalities. In our observations, the behaviour of each bird was likely affected by the behaviour of all flock-mates, so the relative aggressiveness of a given individual was likely a function of its flock-mates' behaviour. For example, aggressive interactions are more frequent between individuals of similar fighting abilities in several species (Hardy & Briffa 2013).

Attacking flock-mates with high body mass index might pay off, for example, if these individuals are less motivated to fight due to their higher levels of energy reserves. Individuals that have more to gain by winning a contest were found to be more dedicated opponents in several cases (Morrell et al. 2005). For

example, house sparrows with low body condition use aggressive scrounging more often than their flock-mates with better condition (Lendvai et al. 2004). Similarly, male house finches (*Carpodacus mexicanus*) with drab plumage coloration (indicating poor condition) are more aggressive than colourful males (McGraw et al. 2007), and male fiddler crabs (*Uca annulipes*) with regenerated claws (weaker competitors) sometimes fight harder over resources than intact males (Callander et al. 2012). However, in our study, there was no correlation between the birds' aggressiveness and their body mass index, not supporting the above idea. Similarly, relative body size and relative body condition do not affect aggressiveness in male crickets (Brown et al. 2006). Thus, whether and how body condition and aggressiveness affect the likelihood of being attacked in agonistic interactions remains to be evaluated in further studies.

In sum, our experimental results suggest that some common social interactions (aggression, spatial association) are not influenced by the apparent problem-solving ability of the group-mates in house sparrows. On the other hand, our correlative results indicate that sparrows may take into account their flock-mates' aggressiveness, body mass index and actual problem-solving success in aggressive interactions. The correlation between flock-mates' actual innovativeness and the focal birds' aggression suggests that the animals might be able to use subtle cues to assess the problem-solving ability of their companions instead of relying on the observation of their performance in brief foraging situations. This interesting possibility requires further testing.

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### Supporting Information

Additional supporting information may be found in the online version of this article:

**Figure S1.** Timeline of the procedures in the study applied for each group of sparrows.

**Figure S2.** Feeders used in the experiment.

**Table S1.** Initial models of focal individuals' behaviour in relation to their innovation rank and their flock-mates' various traits.

**Table S2.** Bivariate relationships of potential confounding variables with the flock-mates' (27 males and 31 females) innovation rank and the focal individuals' (7 males and 8 females) relative attack frequency.