



The origin and spread of innovations in starlings

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There are numerous reports of novel learned behaviour patterns in animal populations, yet the factors influencing the invention and spread of these innovations remain poorly understood. Here we investigated to what extent the pattern of spread of innovations in captive groups of starlings, *Sturnus vulgaris*, could be predicted by knowledge of individual and social group variables, including association patterns, social rank orders, measures of neophobia and asocial learning performance. We presented small groups of starlings with a series of novel extractive foraging tasks and recorded the latency for each bird to contact and solve each task, as well as the orders of contacting and solving. We then explored which variables best predicted the observed diffusion patterns. Object neophobia and social rank measures characterized who was the first of the group to contact the novel foraging tasks, and the subsequent spread of contacting tasks was associated with latency to feed in a novel environment. Asocial learning performance, measured in isolation, predicted who was the first solver of the novel foraging tasks in each group. Association patterns did not predict the spread of solving. Contact latency and solving duration were negatively correlated, consistent with social learning underlying the spread of solving. Our findings indicate that we can improve our understanding of the diffusion dynamics of innovations in animal groups by investigating group-dependent and individual variables in combination. We introduce novel methods for exploring predictors of the origin and spread of behavioural innovations that could be widely applied.

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In recent years there has been fresh interest in the topic of behavioural innovation in animals, fuelled by numerous reports of novel behaviour patterns spreading rapidly through animal populations (Reader & Laland 2003). Innovations may enable organisms to cope with environmental change and challenging conditions (e.g. Kawai 1965; Rogers 2003; Sol et al. 2005), but may also indicate creativity in unchanged conditions (Reader & Laland 2003). Upon their initiation by one individual, or a few individuals, behavioural innovations can rapidly spread by social learning (Lefebvre & Palameta 1988; Reader 2004)

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and can potentially lead to the establishment of cultural variation across populations (e.g. Whiten et al. 1999; van Schaik et al. 2003). Behavioural innovations are an important source of phenotypic plasticity in animals, with potentially significant ecological and evolutionary consequences (Nicolakakis et al. 2003; Reader & Laland 2003). However, the factors influencing the origin and spread of novel learned behaviour patterns remain poorly understood.

Thus far, both theoretical (e.g. Cavalli-Sforza & Feldman 1981; Boyd & Richerson 1985) and empirical (e.g. Lefebvre 1986; Reader & Laland 2000) studies on the diffusion of innovations have focused primarily on population-level patterns. For instance, such studies have addressed the hypothesis that a sigmoid curve can describe the increase in the number of adopters of innovations in a population (reviewed in: Lefebvre 1995a, b; Reader 2004). However, a finer-grained understanding of the temporal and spatial patterns of spread requires knowledge of population members' characteristics and the social interactions that lead

particular individuals to adopt the trait at particular times, factors that have rarely been addressed in animals (but see Giraldeau & Lefebvre 1987).

Here we relate the diffusion dynamics of foraging innovations, elicited in groups of captive animals, to several individual and group characteristics. Group characteristics include association patterns, which may determine the routes of spread of innovations if individuals differentially learn from close associates (Coussi-Korbel & Fragaszy 1995). We also focus on social rank orders, important if dominants monopolize new resources and/or impede subordinates' performance (Langen 1996; Drea & Wallen 1999), or if subordinates need to use novel foods because of a lack of success at obtaining familiar foods (Reader & Laland 2001). In addition, we consider individual characteristics such as novelty responses, which might affect the latency with which individuals exploit novel resources or address new problems (Webster & Lefebvre 2001; Greenberg 2003). Finally, we explore the predictive power of asocial learning performance, measured in isolation, where we might expect that good learners would acquire innovations before poor learners (Reader & Laland 2003; Kendal et al. 2007). Unlike previous studies, we consider these potential predictors simultaneously, while conducting controlled and replicated diffusion experiments in the laboratory. The data thus collected allow us to draw inferences about the likelihood that social learning is involved in the spread of the solutions to novel foraging tasks.

We studied the origin and spread of novel foraging behaviour in wild-caught starlings, *Sturnus vulgaris*, by presenting small groups of birds with novel tasks in the form of puzzle boxes to solve to gain access to a desired food. The starling is a gregarious bird species that shows a relatively high rate of foraging innovation in the wild (Lefebvre et al. 1997). Social interactions may affect the spread of foraging innovations in starlings; others have shown that starlings monitor conspecific behaviour while foraging (Templeton & Giraldeau 1996; Fernández-Juricic et al. 2005) and learn novel extractive foraging tasks from conspecifics in the laboratory (Templeton 1998; Campbell et al. 1999; Fawcett et al. 2002). The strength of associations between male starlings correlated positively with the extent to which they shared songs in captivity (Hausberger et al. 1995) and dominance rank influenced individuals' positions in wild starling roosts (Summers et al. 1987), suggesting that association patterns and social rank orders might also affect the diffusion dynamics of foraging innovations.

Previously we determined the agonistic rank orders (based on the outcome of agonistic encounters) and competitive rank orders (based on priority of access to limited resources) for each of three groups of five male wild-caught starlings (Boogert et al. 2006). We also tested each starling in isolation on its latency to feed in a novel environment, its latency to feed next to a series of novel objects as compared to its control latency to feed ('object neophobia'), and its latency to solve an extractive foraging task ('asocial learning performance'). We found that the fastest asocial learners dominated others in competition over desirable resources within the group and that fast

asocial learning correlated positively with the speed with which isolated individuals began feeding in a novel environment.

The present study presents novel extractive foraging tasks to the same groups of captive starlings. We use the data on social rank orders, novelty responses and asocial learning performance reported by Boogert et al. (2006) to determine whether these factors correlate with the origin and spread of the foraging innovations. We add measurement of each starling group's association pattern to the candidate predictors described in Boogert et al. (2006). We then test for relations between the previously determined association patterns, social rank orders, novelty responses and asocial learning performances on the one hand, and the probability and latency with which individuals contacted and solved these novel tasks on the other.

METHODS

Subjects and Apparatus

Subjects were 15 adult male starlings, organized into three groups of five. Boogert et al. (2006) provide details on the starlings' capture, the housing conditions, the methods adopted to determine social rank orders, novelty responses and asocial learning performance, the statistics of the correlations between these variables and an ethical note. Figure 1 describes the six novel extractive foraging tasks used in the diffusion studies.

Procedure

For each group, we spent 5 days determining social rank orders and association patterns, followed by 14–21 days of individual tests and 14 days of diffusion studies. We conducted the experiment in three sequentially performed replicates, one for each group. One day before the start of each replicate, we transferred the starling group to be studied to another room to avoid visual and/or acoustic interactions with the two other groups during tests. We returned the studied group to the housing room after completion of each experiment. We gathered all data directly on datasheets without the use of audiovisual equipment. Below, we describe how we constructed the association patterns and conducted the diffusion studies.

Association patterns

Over 5 days, we focal sampled each starling twice daily, at 1100–1130 and 1530–1600 hours (Martin & Bateson 1993). Every 30 s for 5 min we scored the focal individual's location in the cage (i.e. left/right and back/front within each of six parts of the cage: the left and right halves of the upper, middle and lower thirds), the identity of its nearest neighbour and the relative distance (close = within pecking distance, medium = in the same 1/6th volume of the cage, or far = in another 1/6th volume of the cage) to its nearest neighbour. We randomized the order of focal birds across days.

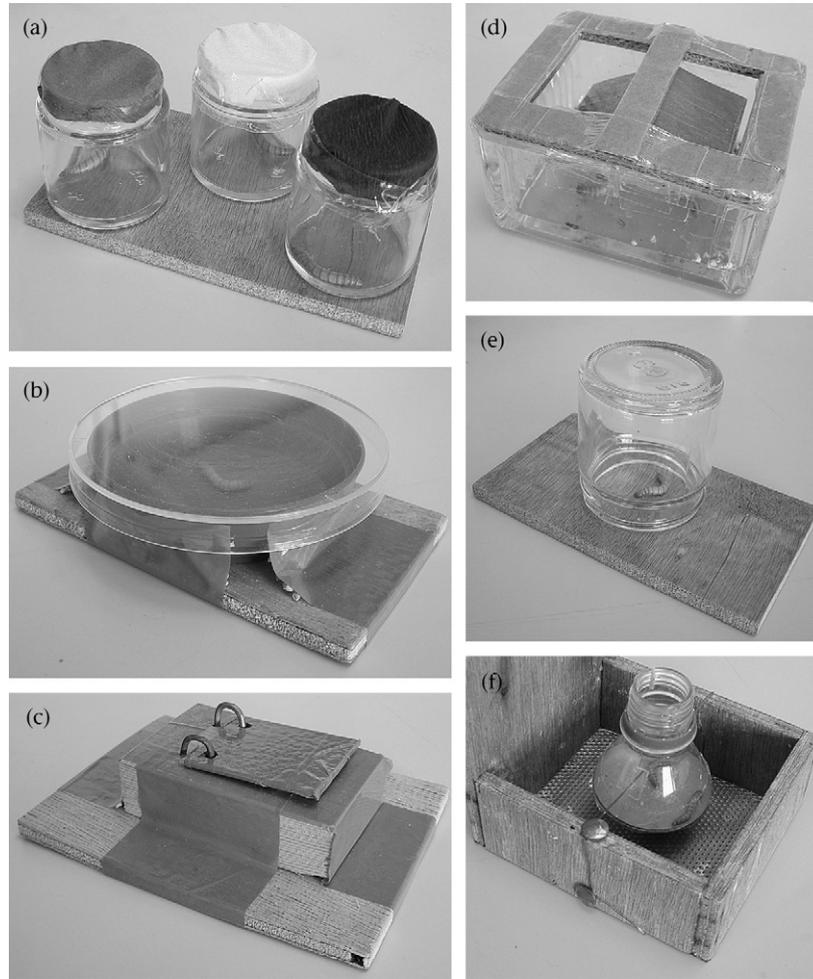


Figure 1. Extractive foraging tasks used in diffusion studies 1–6. (a) Three transparent glass jars (diameter 4 cm, height 4.6 cm) were taped to a wooden plate ($8 \times 11.5 \times 0.5$ cm high); each jar contained one mealworm; openings of the three jars were covered with brown, white and green paper, respectively. Subjects had to pierce the paper to reach the mealworm in the jar. (b) A brown plastic flowerpot saucer (diameter 7.9 cm, height 2 cm) was taped to wooden plate ($8 \times 11.5 \times 0.5$ cm high); the saucer contained one mealworm and was covered with a transparent petri dish lid (diameter 9 cm, height 0.9 cm). Subjects had to peck the lid upwards, off saucer, to reach the mealworm. Although this diffusion task superficially resembled the individual learning task in Boogert et al. (2006), distinct behaviour patterns (pecking upwards versus pecking to the side, respectively) were required to open the two tasks. (c) A wooden block ($4.5 \times 7 \times 2.2$ cm high) was taped to a wooden plate ($8 \times 11.5 \times 0.5$ cm high); the block contained a conical bore-hole with one mealworm; the bore-hole was covered with a brown synthetic lid (3.4×4.3 cm); the lid was attached to the block with two iron hinges. Subjects had to peck the lid upwards to reach the mealworm. (d) A transparent glass container ($7 \times 9 \times 4.4$ cm high) was covered with a piece of cardboard with two holes (2.5×4.3 cm) that provided access to blue and red cardboard pendulum doors with three mealworm halves underneath. Subjects had to peck one of the two pendulum doors downwards to reach the mealworms. (e) A wooden plate ($8 \times 11.5 \times 0.5$ cm high) with one mealworm on top; the mealworm was covered with an inverted transparent glass jar (diameter 5 cm, height 5.2 cm). Subjects had to peck the jar over to reach the mealworm. (f) A transparent plastic bottle (diameter bottle neck 2.3 cm, height 6.4 cm) with a cardboard bottom (diameter 5.6 cm) to which a 2 pence coin was taped to provide counterweight; the bottle was suspended using a synthetic wire; the wire was attached to the short sides of a wooden frame bird feeder ($11 \times 12.8 \times 4.5$ cm) and made rotation of the bottle possible; the bottle contained two mealworms. Subjects had to peck the bottle over so that the mealworms fell out of the bottle and within reach of the subject.

Diffusion studies

We presented each starling group with six different novel extractive foraging tasks sequentially (Fig. 1). Each task, presented repeatedly over 1–2 days, represented one diffusion study. On each diffusion study day, we deprived the starling group of food from 0800 to 0930 hours. We then distributed five identical novel extractive foraging task apparatuses (i.e. one per bird, to reduce monopolization) over the cage floor. For each diffusion study, each of the five apparatuses contained the same number of mealworms: each apparatus

contained one mealworm in diffusion studies 1, 2, 3 and 5, 1.5 mealworms in study 4 and two mealworms in study 6. The apparatuses had the same positions on the cage floor across all six diffusion studies. We recorded all birds' contacts with, and solutions of, the tasks, the latter defined as successfully accessing a mealworm. When the starlings solved all tasks within the 45 min of a trial, we removed the apparatuses, refilled them with mealworms and presented them again on the cage floor. We assumed that individuals were habituated to the type of human interference

required to replenish the apparatuses during the trials; the same experimenter (N.J.B.) had fed the birds daily for the 6 months prior to the diffusion studies.

We finished a diffusion study when (1) all birds had solved the task, (2) the proficiency of some individuals in solving the tasks and their monopolization of the rewards made it impossible for the nonsolvers to approach and attempt to solve the tasks for the duration of a trial or (3) no birds approached the tasks within two consecutive trials. We separated trials by 90 min intervals in which we removed the apparatuses. The number of trials ranged from two to five (median three) for the six diffusion studies in the three starling groups.

Each test day ended between 1700 and 1800 hours and starlings could feed until 0800 hours the next diffusion study day (lights off at 2100 hours, on at 0700 hours). When presented with food ad libitum after the final trial of a test day, starlings always started to feed immediately (personal observation). Satiation is thus unlikely to have affected birds' performances in the diffusion studies.

Analyses

Our aim was to determine which of the previously measured behavioural variables (i.e. association patterns, social rank orders, novelty responses, asocial learning performance) predicted the first contactors/solvers and the subsequent spread of contacting/solving through the groups. However, we cannot make any claims about causal relationships here, as we did not experimentally manipulate our putative predictors, and our data are inappropriate for statistical procedures such as causal path modelling (e.g. Shipley 2000). Instead, we explored the presence of correlations and the predictive value of association patterns, social rank orders, novelty responses and asocial learning performance with linear regression models. Our use of linear models is consistent with statistical authorities' guidelines (e.g. McConway et al. 1999); one can predict responses for future individuals from values of their explanatory variables by using the relationships currently observed to exist between response and explanatory variables. We conducted all analyses using R (R Development Core Team 2006). We fitted linear mixed models (LMM) using the nlme package (Pinheiro et al. 2006) and generalized linear mixed models (GLMM) using the glmmPQL function of the MASS package (Venables & Ripley 2002).

Association patterns

For each group, we constructed an association pattern by computing the association strengths for all possible dyads ($N = 10$). We computed association strengths by averaging the number of observations in which the focal bird of each dyad was in close proximity (i.e. within pecking distance) to the other bird in the dyad (Hausberger et al. 1995). Whenever two birds sat within pecking distance to each other on the same location for two or more successive 30 s focal observations, we treated this association as a single datum to correct for nonindependence.

We addressed the observed pathway by which contact or solution of a task spread through the group for each

group and task. We summed the previously determined association strengths for each 'pairwise interaction' along the chain of contacting/solving birds. Note that we did not observe these pairwise interactions as such; we inferred them from the order in which birds contacted and solved. We computed this value for each diffusion, then summed values across groups and tasks to obtain a single overall metric for path strengths of contacting and a single overall metric for solving. We generated a sampling distribution of path strengths to estimate the likelihood of such path strengths arising through chance. We drew the first and all subsequent contactors/solvers at random, 1000 times, and summed them as above. In each case, we restricted the number of contactors/solvers to the number observed for that group/task in the actual data. This analysis assumes that social learning occurs along a linear pathway ($A \rightarrow B \rightarrow C$ etc), whereas, in theory, naïve individuals could learn from any informed individual. We therefore generated a second path strength metric and associated sampling distribution that used the average association of each target learner with all informed individuals, at that time, in that group, for that task. In each case we compared the observed path strength with the associated random sampling distribution, rejecting the null hypothesis of a random pathway if the observed path strength metric was in a tail ($\alpha = 0.025$) of the distribution.

Origin of contacting and solving

For each bird we summed the number of diffusion studies in which it was the first of its group to (1) contact ('first contactors') or (2) solve the tasks ('first solvers'). When multiple birds started to contact or solve tasks at approximately the same moment (within ca. 2 s), we assigned them tied ranks. We natural log transformed scores for the first contactors as these were not normally distributed. We used Z scores to convert each bird's first contactor and first solver data into the number of standard deviations from its group's mean. We then analysed the data for the three starling groups together. We ran linear mixed models with group as a random effect and agonistic rank, competitive rank, latency to feed in a novel environment, object neophobia and asocial learning performance as fixed effects. We assessed which of these fixed effects significantly correlated with the number of diffusion studies in which each bird was the first of its group to contact and/or solve the tasks. We used backward selection to obtain the minimal adequate model with a selection criterion of $\alpha = 0.05$. Asocial learning performance and competitive rank were collinear with respect to these response variables. Where either of these predictor variables was significant in the model, we explored the effect of forced replacement of it with the other.

Spread of contacting and solving

We used linear mixed models to determine whether social rank orders, novelty responses and/or (a)social learning correlated significantly with the latencies with which birds contacted and solved the tasks. For each group, we omitted the data of the first contactors and first

solvers to examine the subsequent spread of contacting and solving among the rest of the group. If individuals only contacted or solved a task after the first trial, their contacting/solving latency was the cumulative time, summed across trials, up to the point in time at which they contacted/solved. We analysed the data for the three starling groups together by running linear mixed models that incorporated bird nested within group as random effects. We included agonistic rank, competitive rank, latency to feed in a novel environment, object neophobia, asocial learning performance and task as fixed effects. We used backward selection to obtain a model with fixed effects statistically significant at $\alpha = 0.05$.

We inferred the likelihood that social learning influenced the diffusion dynamics of innovations by examining the relation between contact latency and solving duration. We defined solving duration as latency to solve minus latency to contact (Day 2003). We computed solving durations for all birds (including the first contactors) for all diffusion studies and analysed them for the three starling groups together. We ran a generalized linear mixed model on solving durations to accommodate the nonlinear distribution of these data. We used the same random and fixed effects as for the linear mixed models of the spread of contacting/solving described above but added contact latency as a fixed effect. A negative correlation between contact latency and solving duration could suggest that individuals later in the diffusion benefited from increased opportunities to observe groupmates' demonstrations of the task solution by reducing the time that these 'observers' required to learn how to solve the task (Day 2003). To validate interpretation of this relationship as indicative of social learning, we repeated the analysis on data of the same individuals when tested in isolation on an extractive foraging task (i.e. the individual learning test in Boogert et al. 2006). Birds in the individual learning test could not profit from observing others, so obviously social learning could not have influenced their asocial learning test performance. However, if we were to find a negative correlation between latency to contact and solving duration for the individual learning test, in addition to the diffusion studies, it would suggest that this relationship could arise through entirely asocial processes. Under such circumstances we could not claim that this negative association indicated some specifically social learning process in the diffusion study data.

RESULTS

General Information

In five of the 18 diffusion studies (three groups \times six tasks), all birds solved the tasks. In one diffusion study, no birds approached the tasks within two consecutive 45 min trials. In 14 of the 18 diffusions, three or more individuals solved the task. We designed the diffusion tasks to minimize opportunities to exploit others' food discoveries (i.e. to 'scrounge'; Barnard & Sibly 1981): tasks 1–3 and 5 contained a single mealworm, while the solvable

parts of tasks 4 and 6, containing 1.5 and two mealworms, respectively, swung back to their original positions after the solver had acquired a reward (see Table 1). We rarely observed food stealing, as most solvers acquired such great proficiency and speed at obtaining the food reward that groupmates were usually too slow in their attempts to scrounge. Indeed, in 12 of the 18 diffusions, the one to three solvers became so proficient that the nonsolvers did not get the chance to approach and attempt to solve a rewarding task apparatus.

First Contactors and First Solvers

Object neophobia correlated most strongly with the total number of studies in which a bird was the first of its group to contact the novel tasks (Table 1). Less neophobic birds were first contactors more frequently than were more neophobic birds. Competitive rank was also a significant variable in the minimal adequate model of first contactors, with dominant birds tending to contact the task first (Table 1). When we forced asocial learning performance into the model, competitive rank was no longer a significant predictor of first contactors (LMM: $t_9 = 1.22$, $P = 0.255$), illustrating their collinearity. When we removed competitive rank from the model, asocial learning performance approached significance as a predictor of the number of times that a bird was a first contactor

Table 1. Results of a linear mixed model analysis showing significant (minimal adequate model) and nonsignificant (nonsignificant fixed effects) predictor variables for the number of times that a bird was first contactor/solver

| <i>First contactor</i> | Effect \pm SE | <i>t</i> | <i>df</i> | <i>P</i> |
|-------------------------------------|-----------------------|----------|-----------|----------|
| <i>Minimal adequate model</i> | | | | |
| Object neophobia | -0.54 ± 0.18 | 3.07 | 10 | 0.012 |
| Competitive rank | -0.31 ± 0.12 | 2.65 | 10 | 0.025 |
| <i>Nonsignificant fixed effects</i> | | | | |
| Novel environment | | 0.35 | 9 | 0.732 |
| Agonistic rank | | 0.09 | 9 | 0.930 |
| Asocial learning | | 0.01 | 9 | 0.991 |
| <i>Random effects</i> | | | | |
| SD | | | | |
| Group | 1.06×10^{-5} | | | |
| Residual | 0.63 | | | |
| <i>First solver</i> | | | | |
| Effect \pm SE | | | | |
| <i>Minimal adequate model</i> | | | | |
| Asocial learning | -0.81 ± 0.14 | 5.98 | 10 | <0.001 |
| Agonistic rank | -0.08 ± 0.03 | 3.26 | 10 | 0.009 |
| <i>Nonsignificant fixed effects</i> | | | | |
| Object neophobia | | 0.98 | 9 | 0.352 |
| Competitive rank | | 0.50 | 9 | 0.637 |
| Novel environment | | 0.34 | 9 | 0.745 |
| <i>Random effects</i> | | | | |
| SD | | | | |
| Group | 7.81×10^{-6} | | | |
| Residual | 0.47 | | | |

Nonsignificant fixed effects were added individually to the minimal adequate model. We transformed the response variable to group-wise Z scores for each bird and we analysed these Z scores for the three groups together. We used backward selection to identify a model that retained only the fixed effects that were statistically significant at $\alpha = 0.05$. Both models contained group as a random effect.

($t_{10} = 2.18$, $P = 0.054$). Because of this collinearity between explanatory variables we cannot be sure of the exact causal relationship. Nevertheless, competitive rank predicted first contactors better than did asocial learning performance (Akaike information criterion, AIC = 41.74 versus 42.34).

The total number of studies in which a bird was the first to solve the tasks correlated most strongly with asocial learning performance (Table 1). The faster a bird solved an asocial learning task in isolation, the more often it was the first solver during the diffusion studies. Agonistic rank also significantly predicted the number of studies in which a bird was the first to solve the tasks (Table 1). Competitive rank was a significant predictor of first solvers when asocial learning performance was absent from the model (LMM: $t_{10} = 3.78$, $P = 0.0036$) but was not significant when we included asocial learning performance ($t_9 = 0.50$, $P = 0.63$). Conversely, asocial learning performance remained a significant fixed effect when we forced competitive rank into the model of first solvers ($t_9 = 3.06$, $P = 0.013$). This suggests that competitive rank was only indirectly related to the number of studies in which a bird was the first to solve the tasks, through its relation with asocial learning performance.

Subsequent Spread of Contacting and Solving

Association patterns

Figure 2 shows association patterns constructed from the association strengths of all dyads within each group. We found that, regardless of whether we used a linear or averaging path strength metric, the orders in which individuals contacted and solved the tasks did not differ from that expected by random path generation (contact order: linear metric: $P = 0.19$; averaging metric: $P = 0.68$; solving order: linear metric: $P = 0.36$; averaging metric: $P = 0.14$).

Social rank orders, novelty responses and asocial learning

The latency with which the groupmates of the first contactor contacted the tasks was significantly correlated with their latency to feed in a novel environment (see

Table 2): individuals that were faster to feed in a novel environment in isolation were also faster to contact the novel foraging tasks in the group's diffusion studies. In contrast, social rank orders, novelty responses and asocial learning performance were not significantly correlated with the order in which the groupmates of the first solver solved the tasks (see Table 2).

Solving duration

Contact latency was significantly and negatively correlated with solving duration (latency to solve – latency to contact): individuals that took longer to contact the tasks required less time to solve them (Table 2). Contact latency was the only variable significantly correlated with solving duration, and remained so even when we forced asocial learning into the minimal adequate model (GLMM: $t_{46} = 2.76$, $P = 0.0083$). In contrast, the same birds, when given an asocial learning task in isolation, exhibited a significant *positive* relationship between contact latency and solving duration (Spearman rank correlation: $r_s = 0.67$, $N = 15$, $P = 0.006$). Our finding that contact latency and solving duration were negatively correlated only in the social context of the diffusion studies supports interpretation of this result as indicative of social learning.

DISCUSSION

Our findings suggest that both individual and group-dependent behavioural variables can predict the first individual in a group to interact with and solve novel foraging problems. Within starling groups, the birds that contacted novel extractive foraging tasks first were those least hesitant to feed next to novel objects when tested in isolation. Similarly, the first birds to solve the tasks were those that performed best in an asocial learning test in isolation. Naturally, these findings are preliminary and must be interpreted with caution, given the correlational nature of the study, and we cannot rule out that unconsidered covariates account for the variation. Nevertheless, these observed relationships are encouraging, since our methods may be widely applicable to investigate diffusion dynamics in a broad range of taxa. With our

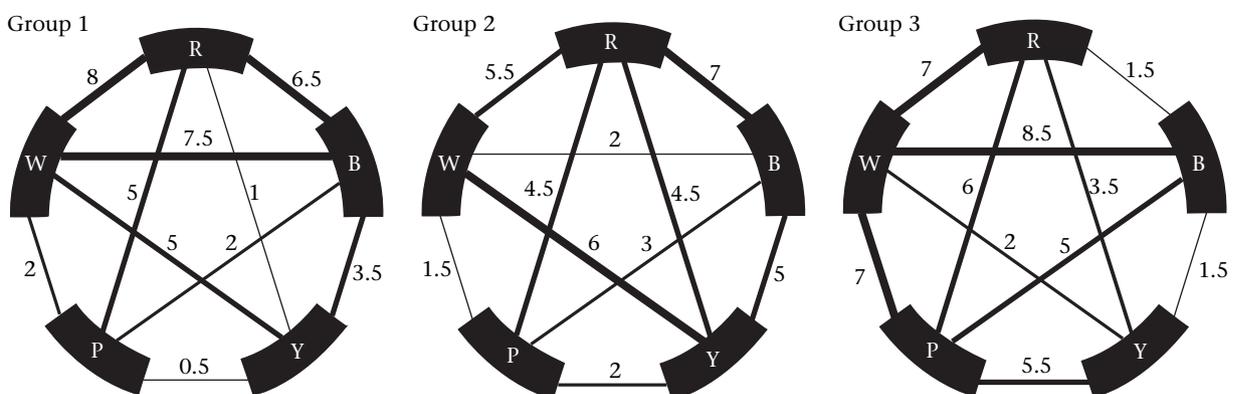


Figure 2. Association patterns for starling groups 1–3. Boxed letters indicate the birds' leg band colours. Lines represent associations between individuals, with numbers and concomitant line thicknesses indicating the strengths of the associations (measured as the mean number of observations in which birds were in close proximity) for all possible dyads. We chose topography of boxed letters and line lengths at random.

Table 2. Results of linear mixed model analyses showing significant (minimal adequate model) and nonsignificant (nonsignificant fixed effects) predictor variables for latency to contact/solve the six diffusion tasks and results of a generalized linear mixed model analysis for solving duration (i.e. latency to solve – latency to contact)

| | Latency to contact* | | | | | Latency to solve† | | | | | Solving duration | | | | | |
|-------------------------------------|---|--------|----------|-----------|----------|-------------------|--------|----------|-----------|----------|---------------------------|---------|----------|-----------|----------|--|
| <i>Minimal adequate model</i> | <i>Latency to feed in a novel environment</i> | | | | | <i>Task</i> | | | | | <i>Latency to contact</i> | | | | | |
| | Effect | SE | <i>t</i> | <i>df</i> | <i>P</i> | Effect | SE | <i>t</i> | <i>df</i> | <i>P</i> | Effect | SE | <i>t</i> | <i>df</i> | <i>P</i> | |
| | 312.38 | 131.33 | 2.38 | 11 | 0.037 | 386.92 | 174.32 | 2.22 | 30 | 0.034 | –2.08e–04 | 7.9e–05 | 2.63 | 46 | 0.012 | |
| <i>Nonsignificant fixed effects</i> | | | | | | | | | | | | | | | | |
| Agonistic rank | 29.89 | 51.92 | 0.58 | 10 | 0.578 | –50.87 | 62.64 | 0.81 | 10 | 0.436 | –4.6e–03 | 0.03 | 0.15 | 11 | 0.863 | |
| Competitive rank | 22.58 | 190.40 | 0.12 | 10 | 0.908 | 190.15 | 245.67 | 0.77 | 10 | 0.457 | 0.06 | 0.10 | 0.60 | 11 | 0.557 | |
| Feeding in novel environment | | | | | | –5.71 | 165.16 | 0.04 | 10 | 0.973 | 0.02 | 0.07 | 0.29 | 11 | 0.810 | |
| Object neophobia | 265.94 | 275.00 | 0.97 | 10 | 0.356 | –363.15 | 326.00 | 1.11 | 10 | 0.291 | 4.96e–03 | 0.14 | 0.04 | 11 | 0.973 | |
| Asocial learning | –86.28 | 307.31 | 0.28 | 10 | 0.785 | 377.54 | 355.76 | 0.89 | 10 | 0.314 | 0.17 | 0.15 | 1.13 | 11 | 0.277 | |
| Task | 120.79 | 135.68 | 0.89 | 53 | 0.377 | | | | | | 0.14 | 0.08 | 1.75 | 45 | 0.100 | |
| <i>Random effects (SD)</i> | | | | | | | | | | | | | | | | |
| Group | 1429.69 | | | | | 895.72 | | | | | 1.19e–09 | | | | | |
| Bird nested within group | 0.17 | | | | | 558.60 | | | | | 4.07e–05 | | | | | |
| Residual | 1929.28 | | | | | 1704.03 | | | | | 41.46 | | | | | |

We included latency to contact as a fixed effect in the model for solving duration, but otherwise used the same fixed effects as in the models for latency to contact/solve. For all analyses, we first fitted a model that included all fixed effects, then used backward selection with a significance criterion of $\alpha = 0.05$. All models contained a random effects structure with bird nested within group to represent our hierarchical study design.

*Excludes first contactor in each diffusion study per group.

†Excludes first solver in each diffusion study per group.

approach, one could identify potential predictor variables and subject them to more direct experimental investigation. For example, one could systematically vary group composition to determine which combinations of traits or individuals facilitate or impede the initiation and spread of innovations.

Most strikingly, our findings raise the possibility that problem-solving propensities are relatively consistent across asocial and social contexts. Apparently, the presence of groupmates did not inhibit the first contactors/solvers from performing in a manner similar to that outside the group. These first contactors and first solvers were of high competitive rank, as they monopolized familiar desired resources (mealworms and bathing water) in our previous social rank assessments (Boogert et al. 2006). These results contrast with findings in primates, fish and birds that suggest low rank may correlate positively with problem solving or innovation frequency (Laland & Reader 1999; Reader & Laland 2001, 2003). Several factors may explain the greater propensity of dominants to innovate within the groups in our study compared to that in previous studies. For example, the visibility of food rewards in the transparent diffusion study tasks meant that birds did not need to explore the objects to see the rewards. Such object exploration may be more frequent in lower-ranking individuals who are driven to explore by need (Reader & Laland 2003). In addition, regular and easily obtainable food sources were absent.

While we cannot directly determine the extent to which social learning affected the spread of contacting and solving in the first place, we can draw inferences from statistical analyses. We found a significant negative relationship between contact latency and solving duration in the diffusions. Conversely, in an asocial learning test of the same individuals, contact latency and solving duration showed a significant positive correlation. We would predict a negative correlation in the asocial test if the time available to view the tasks before attempting them facilitated faster solving. These results suggest that in the diffusions, individuals that took longer to contact the tasks benefited from increased opportunities to observe groupmates' demonstrations of the task solutions, thereby reducing the time they required to solve the task (Day 2003). This implies that social learning underlies the diffusions, and the data are consistent with a range of psychological mechanisms of social learning, including local and stimulus enhancement and imitation (Heyes 1994).

To reinforce the case for social learning, researchers could measure social learning performance outside the group by adopting the traditional experimental set-up of a subject observing a single demonstrator performing an unfamiliar task solution (Lefebvre & Palameta 1988; Bouchard et al. 2007). Future experiments could then assess the predictive value of individuals' social learning performance outside the group for the diffusion dynamics of innovations within the group. In addition, birds that do not solve the tasks during the diffusion studies could be tested again in isolation. In principle, these individuals may learn the tasks' solutions but be inhibited from performing by the first solvers' monopolization of the task rewards.

The negative association between contact latency and solving duration provides evidence for social learning within the groups, but the patterns of spread of contacting and solving the novel foraging tasks did not match prior association patterns. Collectively, these findings suggest that individuals learned task solutions from any member of their group, rather than disproportionately from close associates. Conceivably, individual starlings may not have attended disproportionately to the feeding behaviour of the starlings with which they associated most frequently prior to the diffusion studies. Animals may have different patterns of association during and outside of feeding times. The failure to observe a relationship between association patterns and the spread of contacting and solving tasks may also have reflected the small size of the starling groups, in which each bird was familiar with all other birds. In addition, perhaps the small spatial scale of the enclosure, compared to a natural setting, effectively meant that all birds were continuously in relatively close proximity to each other. Larger groups studied in more spacious environments may provide greater sensitivity to the relationship between association patterns and spread of learned information. Association patterns measured in a similar experimental set-up did influence starlings' vocal learning: in captive groups, the extent to which males shared songs reflected the extent of social associations between them (Hausberger et al. 1995). However, the relationship between vocal and other forms of social learning remains to be established (Heyes & Saggerson 2002). Our findings may encourage students of animal social networks to verify the common assumption that spatial proximity is likely to result in enhanced information transmission (Croft et al. 2004, 2005).

Contact latencies of first contactors' groupmates correlated significantly with the latency with which these individuals had fed in a novel environment in isolation. As we conducted the diffusion studies in an environment familiar to the starlings, this finding suggests that 'latency to feed in a novel environment' is related to, or indicative of, a context-general behavioural process (e.g. vigilance, stress) that may affect birds' performance under a variety of circumstances (Boogert et al. 2006). Together with the finding that object neophobia and asocial learning performance predicted the number of occasions an individual was first contactor and first solver, respectively, these results are consistent with the notion of a behavioural syndrome of covarying traits, with individual differences in particular traits being stable across situations (Sih et al. 2004; Réale et al. 2007). None of the predictor variables correlated with the order in which the first solvers' groupmates solved the diffusion study tasks. However, our small sample size warrants caution in interpreting negative findings; we may have detected additional correlates of diffusion dynamics with more subjects at our disposal and with greater statistical power.

Finally, we encourage future studies to manipulate potential explanatory variables of the diffusion dynamics of innovations and to assess their predictive value directly. In this study, initiations and diffusions of innovations were not linked to association patterns, but did show a strong correlation with previously determined measures

of asocial learning performance, social rank and neophobia. Our findings thus support the view that innovations do not originate and spread randomly through animal populations (Coussi-Korbel & Frigaszy 1995).

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