ANIMAL BEHAVIOUR, 2008, **75**, 1509–1518
doi:10.1016/j.anbehav.2007.09.033

The origin and spread of innovations in starlings

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*(Received 5 October 2006; initial acceptance 30 November 2006;
final acceptance 25 September 2007; published online 3 March 2008; MS. number: A10582R)*

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.

Keywords: diffusion dynamics; dominance; foraging; group; innovation; neophobia; social learning; social network; starling; *Sturnus vulgaris*

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) 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

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0003–3472/08/$34.00/0

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.