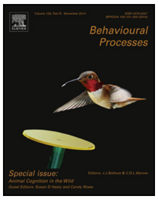
Behavioural Processes 109 (2014) 135–144

Contents lists available at ScienceDirect

Behavioural Processes

journal homepage: www.elsevier.com/locate/behavproc



Perching but not foraging networks predict the spread of novel foraging skills in starlings

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ARTICLE INFO

Article history:
Received 3 May 2014
Received in revised form 1 August 2014
Accepted 19 August 2014
Available online 29 August 2014

Keywords:
Dominance
Foraging
Network-based diffusion analysis
NBDA
Social learning
Starlings

ABSTRACT

The directed social learning hypothesis suggests that information does not spread evenly through animal groups, but rather individual characteristics and patterns of physical proximity guide the social transmission of information along specific pathways. Network-based diffusion analysis (NBDA) allows researchers to test whether information spreads following a social network. However, the explanatory power of different social networks has rarely been compared, and current models do not easily accommodate random effects (e.g. allowing for individuals within groups to correlate in their asocial solving rates). We tested whether the spread of two novel foraging skills through captive starling groups was affected by individual- and group-level random and fixed effects (i.e. sex, age, body condition, dominance rank and demonstrator status) and perching or foraging networks. We extended NBDA to include random effects and conducted model discrimination in a Bayesian context. We found that social learning increased the rate at which birds acquired the novel foraging task solutions by 6.67 times, and acquiring one of the two novel foraging task solutions facilitated the asocial acquisition of the other. Surprisingly, the spread of task solutions followed the perching rather than the foraging social network. Upon acquiring a task solution, foraging performance was facilitated by the presence of group mates. Our results highlight the importance of considering more than one social network when predicting the spread of information through animal groups. This article is part of a Special Issue entitled: Cognition in the wild.

1. Introduction

Recent years have seen an explosion of both scientific and public interest in animal innovation and social learning. The behavioural innovations of one individual can rapidly spread through a group of animals through social learning, leading to the establishment of cultural variation across populations (Allen et al., 2013; Hoppitt and Laland, 2013). Social learning allows, for example, vervet monkeys to avoid toxic food (Van de Waal et al., 2013), meerkat pups to eat scorpions (Thornton and McAuliffe, 2006), warblers to mob nest-parasitic cuckoos (Davies and Welbergen, 2009), and children to solve complex puzzle boxes (Dean et al., 2012). The origin and social transmission of information thus have major ecological and evolutionary consequences (Avital and Jablonka, 2000; Hoppitt and Laland, 2013).

Historically, animal social learning was studied primarily by testing whether relatively artificial behaviour patterns could be transferred between demonstrator–observer dyads confined to small enclosures in captivity, often with the objective of seeking to establish whether animals were capable of human-like imitation (Galef, 1988; Whiten and Ham, 1992; Hoppitt and Laland, 2013). However, recent advances in statistical tools now allow researchers to identify social learning when it occurs in more naturalistic social settings in captivity and in animal populations in the wild (Franz and Nunn, 2009; Hoppitt et al., 2012; Hoppitt and Laland, 2013). Furthermore, these natural(istic) test conditions allow test subjects a free choice of whom to interact with, which in turn might affect whom they are most likely to copy.

Almost two decades ago, Coussi-Korbel and Fragaszy (1995) introduced the concept of “directed social learning”, which occurs when social information does not spread evenly through a group. Instead, demonstrator and observer characteristics, such as sex, age, and social rank, affect the salience of demonstrators to observers and the likelihood that social transmission of information occurs between them. Various studies on (semi-) natural

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http://dx.doi.org/10.1016/j.beproc.2014.08.016

animal groups have provided evidence for directed social learning (Hoppitt and Laland, 2013). For example, captive groups of chimpanzees exposed to two demonstrators copied the older, more dominant and previously successful model more than the younger, subordinate and experimentally naïve model (Horner et al., 2010). Although demonstrator characteristics did not appear to affect social learning tendencies in captive flocks of blue tits, subordinate males were more likely to acquire a novel foraging skill socially than were dominant males, and juvenile females were twice as likely to socially learn as compared to all other flock members (Aplin et al., 2013). Young female chimps spent more time watching their mothers and learned to fish for termites at an earlier age than young males (Lonsdorf et al., 2004). No sex differences in social learning were found in wild meerkats, but pups and juveniles were more likely than adults to join demonstrators and scrounge from them, and learned to obtain food from a novel foraging task as a result (Thornton and Malapert, 2009).

The latter study suggests that demonstrators' social tolerance of, and physical proximity to, naïve observers might affect the latters' access to information regarding novel foraging techniques. Coussi-Korbel and Fragaszy (1995) hypothesised that patterns of group members' physical proximity to each other in time and space would predict the pattern of information spread through the group, as well as the similarity to the demonstrator's behaviour achieved by the observer (Coussi-Korbel and Fragaszy, 1995). Researchers can now formally test this hypothesis using network-based diffusion analysis (NBDA), pioneered by Franz and Nunn (2009) and extended by Hoppitt et al. (2010a) and Nightingale et al. (2014). Using NBDA, novel foraging skills or novel foraging patch discoveries have been shown to spread following the social network in for example tits (Aplin et al., 2012), three-spined sticklebacks (Atton et al., 2012; Webster et al., 2013), squirrel monkeys (Claidière et al., 2013), and humpback whales (Allen et al., 2013). However, social networks did not predict the spread of information in captive starlings (Boogert et al., 2008), wild ring-tailed lemurs (Kendal et al., 2010) or redfronted lemurs (Schnoell and Fichtel, 2012).

One potential methodological reason that NBDA has generated negative findings is that researchers adopting NBDA have thus far always relied on a single social network in their analyses. Kendal et al. (2010) pointed out that it is crucial to use a social network that is relevant to the skill to be socially transmitted, and suggested that a foraging network might have predicted the spread of a novel foraging skill in wild ring-tailed lemur groups better than the non-foraging spatial proximity network adopted in their study (Kendal et al., 2010). Similarly, the studies by Boogert et al. (2008) and Schnoell and Fichtel (2012) each used a single social network based on physical proximity and affiliative interactions, respectively, to predict the spread of novel foraging task solutions, instead of a potentially more relevant foraging network. The suggestion that social networks constructed using different behavioural measures might not be strongly correlated was recently confirmed by a study on wild chacma baboons: Castles et al. (2014) compared five different social networks constructed from two interaction and three proximity sampling methods, and found them to be uncorrelated at both individual and network levels (Castles et al., 2014). However, to our knowledge no published study has compared the performance of different social networks in predicting the spread of novel foraging skills in animal groups. Furthermore, individual-level characteristics that might affect directed social learning, such as dominance, age and sex, have rarely been taken into account in NBDA until now.

In the present study, we tested which individual characteristics and social networks explained the patterns in which novel foraging skills spread through small groups of starlings held in captivity. We measured the foraging and perching networks, as well as the foraging and perching dominance ranks, for each of four starling groups composed of wild-caught juvenile and adult females and males. We then trained one subordinate and one dominant starling from each group to solve a novel foraging task using alternate actions and options. Once these demonstrators were trained, they and their group mates were presented with multiple replicates of the novel foraging task, and we scored who solved the task using which of the two task solutions, when and how. To analyse our data, we used our recent extension of NBDA (Nightingale et al., 2014) to incorporate individual and group-level random effects (i.e. allowing for the fact that individuals might be correlated in their rate of solving), alongside individual-level fixed effects (i.e. solvers' sex, age, body condition, social ranks) and performed model discrimination in a Bayesian context. Surprisingly, our results show that the spread of the novel foraging task solutions followed the perching rather than the foraging network, and individual characteristics did not seem to affect the diffusions.

2. Materials and methods

2.1. Subjects

Experimental subjects were 36 European starlings (*Sturnus vulgaris*), of which 13 were adult males, 13 were juvenile males (hatched in the year of catching) and 10 were juvenile females. We caught these starlings in Finstown on the Orkney Islands on October 1st 2011 using a clap net, and the lack of adult females in this single catch is likely to be random (wild starling flocks are not known to have obvious sex/age biases in composition). Upon capture, we recorded each starling's age (juvenile or adult), sex, weight and wing length, and fitted each bird with a unique British Trust for Ornithology metal ring. We transported birds to the University of St. Andrews on the day of capture. Upon arrival in St. Andrews, we gave each starling a unique combination of coloured plastic rings (A.C. Hughes), and randomly allocated it to one of four indoor enclosures, resulting in groups of 10, 9, 9 and 8 birds, respectively. Each enclosure measured 3 × 1.20 × 2.30 m and was fitted with full-spectrum fluorescent lights, sawdust and hay bedding, and a large bird bath (76 × 45 × 9 cm). Rope perches and branches spanned the length and height of the enclosure, respectively, and provided at least 7 m of perching space, allowing all birds to perch without being within pecking distance of each other. Softened high-protein dog kibble in 28 cm diameter saucers was available ad libitum except for the duration of the diffusion experimental trials (see below). Trays containing dried mealworms hidden in grit were provided regularly to encourage natural foraging behaviours. All food was presented on the floors of the enclosures. Enclosures were kept at 20 ± 1 °C with lights on at 0700 and off at 1900 h.

2.2. Association patterns

2.2.1. Foraging associations

We filmed each starling group for four days between November 22nd and December 3rd 2011. For each of these recording days we analysed 45 min of normal foraging activity by scoring the identity of the birds foraging and the time at which each individual's foraging bout started and ended. To create the foraging association matrix, we first summed the total amount of time that each pair of birds (e.g. birds i and j) was observed to be foraging simultaneously (F_{ij}). We then summed the total amount of time that each bird was foraging regardless of who else was foraging at the same time (F_{iT}). We created an asymmetric foraging association matrix **F**, in which the foraging association of bird i with bird j was F_{ij}/F_{iT}, which represents the proportion of i's foraging time spent in the foraging presence of j. Likewise, the foraging association of bird j with bird i was F_{ji}/F_{jT}.