SHORT COMMUNICATION

Independent appearance of an innovative feeding behaviour in Antillean bullfinches

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Abstract Behavioural innovations have been largely documented in birds and are thought to provide advantages in changing environments. However, the mechanisms by which behavioural innovations spread remain poorly known. Two major mechanisms are supposed to play a fundamental role: innovation diffusion by social learning and independent appearance of the same innovation in different individuals. Direct evidence for the independent emergence of the same innovation in different individuals is, however, lacking. Here, we show that a highly localized behavioural innovation previously observed in 2000 in Barbados, the opening of sugar packets by Loxigilla barbadensis bullfinches, persisted more than a decade later and had spread to a limited area around the initial site. More importantly, we found that the same innovation appeared independently in other, more distant, locations on the same island. On the island of St-Lucia, 145 km from Barbados, we also found that the sister species of the Barbados bullfinch, the Lesser Antillean bullfinch Loxigilla noctis developed the same innovation independently. Finally, we found that a third species, the Bananaquit Coereba flaveola, exploited the bullfinches' technical innovation to benefit from this new food source. Overall, our observations provide the first direct evidence of the independent

S. Ducatez and J. N. Audet contributed equally to the study.

S. Ducatez (⊠) · J. N. Audet · L. Lefebvre Department of Biology, McGill University, 1205, avenue Docteur Penfield, Montréal, Québec H3A 1B1, Canada e-mail: simon.ducatez@mail.mcgill.ca emergence of the same behavioural innovation in different individuals of the same species, but also in different species subjected to similar anthropogenic food availability.

Keywords Behavioural innovation · Cognition · Behavioural flexibility · Social learning · Barbados

Introduction

Innovations are novel behaviours that represent new solutions to ecological problems (Kummer and Goodall 1985), so that individuals/species exhibiting a higher innovation propensity are expected to be more likely to cope with new environmental conditions (Sol et al. 2005a). In this context, innovations are expected to be driven by environmental changes (Reader 2007; Ramsey et al. 2007) and many reported innovations are indeed responses to humaninduced environmental changes (Lefebvre et al. 1997, 2001; Reader and Laland 2002).

Despite the potential importance of innovations for conservation (McDougall et al. 2006) and evolutionary (Nicolakakis et al. 2003; Sol et al. 2005b) issues, the mechanisms leading to the spread of behavioural innovations remain poorly understood. Three mechanisms have been proposed: (1) independent appearance of the same innovation in different individuals; (2) social learning, that is, the diffusion of innovations through direct observation of innovative individuals by non-innovative ones; (3) natural shaping, when the action of an innovator on the environment subsequently favours individual learning by another individual without any direct contact between the innovator and the second individual (Galef 1992). Experiments on black-capped chickadees (Sherry and Galef 1984) and titmice (Kothbauer-Hellmann 1990) suggest that

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all three may have contributed to the classical case of milk bottle opening by Paridae in Britain and Ireland (Fisher and Hinde 1949; Hinde and Fisher 1951, 1972), but do not bring direct evidence of the independent emergence of behavioural innovations.

Distinguishing the relative importance of the three mechanisms can be challenging because of the difficulties of documenting the independent appearance of one particular innovation in the field. Current evidence for the independent origin of innovation is based on observations of the simultaneous emergence of the same innovation in distant places, but these observations do not rule out the possibility that it resulted from dispersal of innovators. Thompson et al. (1996) suggested that the appearance of a foraging innovation (nectar robbing) in territorial blue tits Parus caeruleus in two separate areas in Oxford was the result of different individuals independently adopting the same behaviour, but the hypothesis that innovators dispersed and transmitted the innovation from one area to the other could not be eliminated. Further evidence for multiple independent origins of an innovation was also provided, albeit indirectly, by Lefebvre's (Lefebvre 1995) re-analysis of Fisher and Hinde's (1949) data. The distance-by-time function for all areas where bottle opening was noticed suggested independent innovation by many birds rather than a cultural wave of advance from the site and date where the behaviour presumably originated. Still, those conclusions are based on indirectly inferred data, and no direct evidence for an independent innovation by different birds was brought in this case.

Direct evidence for the independent emergence of the same innovation in different areas is still lacking. Here, we follow up on a previously reported foraging innovation, the opening of sugar packets by Barbados bullfinches (now Loxigilla barbadensis, previously Loxigilla noctis) at a single site in Barbados (Reader et al. 2002). This innovation requires relatively complex motor skills, and only bullfinches were observed performing this task in Barbados, despite the presence of other opportunist species such as the Carib grackle Quiscalus lugubris on the island. Barbados bullfinches are thought to be largely territorial (Reader et al. 2002), although territory size and movements in this species are poorly known, and their life expectancy is estimated at 4 years (www.birdlife.org). We first investigated whether, more than a decade later, the behaviour still existed at the site where it was first seen and if it had spread around the initial site. We then enlarged the study zone to identify new areas where the same innovation could be potentially present. We took advantage of the observation of bullfinches opening sugar packets of a different colour at a new location (where this behaviour had not been previously recorded) to test whether these birds were interested in the sugar packets found at the initial location. If not, it would strongly suggest that the behaviour independently appeared at the two sites. Lesser Antillean bullfinches *L. noctis* living in St. Lucia, an island situated 145 km north-west of Barbados, were also opportunistically observed. This species is closely related to the Barbados bullfinch, the speciation dating from only $\sim 0.2-0.7$ m.y. ago (Buckley and Buckley 2004). Finally, we report exploitation by bananaquits *Coereba flaveola* of sugar packets previously opened by bullfinches, a case of interspecific scrounging.

Methods

Sites were examined between 25 February and 30 April 2012, which coincides with the main tourist season and thus with the peak of food availability for the very tame and opportunistic Barbados bullfinch around terraces and restaurants. Eleven sites were selected in the vicinity of the initial site of the Colony Club (see Fig. 1), where the sugar packet opening behaviour was initially noted in 2000. We focused on surrounding restaurant terraces, but also included one picnic area south of the Colony Club and two sites without anthropogenic food sources north of the Colony Club in order to pinpoint the area where the innovation might have spread. We also examined the nearest area north of the Colony Club where anthropogenic sources of sugar might be available (Royal Pavilion), which was ca. 1 km away (see Fig. 1). Each site was prospected once in the morning (between 8 and 10 a.m.) and once in the afternoon (between 4:30 and 6:30 p.m.) on different days. At each site, we placed six sugar packets within a radius of 5 m and observed from a distance of at least 2 m. We obtained sugar packets similar in colour (white) and design (6 by 4 cm) to those used at the Colony Club. Each observation lasted a maximum of 1 h when no sugar packet opening behaviour was observed. We also included one site situated more than 500 m from any restaurant terrace in order to test whether individuals less familiar with anthropogenic food sources would open sugar packets. At all sites, bullfinches came within 10 cm of at least one packet. We were not able to identify the sex of the birds as Barbados bullfinches are monomorphic (Buckley and Buckley 2004). Finally, we observed Lesser Antillean Bullfinches on the island of St. Lucia (145 km from Barbados) in the morning of 24 April 2012.

Results

Sugar packets were opened at three different sites in the immediate vicinity of the initial place (Colony Club) where the behaviour was first recorded in 2000 (Fig. 2a).

Fig. 2 a Barbados bullfinch

Barbados. b Male lesser Antillean bullfinch L. noctis

Chastanet, St. Lucia



Fig. 1 Sites prospected for sugar packet opening behaviour in Antillean bullfinches L. barbadensis and L. noctis



Bullfinches opened at the Colony Club terrace, the Heron Bay gap (north of the Colony Club) and the Coral Reef terrace (south of the Colony Club) (Fig. 1). On a fourth site, the Chattel Village, 1,200 m from the Colony Club, the birds did not attempt to open the white sugar packets we offered, but we observed them opening brown-coloured ones available on their tables. On the 5 sites situated between the Chattel Village and the Colony Club, bullfinches did not attempt to open sugar packets during our observations. The Chattel Village and the Colony Club were the only two places in the sampled sites where sugar packets were commonly available outside of our experiments. Although the bullfinches were not identified with leg bands, we observed two to three birds opening sugar packets at the same time at the Coral Reef terrace, the Heron Bay gap and the Chattel Village.

At all sites where the birds opened the packets, they did so within the first 5 min of observation, and the method used by the birds to succeed was very similar. Individuals first examined the packet and flipped it over, as if they were observing whether the packet was already open or not, and then either flew away carrying the packet in their beak or started immediately to peck at it, eventually piercing it and eating the sugar inside (see video 1 in the Supplementary Material). At two of the sites where bullfinches opened sugar packets (Coral Reef terrace and Heron Bay gap), we also observed bananaquits (*C. flaveola*) feeding from sugar packets already opened by bullfinches, as previously observed by Reader et al. (2002). Bananaquits did not manipulate sugar packets at the other sites where they were offered, although they were observed within 4 m of the packets at two places, the Surfside and the Royal Pavilion restaurant terraces, where they fed on other anthropogenic food sources. Finally, we observed two different male Lesser Antillean Bullfinches (*L. noctis* is sexually dimorphic) opening sugar packets at Anse Chastanet (hotel terrace) in St. Lucia (see Figs. 1 and 2b and video 2 in Supplementary Material).

Discussion

The sugar packet opening behaviour observed in 2000, restricted only to the initial site of the Colony Club (Reader et al. 2002), was still observed in 2012. Surprisingly, however, the behaviour has spread little (<200 m) from the initial site, despite that the area is full of restaurants and hotels. As sugar packets are not usually distributed at the Coral Reef or in the Heron Bay gap, it is likely that the birds opening the packets at these locations developed this behaviour at the Colony Club terrace. Although we were not able to identify the different birds, two individuals recognizable by plumage features and avian pox lesions were observed at the Coral Reef terrace but never on the other sites, suggesting that the movements were limited between these sites, and that the sugar packet opening behaviour at the three sites around the Colony Club was performed by different individuals. We could expect individuals from territories near to the Colony Club terrace to sometimes visit the terrace, or to have occupied this territory in the past, acquiring the capacity to open sugar packets. These birds may have independently developed the innovation or learned socially from their con specifics. Even if the diffusion pattern we observe (see Fig. 1) favours the hypothesis of social learning around the Colony Club, it remains impossible to determine whether the innovation spread through social or asocial mechanisms at these 3 sites. As proposed by Reader et al. (2002), the territoriality of the birds may have restricted the spread of the novel behaviour to a larger area.

We also found that bullfinches were able to open sugar packets of a different colour at the Chattel Village, at a distance of 1,000 m from the Coral Reef, the nearest place where bullfinches were observed opening sugar packets around the Colony Club. As the sugar packet opening behaviour was not observed between these two sites, the behaviour either arose independently at the two sites or was brought by an immigrant from one site to the other. However, the fact that the Barbados bullfinches from the Chattel Village did not attend to the white packets we offered, similar in colour to those routinely available at the Colony Club, but only to the brown ones available at that site, suggests that the behaviour appeared independently at the two places. We were also informed of a bullfinch opening a white sugar packet at Accra Beach in April 2011 (Dr. R. Russel, pers. comm.), 13-14 km south of the areas we canvassed here (see Fig. 1), suggesting the existence of a third independent appearance of this behaviour. We can, however, not rule out the hypothesis that the opening of sugar packets on this third site resulted from the dispersal of an innovator. Finally, the observation of two Lesser Antillean bullfinches opening sugar packets in St. Lucia clearly demonstrates the independent appearance of the same innovation in two species.

The interest of bananaquits in sugar packets specifically at places where bullfinches are observed opening them suggests the existence of an association between both species, where bananaquits scrounge the innovative behaviour of bullfinches to obtain otherwise inaccessible food (Giraldeau and Caraco 2000). Indeed, bananaquits were not observed opening sugar packets, probably because their beak morphology makes them technically unable to do so. Scrounging of an innovative behaviour by hetero specifics suggests that even species that are technically unable to perform an innovation could benefit from the behaviour of other species to enlarge their own foraging repertoire.

This is the first study that clearly demonstrates the independent appearance of the same innovation in different individuals within a species and in two different species. Our observation thus supports the expectation that independent appearance of innovation may be important in the spread of some innovations. It remains, however, difficult to evaluate the relative importance of the different mechanisms responsible for the spread of an innovation, both within the species studied here and in other cases. It is likely that both a species' ecology (such as territoriality) and the distribution of an innovation source (in our case, the distribution of sugar packets) will largely affect how social and asocial mechanisms drive the spread of an innovation, so that mechanisms may vary according to species, populations and innovations. Nevertheless, our findings clearly document the existence of independent appearances of an innovation, and future observations should carefully address that possibility when analysing innovation mechanisms.

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