Animal Behaviour 85 (2013) 1225–1232

Contents lists available at SciVerse ScienceDirect

Animal Behaviour

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

Milk bottles revisited: social learning and individual variation in the blue tit, *Cyanistes caeruleus*

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A R T I C L E I N F O

Article history:
Received 17 December 2012
Initial acceptance 14 January 2013
Final acceptance 14 February 2013
Available online 17 April 2013
MS. number: 12-00956

Keywords:
blue tit
Cyanistes caeruleus
innovation
observational learning
social information
two-action method

Blue tits are famous for the 'milk bottle' innovation, which emerged at numerous sites across Britain in the early 20th century. However, overall we still know little about the factors that foster or hinder the spread of innovations, or of the impact of individual differences in behaviour on social transmission. We used a two-action and control experimental design to study the diffusion of innovation in groups of wild-caught blue tits, and found strong evidence that individuals can use social learning to acquire novel foraging skills. We then measured six individual characteristics, including innovative problem solving, to investigate potential correlates of individual social-learning tendency. Consistent with a hypothesis of common mechanisms underlying both processes, we found evidence for a relationship between social learning and innovativeness. In addition, we observed significant age- and sex-biased social learning, with juvenile females twice as likely to acquire the novel skill as other birds. Social learning was also more likely in subordinate males than dominant males. Our results identify individual variation and transmission biases that have potential implications for the diffusion of innovations in natural populations.

There have been numerous reports of novel behaviours emerging and spreading in animal populations, from potato washing in Japanese macaques, *Macaca fuscata*, to lobtail feeding in humpback whales, *Megaptera novaeangliae* (Kawai 1965; Weinrich et al. 1992; Reader & Laland 2003). While there is a growing understanding of the phylogenetic and ecological predictors of these innovations (Lefebvre et al. 2004; Morand-Ferron & Quinn 2011), we still have little understanding of what factors may promote or retard their spread (Dean et al. 2012). There are two nonmutually exclusive potential mechanisms by which the uptake of novel behaviour could occur: many independent acquisitions of the same innovation in response to a common environmental stimulus, or a single innovation followed by social learning, whereby naïve individuals learn from observing knowledgeable individuals (Kendal et al. 2005). Such social learning may lead to behavioural differences between groups, to traditions, and ultimately to culture (Kendal et al. 2005; Laland et al. 2011), and it is hypothesized that it may be important in providing an alternative means of cultural adaptation that is more rapid than genetic transmission (Whiten & Mesoudi 2008).

It can be difficult to distinguish asocial and social learning, particularly with observational studies in the wild (Kendal et al. 2010). Experimental work can overcome these problems but may be of little ecological relevance, particularly if social learning is only tested between dyads (Whiten & Mesoudi 2008; Reader & Biro 2010). One powerful method of testing social learning is the two-action and control design, where two groups are exposed to different demonstrators, each trained on one of two possible solutions to a novel problem (Heyes & Dawson 1990; Whiten & Mesoudi 2008). A third group with no demonstrator serves as a control for asocial learning. This method makes it possible to distinguish between asocial learning and social learning, and also teases apart potential social-learning mechanisms. Local enhancement (where the demonstrator attracts others to the locale; Heyes 1994) can be distinguished from asocial learning, as the former results in a difference between experimental groups and control group, but no difference between experimental groups. Observational social learning (where naïve individuals produce a certain pattern of behaviour through observation of tutor position, action and behaviour; Heyes 1994) results in a difference both between the experimental groups and between experimental and control. Because the two-action method can be conducted in groups and

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http://dx.doi.org/10.1016/j.anbehav.2013.03.009

not only in dyads, this approach also has the potential to elucidate social dynamics and individual differences that may affect the spread of behaviour.

The factors that influence individual propensity to use social learning remain poorly understood, with some studies assuming that all individuals are equally likely to receive or transmit new behaviours (Coussi-Korbel & Fragaszy 1995). In contrast, theories of directed social learning state that the social context should influence opportunities to learn from certain individuals (Coussi-Korbel & Fragaszy 1995; Aplin et al. 2012). At its simplest, this may reflect patterns of affiliation and tolerance, for example in canaries, *Serinus canaria domestica*, in which aggression between males was found to preclude social transmission (Cadieu et al. 2010). However, it is also possible that individuals may follow adaptive social-learning ‘strategies’ when deciding to use social information; for example individuals may copy when unsuccessful, or only copy individuals of a higher dominance rank (Nicol & Pope 1994; Galef & Laland 2005; Kendal et al. 2005). One of the few studies to find empirical evidence for social-learning strategies is in domestic fowl, *Gallus gallus domesticus*, in which individuals preferentially learn from those of higher dominance rank (Nicol & Pope 1994).

In addition to adopting flexible social-learning strategies, individuals may also differ consistently in their tendency to use social learning (Rosa et al. 2012). This could be related to developmental trajectories, or to intrinsic characteristics such as sex, innovativeness or neophobia. In guppies, *Poecilia reticulata*, females are more exploratory, innovative and more likely to use social learning, suggesting that females may invest more in resource acquisition (Reader & Laland 2000). Innovativeness and social learning are also positively correlated in pigeons, *Columbia livia* (Bouchard et al. 2007). Individual differences in propensity for social learning may also be related to social skills such as dominance rank and competitive ability: dominants have been shown to monopolize social-learning opportunities (Kappeler 1987), but in other cases young individuals and subordinates are the best social learners, perhaps as they prioritize novel skill acquisition (Langen 1996; Thornton & Malapert 2009). The existing evidence as to direction is mixed (Boogert et al. 2008a), with no clear predictions. However, if individuals consistently differ in their propensity to use social information then this may have important implications for population-level processes, as social transmission becomes restricted to particular groups or ‘transmission pathways’.

One of the most widely cited examples of a diffusion of innovation is milk bottle opening in British tits (great tits, *Parus major*, and blue tits), where birds famously learnt to pierce through the foil caps of milk bottles left on doorsteps in order to drink the cream. The innovation was first observed at one site in 1921, but by 1947 it had been recorded at almost 30 sites across the U.K. (Fisher & Hinde 1949; Hinde & Fisher 1951). None the less, the processes behind this striking spread of novel behaviour have remained controversial, and the original authors later favoured the view that multiple innovations were occurring at different sites, followed by some local social learning (Hinde & Fisher 1972; Lefebvre 1995). In a later analysis by Lefebvre (1995), the observations were compared to population-level models of social learning. These results suggested that the milk bottle opening innovation had indeed originated at several independent sites, but had also spread extensively at each location with an accelerated rate suggestive of social learning. Sherry & Galef (1984, 1990), exposed black-capped chickadees, *Poecile atricapillus*, to open or closed milk bottles in the presence of either tutors or naïve conspecifics. Birds provided with a tutor did not learn at a higher rate than those exposed to a naïve conspecific, challenging the social-learning assumptions of the milk bottle innovation diffusion (also see Kothbauer-Hellman 1990). However, these studies assessed social transmission between physically separated dyads in an artificial environment.

We investigated social learning in blue tits using a two-action and control experimental design in groups of wild-caught birds. In experimental groups, demonstrators were trained to obtain food from a novel foraging task using one of two possible solutions. Control groups were exposed to the task without a demonstrator. We predicted that if social transmission was occurring, then individuals from experimental groups would be more likely to acquire the novel skill than individuals in control groups. If observational learning was occurring, then individuals should use the same solution as that demonstrated in their group. We then tested whether there is an effect of individual variation on social-learning propensity by measuring six individual characteristics (sex, age, body condition and innovativeness, competitive ability and dominance rank), and examined these characteristics as predictors of latency and probability of social learning.

METHODS

Subjects and Housing

Twelve groups of eight blue tits were caught from the wild using mist nets. In total, 96 birds were caught between December 2010 and March 2011 and between October 2011 and February 2012 from three Oxfordshire sites: Wytham Woods, Tubney Woods and the John Krebs Field Station. Horizontal social learning should be facilitated in the winter season, when blue tits form nonterritorial feeding flocks (Thompson et al. 1996). By catching birds at the same site and using one net, the catching procedure was targeted to maximize the likelihood that each group of birds caught were part of the same wild flock, and after each trial the birds were released together at the capture site with 2 days of supplementary food. Upon capture, birds were fitted with a British Trust for Ornithology metal leg ring, colour-ringed to allow visual identification, and fitted on the other leg with a plastic ring containing a uniquely identifiable passive integrated transponder (PIT) tag (see Farine et al. 2012). Individuals were also aged as adult or juvenile, weighed, and sexed using a combination of biometrics, molecular testing from noninvasive mouth swabs, and subsequent breeding captures.

Groups were initially housed individually indoors in eight adjacent wire-mesh cages (45 × 45 cm and 68 cm high), each provided with roost boxes, and fed on a diet of sunflower seed, peanut granules and mealworms. Housing rooms were kept under a natural light regime and at ambient temperature. After a settlement period of 24 h, birds were released into a large outdoor aviary (5 × 5 m and 3 m high) fitted with a complex environment of tree branches, roost boxes and bathing dishes. The same diet as above was provided at multiple feeders. After the social-learning experiment (day 4), birds were trapped in the roost boxes after dark and transferred back to the indoor cages; the colour rings were removed before release the following day. Throughout the period of captivity, contact with humans was minimized and observations were made either from a hide or through one-way glass.

Experimental Procedure

Demonstrator training

Social learning was tested using a two-action novel foraging task. The task was a grid of 72 cells, presented in three trays, arranged next to each other on the aviary floor. Each cell contained a waxworm (a highly preferred food type). Cells were topped with an equal mix of foil caps, which could be pierced then torn to expose the worm, and cardboard lids that needed to be flipped over; these were regularly ordered across grids and trays (Fig. 1a, b and see video in the Supplementary Material). One individual in each group was haphazardly chosen as the demonstrator. Demonstrators thus represent the average demography of groups, and were a mix of sexes (female = 5, male = 3), ages (adult = 2, juvenile = 6) and dominance status (high = 3, low = 5). Training began 1 h after initial capture and housing, and demonstrators were assigned one of three training regimes in random order: 'control' ($N = 4$), where the individual was subjected to equal levels of disturbance but not exposed to the task; 'foils' ($N = 4$), where the individual was only trained on the foil solution; and 'lids' ($N = 4$), where the individual was only trained on the lid solution. A step progression method was used: the task was originally presented as solved and then presented in increasingly difficult states until the individual had learned and performed the full solution every time it received the task. Training took place in the individual's indoor cage (with no visual contact to other individuals), and usually took between 3 and 6 h. Demonstrators were food deprived for no more than 1 h before training sessions.

Competitive rank order

Competitive ability was judged by the length of time each individual spent monopolizing the main sunflower feeder in the outdoor aviary over the 3 days preceding the social-learning experiment, and was distinguished from the more direct antagonistic (dominance) rank as per Boogert et al. (2006, 2008b). To measure time spent feeding by birds, feeders were fitted with two PIT tag reading antennae that recorded visits every 16th of a second (Francis Scientific Instruments, Cambridge, U.K.). Total feeding duration was calculated as the sum of all visits, and all eight group members were then ranked, with the individual observed most often on the feeder given the highest rank (Boogert et al. 2006; Cole & Quinn 2012). Competitive ability increased with age (linear mixed model, LMM: $t_{54} = 3.99$, $P = 0.05$), but was unrelated to body size, sex, innovativeness or dominance score (all $P > 0.05$).

Dominance hierarchy

Antagonistic interactions (posturing and contact) were measured over two blocks of 2 h for each group on the 2 days preceding the social-learning experiment (days 2–3). During this time, all food sources were removed from the outdoor aviary and a single-access feeder containing peanut granules (approximately 2 mm^2) installed. These small food items constrain birds to stay on the feeder for prolonged periods, effectively increasing competition (Cole & Quinn 2012). A video camera recorded all interactions; video files were later analysed with colour rings providing visual identification. Only interactions with clear winners and losers (where one displaced the other) were used. A dominance hierarchy for each group was then constructed using David's score (David 1987), using the methodology from Gammell et al. (2003), and calculating the dominance of each individual using a corrected normalized David's score. Dominance score was positively correlated with wing length (LMM: $t_{54} = 7.41$, $P < 0.01$). Wing length is commonly used as a measure of body size and was also correlated with mass (linear model, LM: $F_{1,74} = 40.28$, $P < 0.001$). Males were usually dominant over females (LMM: $t_{54} = 9.04$, $P < 0.01$), and there was a positive, nonsignificant correlation with age (LMM: $t_{53} = -1.77$, $P = 0.08$; see Fig. 2).

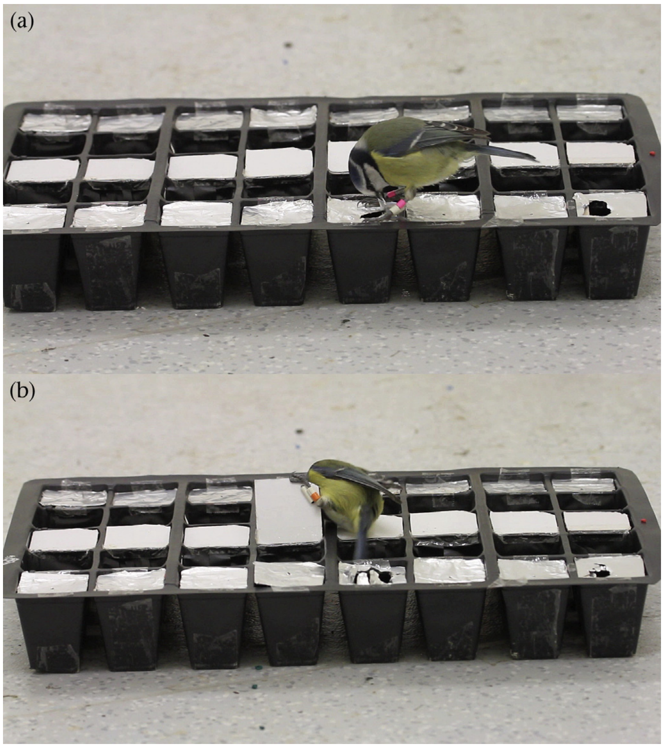

Figure 1. Individuals using alternative solutions to the same novel task to get access to worms inside cells. (a) Piercing and tearing foil caps, (b) flipping up lids. Demonstrators were trained on one of two possible solutions using a gradual shaping procedure.

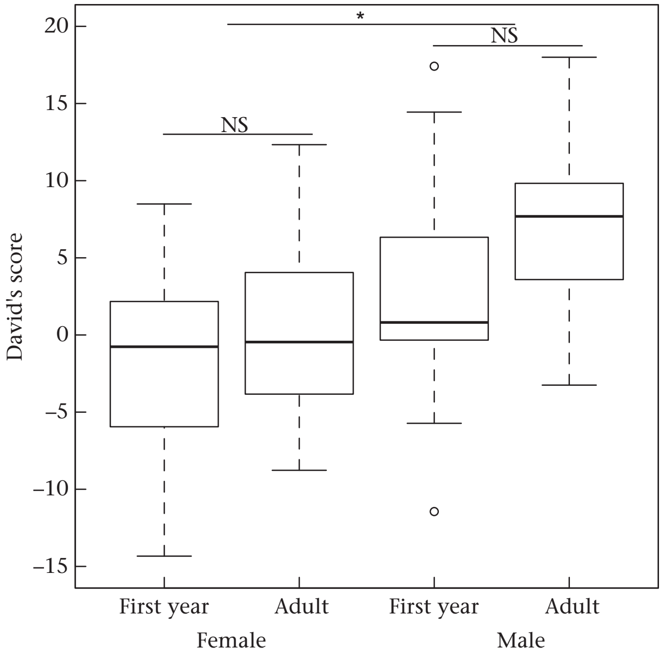

Figure 2. Dominance score (David's score) for individuals from all groups combined ($N = 61$): first-year females: $N = 20$; adult females: $N = 17$; first-year males: $N = 12$; adult males: $N = 12$. The box plots show the median and 25th and 75th percentiles; the whiskers indicate the values within 1.5 times the interquartile range, and circles are outliers. Sexes and age groups are shown separately and higher scores indicate greater dominance. *$P < 0.05$.

Innovativeness

Innovativeness was quantified with a novel problem-solving task, consisting of a clear tube containing three waxworms on a platform supported by a removable lever with a ‘free’ waxworm provided below. This lever-pulling task is further described in Cole et al. (2011). Of 96 birds, 80 were provided with a lever-pulling task in the individual cages on the last night of captivity for 3 h without disturbance, 1 h before darkness and 2 h in the morning. Almost all individuals (76/80) ate the ‘free’ waxworm, and 41% of all individuals solved the lever-pulling task. Success was unrelated to individual traits (all $P > 0.5$). In great tits, a similar proportion solved the task (44%), and success in the lever-pulling task was unrelated to motivation, individual morphological or personality traits, suggesting that the variation largely represents inherent individual differences in innovativeness (Cole et al. 2011). For a full description, its repeatability and characterization, see Cole et al. (2011, 2012) and Cole & Quinn (2012).

Social-learning experiment

At 0800 hours on the fourth day in the group aviary, the social-learning task was placed on the aviary floor. During this day, live food (mealworms) was removed; however, sunflower seeds remained readily available at all times. Observations were conducted over a 4 h period starting when the demonstrator first solved the task (usually within 10 min of the task being introduced), or at the first visual inspection of the task by any individual in the control groups. All interactions with the task were recorded and scored as either (1) visual inspection of the task (a directed gaze within 1 m), (2) physical contact with the grid, (3) manipulation of the task, and (4) solving the task with or (5) without reward. The identity of the focal individual and the solution used (foil or lid) were also recorded. Records were made of all agonistic interactions between individuals at the task.

We were interested in testing whether the learnt behaviour was retained, and whether the group environment affected the expression of learnt behaviour (Drea & Wallen 1999). To do so, we also presented a smaller version (four cells: two foils, two lids) of the social-learning task to all birds when isolated in individual cages on the last night and morning of captivity (3 h).

Data Analysis

For the analysis of social learning, we calculated the proportion of individuals in each group that solved the task, and compared experimental with control groups. In experimental groups we also calculated the proportion of all individuals that performed the same solution as the demonstrator. To test whether differences in neophobia or motivation could help explain the likelihood of solving the task in the social-learning context, we compared the contact latency to the task of ‘solvers’ and ‘nonsolvers’ and examined the relationship between individual body condition (calculated as mass divided by wing length) and solving probability. Contact latency was used as a proxy for neophobia, while body condition was used as a proxy for motivation. We used LMMs in R (lme4 package; lme4 package; Bates & DebRoy 2004), including solving latency as the response variable, demonstrator condition (foil or lid) as a fixed effect, and replicate (group) as a random effect.

To investigate the relationship between individual variation and social learning we used a generalized linear mixed model (GLMM) and LMM in R to compare solving (yes/no) and solving latency (first contact to first successful solve), in response to age, problem-solving performance, competitive rank and dominance score, controlling for demonstrator type (foil or lid). Birds that did not solve the task were given a ceiling latency of 250 min. Replicate was included as a random intercept and a final model was formed by backward stepwise removal of nonsignificant terms.

Ethical Note

All work was subject to review by the Department of Zoology ethical committee, University of Oxford, and the Animal Experimentation Ethics Committee, Australian National University, adhered to U.K. standard requirements and was carried out under a Home Office licence and Natural England licence 20104175 and 20114175. Birds were caught and ringed under British Trust for Ornithology (BTO) licence C5714 and C5791. They were transported from the wild to captivity in cloth bags (BTO standard), and installed in individual cages with food, water and roost boxes within 1.5 h of capture. Birds always began feeding shortly after being put into the cages, and were monitored regularly during the first day in captivity. When the birds were in the group aviary, there was minimal aggressive behaviour between individuals, and no injuries were observed. To ensure this outcome, birds were monitored for 4 h after release into the group aviary, and (excepting during dominance trials) multiple roost boxes and food and water points were provided to reduce resource monopolization. Changes in body mass between capture and release (mean $= -0.36$ g, 3.5%) were within the natural range of diurnal mass fluctuations (Haftorn 1992), and birds were released at the site of capture with a supply of supplementary food.

RESULTS

Social-learning Experiment

There was a clear difference between the acquisition of the task in experimental and control groups. When provided with a demonstrator, 54% of all naïve individuals learned to solve the task. In contrast, no individual in the control groups (four groups comprising 32 individuals) solved the novel foraging task (Fig. 3).

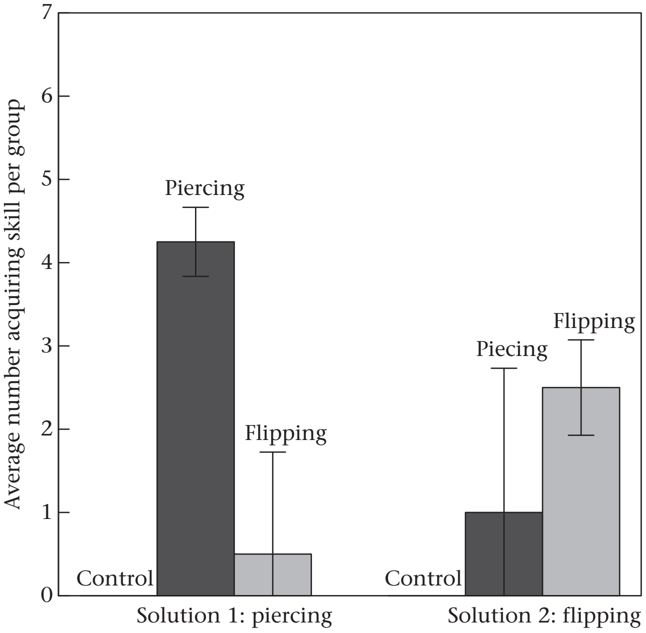

Figure 3. The average number of individuals in each group that used either solution 1 (piercing foil) or solution 2 (flipping lids) to solve the novel foraging task. There were four groups of each of the control with no demonstrator, a demonstrator trained on the foil solution and a demonstrator trained on the lid solution. The first cluster of bars represents groups presented with a demonstrator trained on ‘piercing’; the second cluster represents groups presented with a demonstrator trained on ‘flipping’. Error bars represent SEs.

This could not entirely be explained by a lack of awareness of the task in control groups, as 85% of individuals in control groups showed some investigation of the task (group mean = 7 of 8). There was a high degree of variation in solving the task in the experimental groups, but at least one naïve individual learnt in all experimental groups. Finally, in the vast majority of cases, performance on the task when alone reflected performance in the group context, with 18 of 25 ‘solvers’ also solving the task in isolation, and only an additional two of 31 ‘nonsolvers’ solving it once alone. This suggests that (1) there was no inhibitory effect of social context, and (2) that the social-learning information was retained, and used after demonstrator effects were removed.

Within the eight experimental groups, half of the demonstrators ($N = 4$) were trained on solution 1 to the task (piercing foil lids), while the other half ($N = 4$) were trained on solution 2 (flipping up lids). More individuals performed the same solution as that demonstrated rather than the alternative (chi-square test: $\chi^2_1 = 10.42$, $P < 0.01$; Fig. 3). Solution 2 seemed more difficult to learn, with an average of 36% of individuals exposed to the ‘lids’ solution solving ‘lids’ compared to 61% of those exposed to the ‘foil’ solution (Fig. 3). Taken together, these results from the two-action test provide very strong evidence that blue tits can use social learning to acquire novel foraging skills.

Individual Differences in Social Learning

Within the experimental groups, 53% of all naïve individuals acquired the novel foraging skill. To test whether this variation could be explained by individual differences in neophobia, we investigated the relationship between contact latencies and social learning. There was a positive, nonsignificant correlation between contact latency and latency to solve the task after first contact (LMM: $t_{54} = 1.75$, $P = 0.08$). However this result was skewed by five individuals that never approached the task. When they were removed from the analysis, there was no difference in contact latency between ‘solvers’ and ‘nonsolvers’ (LMM: $t_{48} = 0.38$, $P = 0.70$; Appendix Table A1). Second, while all individuals had access to a sunflower feeder during the task, there might have been differences in motivation to gain access to the novel food owing to underlying body condition. Yet our results also showed no evidence of differing motivation, when we tested the relationship between solving latency and body condition at either capture (LMM: $t_{50} = 0.49$, $P = 0.97$) or release (LMM: $t_{29} = 0.41$, $P = 0.68$; Appendix Table A2).

There was no support for a relationship between competitive rank or age and latency to solve the task (rank: LMM: $t_{47} = -0.519$, $P = 0.45$; age: LMM: $t_{54} = -1.47$, $P = 0.14$). Rather, there was evidence for an effect of dominance (LMM: $t_{46} = 3.14$, $P < 0.01$) and innovative problem solving (LMM: $t_{46} = -2.18$, $P = 0.04$), with subordinate individuals and successful problem-solvers being more likely to learn socially (Appendix Table A3). The effect of dominance was striking, with 63% of subordinates acquiring the skill compared with 38% of dominant individuals. Females were also more likely to solve the task than males (LMM: $t_{54} = 2.20$, $P = 0.03$; 61% of females learnt compared with 30% of males); however, sex was strongly correlated with dominance (Welch two-sample test: $T = -3.04$, $N = 55$, $P < 0.01$; Fig. 2), making it difficult to include both in the same model. We therefore analysed the sexes separately.

In males, subordinates and successful problem-solvers were most likely to learn the task (dominance: LMM: $t_{17} = 3.08$, $P < 0.01$; Fig. 4; problem solving: LMM: $t_{17} = -3.20$, $P < 0.01$), but there was no correlation with any of the other measured variables (all $P > 0.05$; Appendix Table A4). However, for females, we found no evidence for an effect of dominance or innovative problem solving on probability or latency of social learning (dominance: LMM: $t_{29} = 0.19$, $P = 0.85$; problem solving: LMM: $t_{29} = -0.84$, $P = 0.41$; Appendix Table A5). Rather, there was a significant effect of age, with juvenile females being twice as likely to learn as adult females (GLMM: $t_{31} = -2.45$, $P = 0.04$; Fig. 5, Appendix Table A6) and also significantly more likely to learn than all males (GLMM:

Figure 4. The distribution of social learners by dominance in males. The box plots show the median and 25th and 75th percentiles; the whiskers indicate the values within 1.5 times the interquartile range. Dominance is given by David's score; higher scores indicate greater dominance.

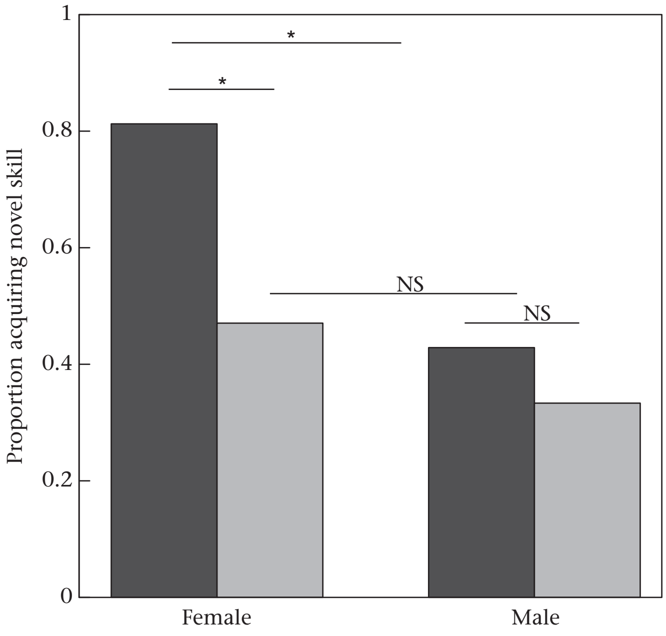

Figure 5. The distribution of individuals using social learning by sex and age. Adults are shown in light grey, juveniles in dark grey. The proportion of all individuals in that class across all groups that solved the task is shown. *$P < 0.05$.

$t_{38} = -2.52$, $P = 0.01$). When age classes were thus considered, it was clear that juvenile females drove the sex difference, with no significant difference in social learning between adult females and males (LMM: $t_{40} = 0.85$, $P = 0.40$; Fig. 5). In both sexes, those adults that learnt had shorter latencies to do so than juvenile learners (Welch two-sample test: $T = -2.06$, $N = 48$, $P = 0.05$), suggesting either that there is an interaction between dominance and variation in cognition or that juveniles might have been more persistent in their attempts to learn.

Finally, the sex, dominance score or age of the demonstrator made no difference to the proportion of the group or type of individual that learnt. There did not appear to be any preferential attention paid to dominants, as suggested in some previous work (Nicol & Pope 1994); however, it is difficult to form any substantive conclusions with the sample size available ($N = 8$).

DISCUSSION

Our experiment provides much needed empirical evidence that parids can use social learning to acquire novel foraging skills. This is consistent with an early descriptive study (Fisher & Hinde 1949; Hinde & Fisher 1951) and captive study (Sasvari 1979). Contrary to the findings of Sherry & Galef (1984, 1990), we also found evidence for social-learning mechanisms other than local enhancement, with individual blue tits being much more likely to solve the task with the same action as that shown by the demonstrator. Our results provide the first demonstration of social learning of a novel foraging skill in this species using an experimental design that can exclude asocial learning and local enhancement as alternative explanations. In doing so, they provide support for the view that the milk bottle innovation observed and commonly cited as an example of cultural transmission could indeed have spread via observational learning mechanisms (Lefebvre 1995). Finally, blue tits are a flocking species, for which the social context of social transmission of information is potentially very important. By studying social learning in a group experiment with wild individuals of mixed sex and age, we attained a higher degree of biological relevance than could be gained through more traditional approaches.

Social learning encompasses a wide range of possible mechanisms, ranging from social information about food sites (Aplin et al. 2012) to complex imitative behaviour, where the exact body action of the demonstrator is copied (Voelkl & Huber 2000). Our task consisted of multiple cells, each topped with either a lid that could be flipped over or a foil cap that could be torn to get access to a waxworm (Fig. 1). There was likely to be some level of local enhancement operating in our experiment, with demonstrators attracting the attention of naïve individuals to the task. Beyond this, we found a significant difference between the techniques used by groups seeded with alternative solutions, providing strong evidence for some form of observational learning (Fig. 3). However, we do not claim to distinguish between the further alternative mechanisms of imitation (where the exact motor action of the demonstrator is copied) and fine-scale stimulus enhancement (where the activity of the demonstrator draws the observer's attention to a specific object or part of an object, which it then generalizes; Heyes 1994; Voelkl & Huber 2000).

Approximately half of all individuals in our experiments were able to acquire the novel foraging skill through social learning. We were able to exclude differences in neophobia or motivation caused by body condition as potential predictors of this variation. Probability of social learning was also unrelated to competitive ability. Rather, we found a potentially important relationship between social learning and dominance, sex and age. The predictors of social-learning propensity appeared to differ within each sex. Within females, age was important, with more first-year individuals learning than adults (Fig. 5). In males, social learning was negatively correlated with dominance and there was no effect of age (Fig. 4). Within males the results are consistent with the 'necessity is the mother of invention' hypothesis, and 'copy-if-dissatisfied' social-learning rule (Galef & Laland 2005; Kendal et al. 2005), which argues that individuals should prioritize social information over personal information when their current position is suboptimal (Galef et al. 2008). It is interesting to consider whether this transmission bias is context dependent, with individuals dynamically assessing their relative dominance based on their current social grouping, or whether it may be more generally state based, with individuals basing their assessment of dominance on past experience and future expectations irrespective of current social context.

Juvenile females were almost twice as likely to acquire the novel skill than any other type of individual in our study (Fig. 5). In Reader & Laland (2000), foraging information spread faster through subgroups of female guppies than through male subgroups. The authors suggested this sex difference reflected a parental investment asymmetry, with females prioritizing resource acquisition comparatively more than males. Similarly, females are faster social learners in two species of lemur (Kappeler 1987; Schnoell & Fichtel 2012), which may be caused by increased motivation resulting from higher nutritional needs. In contrast to these studies, wild meerkats, *Suricata suricatta*, show no sex bias in social learning. Rather, young meerkats are most likely to acquire social information; this is attributed to knowledge asymmetry between juveniles and adults (Thornton & Malapert 2009). While it is possible that female blue tits have higher nutritional needs than males owing to their greater reproductive investment, this seems unlikely to be important over the winter season. Furthermore, this cannot explain differences between adults and juveniles, and thus a 'greater-needs' hypothesis seems unlikely to apply. Rather, in our study population, dispersal is biased towards first-year females (Paradis et al. 1998). It is interesting to speculate whether females are more receptive to social information during their main dispersal phase, when such information may be important in coping with the challenges posed by the novel physical and social environments into which they move.

Problem-solving performance was also positively correlated with social learning in our study, in terms of both overall social-learning probability and speed from first contact to solution. Such problem solving, when tested using the same assay in the closely related great tit, has been shown to be both repeatable (Cole et al. 2011) and related to multiple life history traits determining reproductive fitness (Cole et al. 2012). While it is impossible to eliminate all possible confounding variables that might influence such a relationship, if there is a positive correlation between innovation and social learning then this suggests that there might be a common mechanism mediating both processes, or at least no trade-off between them (Galef 1996; Reader 2003; Heyes 2012). However, such evidence has been found in only two other species (Reader & Laland 2000; Bouchard et al. 2007). Our results add further weight of evidence to these studies.

In conclusion, we report the first evidence of social learning in parids using a two-action and control experimental design. This experiment not only provides evidence for local enhancement, but also implies a role for more complex observational learning. Furthermore, we find significant variation in individual tendency to use social learning, unrelated to the latency to make contact with the novel task. Most individuals that used social learning to acquire a novel foraging skill were females in their first year. In males, acquisition was also negatively correlated with dominance. This suggests a link between life history state and social-learning propensity in this species, invoking a 'copy-if-dissatisfied' social-learning strategy, and a possible link with dispersal, which needs to be investigated further. Such transmission biases may have implications for the patterns and process of cultural diffusion of innovation, particularly if there is a further cognitive feedback between innovativeness and social-learning propensity. More work is needed to assess the potential for these transmission biases in the wild, and to investigate their implications for influencing the diffusion of innovations and movement of information at a larger population scale.

Acknowledgments

We thank the E.G.I. Social Networks Group, Julian Howe and Adele Mennerat for help with fieldwork, and Andrew Cockburn for help with data analysis. Particular thanks to Damien Farine for help with data collection and video composition. Finally, we would like to thank the two anonymous referees for their helpful comments. L.M.A. was funded by an Australian Postgraduate Award and by an International Alliance of Research Universities travel grant. J.M.F. was funded by a postdoctoral fellowship of the Natural Sciences and Engineering Research Council of Canada. The work was supported by a European Research Council grant to B.C.S. (AdG 250164).

Supplementary Material

Supplementary material associated with this article is available, with the online version, at http://dx.doi.org/10.1016/j.anbehav.2013.03.009.

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Appendix

Table A1
LMM on the relationship between solving latency and contact latency

	Test statistic (t)	P	Effect size	SE
Contact latency	0.38	0.705	0.09	0.24
Treatment (foil, lid)	1.58	0.121	63.05	39.92

Five individuals that never made contact with the task have been removed from analysis. Replicate (group) was fitted as a random term (estimated variance component ± SD: 1547.30 ± 39.34).

Table A2
LMM on the relationship between the solving latency of all individuals and body condition at either capture (model 1) or release (model 2)

	Test statistic (t)	P	Effect size	SE
Full model 1				
Body condition (at capture)	−0.17	0.623	134.47	291.02
Treatment (foil, lid)	1.30	0.198	57.52	44.11
Full model 2				
Body condition (at release)	0.45	0.654	188.41	416.44
Treatment (foil, lid)	0.89	0.378	62.62	69.95

Replicate (group) was fitted as a random term (estimated variance component ± SD for model 1: 2409.80 ± 49.09; estimated variance component ± SD for model 2: 4505.4 ± 67.12).

Table A3
LMM on factors affecting the solving latency of all individuals

	Test statistic (t)	P	Effect size	SE
Treatment (foil, lid)	1.28	0.206	62.17	48.38
Dominance score	3.14	0.003	5.62	1.79
Problem-solving success	−2.13	0.038	−61.78	28.95
Age (adult, juvenile)	1.75	0.331	0.22	0.13

Replicate (group) was fitted as a random term (estimated variance component ± SD: 2805 ± 52.96).

Table A4
LMM on factors affecting the solving latency of males

	Test statistic (t)	P	Effect size	SE
Treatment (foil, lid)	0.57	0.576	30.99	54.14
Dominance score	3.17	0.007	7.91	2.50
Problem-solving success	−3.31	0.005	−123.90	37.45
Age (adult, juvenile)	0.78	0.449	30.35	38.97

Replicate (group) was fitted as a random term (estimated variance component ± SD: 2476 ± 49.76).

Table A5
LMM on factors affecting the solving latency of females

	Test statistic (t)	P	Effect size	SE
Treatment (foil, lid)	0.48	0.636	37.09	77.42
Dominance score	−0.19	0.853	−0.52	2.75
Problem-solving success	−0.84	0.407	−28.58	33.90
Age (adult, juvenile)	−1.72	0.098	−53.27	30.97

Replicate (group) was fitted as a random term (estimated variance component ± SD: 8592.1 ± 92.69).

Table A6
GLMM on factors affecting solving probability of females (solve: no/yes)

	Test statistic (z)	P	Effect size	SE
Treatment (foil, lid)	−0.78	0.442	−2.45	3.19
Age (adult, juvenile)	2.05	0.040	3.57	1.74

Replicate (group) was fitted as a random term (estimated variance component ± SD: 15.75 ± 3.97).