Immigrant birds learn from socially observed differences in payoffs when their environment changes

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Short title: Immigrant birds' learning strategies under spatial variability

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Keywords: social learning, social learning strategies, animal culture, cultural evolution, reinforcement learning, Parus major, spatial variability

Author contributions

Conceptualisation, M.C., L.M.A.;
Methodology, M.C., G.A.N., L.M.A;
Software, M.C.;
Investigation, M.C.;
Resources, G.A.N., M.C.;
Writing - Original Draft, M.C.;
Writing - Review & Editing, M.C., G.A.N., L.M.A.;
Visualization, M.C.;
Supervision, L.M.A.;
Funding Acquisition, L.M.A.

Abstract

Longstanding theory predicts that strategic flexibility in when and how to use social information can help individuals make adaptive decisions, especially when environments are temporally or spatially variable. A short-term increase in reliance on social information under these conditions has been experimentally shown in primates, including humans, but whether this occurs in other taxa is unknown. We asked whether migration between spatially variable environments affected social information use with a large-scale cultural diffusion experiment with wild great tits (*Parus major*) in captivity, a small passerine bird that can socially learn novel behaviors. We simulated an immigration event where knowledgeable birds were exchanged between groups with opposing preferences for a socially learned foraging puzzle, living in similar or different environments. We found evidence that both immigrants and residents were influenced by social information and attended to the rewards that others received. Our analysis supported the use of a payoff-biased social learning by immigrants when both resources and habitat features were spatially variable. In contrast, immigrants relied more-so on individual learning when payoffs or the environment were unchanged. In summary, our results suggest that great tits assess the payoffs others receive, and are more influenced by socially observed differences in payoffs when environmental cues differ in their new environment. Our results provide experimental support for the hypothesis that spatial variability is a strong driver for the evolution of social learning strategies.

Introduction

When animals move from one place to another through dispersal, migration or nomadism, they often experience spatial variability, whereby environmental factors change across a transect. Spatial variability can be observable (e.g. a change in habitat cues), but also might be un-observable, such as subtle changes in the rewards earned from familiar behavior. Exposure to observable variability may cause neurological changes that trigger learning [1], leading animals to explore the new environment to identify novel resources or risks [2, 3]. Yet, trial and error exploration and learning in new environments may be extremely costly. For example, toxicity risks of novel food items may be largely unknown to the individual [4]. Longstanding theory has thus predicted that it should be advantageous to preferentially rely on social information as a less costly alternative to individual learning [5, 6]. However, as the proportion of social learners increases, they rely on an ever smaller set of individual learners who are actively sampling the environment, causing the average fitness of the population to fall—an outcome referred to as Rogers' paradox [7]. Furthermore, the social learning might also come at some cost, especially under resource scarcity, either as an opportunity cost for time spent observing rather than foraging, or as increased likelihood of aggressive interactions due to resource defense [8].

Thus, individuals should not always socially learn, and an abundance of theoretical work supports the evolution of selective, flexible learning strategies [9, 10, 11, 12, 13, 14, 6]. Strategies should evolve that allow individuals to alternate between the acquisition and exploitation of socially learned behavior, at least until further variability is, or is expected to be, encountered [11, 15]. Additionally, social learners should not necessarily copy all information equally, but rather strategically decide on who or what to copy [14]. Selective reliance on social learning in uncertain conditions has been identified by various experiments across taxa (see Kendal et al. [16] for review), although environments or rewards have rarely been deliberately manipulated.

One particularly uncertain context for wild animals is after migration or dispersal, as they are exposed to new physical and social environments. Several key studies give insight into how immigrants use social information. Migrant pied flycatchers (*Ficedula hypoleuca*) were shown to benefit from social information gleaned from resident great tits in the context of nest site selection selection [17, 18]. Newly immigrated meerkats (*Suricata suricatta*) were found to adopt the wake-up time of residents of their new social group [19]. In chimpanzees (*Pan troglodytes*), female immigrants adopted residents' nut-cracking tradition, even if it was less effective than their own preferred tradition [20]. However, captive chimpanzees were shown not to adopt resident dietary preferences after migration [21]. Migrant male orangutans (*Pongo abelii*) were found to preferentially peer at local residents [22]. In vervet monkeys (*Chlorocebus pygerythrus*), males (the dispersing sex) were shown to preferentially copy dominant females who form the stable core of their social system [23]. When rewards were varied, males employed a pay-off biased learning strategy that overrode their model bias, while philopatric females continued to prefer to learn from other dominant females [24].

Formal models and experiments have addressed why immigrants should strategically use social learning after moving to a new environment. Firstly, under spatial variability, migration can introduce non-adaptive behavior that favors strategic learning that acts as a filter for both immigrants and residents [25]. This filtering is not as useful under temporal variability, as the entire population might possess non-adaptive behavior after a temporal change. Furthermore, migration results in experience-structured populations where residents would be preferred demonstrators because they might have gained more adaptive information as a result of longer experience in a particular environment [26]. A recent virtual foraging experiment on humans supported this difference between types of variability, showing that immigration across spatially variable environments temporarily increased reliance on social information more-so than temporal changes in rewards [26].

Great tits' social system and learning abilities have made them a proven study system for questions linking social learning to social network structure and dynamics. During the winter months, great tits adopt a fissionfusion social system whereby birds join and leave mixed-species foraging flocks over the course of the day [27]. Tits are more socially tolerant compared with the spring breeding season, and belonging to winter flocks enhances their foraging abilities, either for patch discovery or the social transmission of novel foraging behavior [28, 29, 30, 31]. Prior empirical studies have shown that naive great tits can acquire foraging behaviors with a conformist transmission bias, meaning that they disproportionately learned the most frequently observed option [29, 32, 33, 34]. A follow up study found that this conformist bias did not create a trap in temporally variable environments where the rewards of options abruptly changed [32]. Tits adjusted their behavior to this change by relying mostly on individual learning, but retained a frequency-dependent conformity production bias [32]. However, the effect of spatial variability on tits' social learning has not yet been tested, even though spatial variability is hypothesized to drive the evolution of social learning strategies more-so than temporal variability [25], and could be more likely to trigger adaptive changes in learning strategies.

To test the effect of spatial variability on social information use, we conducted a cultural diffusion experiment in captivity using 18 micro-populations, each containing 8 wild-caught great tits ($N = 144$ birds). Each population was provided with an automated puzzle-box with two possible solutions that gave access to either the same, or

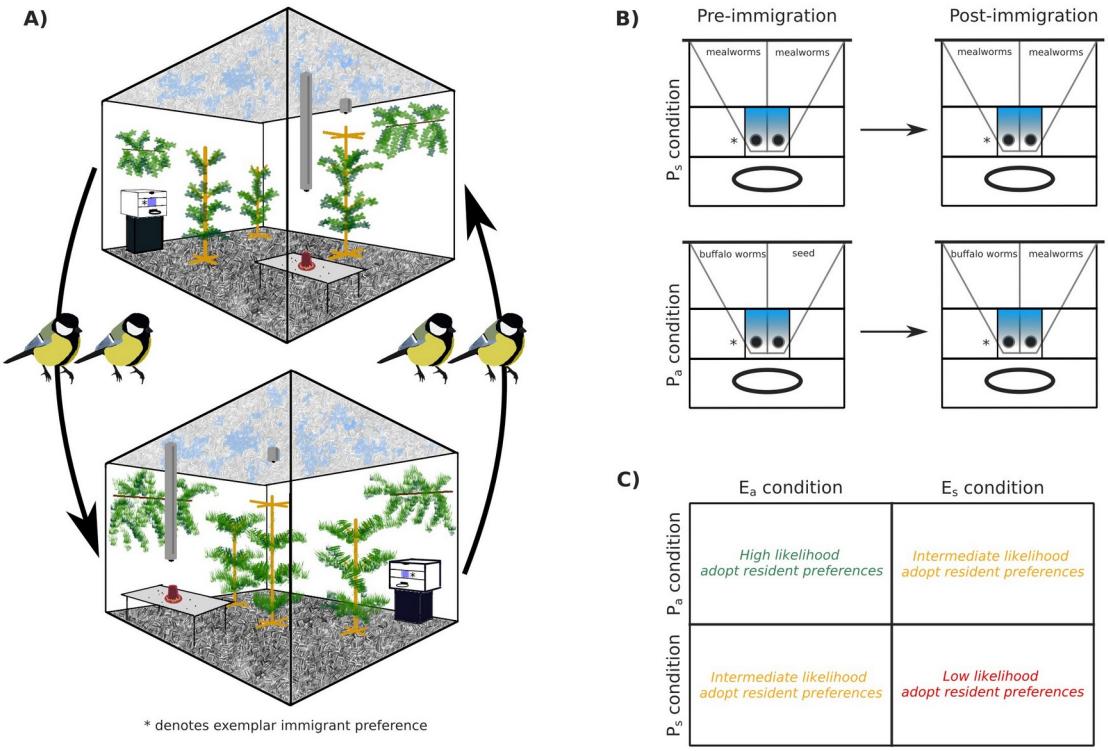

Figure 1: Diagrams of experimental design and hypothesis. A) An example of immigration between two populations in the asymmetric environment condition (E_a), where 2 birds were swapped between populations with different habitat cues: deciduous (top) and pine (bottom) with opposing puzzle solutions. Prior to immigration, immigrants socially learned a seeded solution, demonstrated by the tutor (denoted by *). Seeded solutions were balanced across conditions. B) Illustration of symmetric (P_s) and asymmetric (P_a) payoff conditions. In P_a prior to immigration, the seeded solution was rewarded with buffalo worms, while the alternative solution was rewarded with sunflower seeds. After immigration, immigrants' preferred solution still gave access to buffalo worms, but the alternative resident solution gave access to the more preferred mealworms. C) Diagram of our expectations about immigrant preferences under each condition in the 2x2 design. We expected that immigrants in E_a,P_a (representing the maximal spatial variability) would be most likely to adopt the resident solution after immigration. The data underlying this figure can be found in our data and code repository [53].

differing reward, and one "tutor" individual that was trained to use one solution. After this "seed" solution had spread and established as a behavioral tradition, we simulated immigration events between pairs of populations with opposing established traditions. For example, immigrants from a source population that preferred pushing the puzzle door right would be moved to a destination population that preferred left.

Each pair of source and destination populations was in 1 of 4 conditions, defined by a 2x2 factorial design. We manipulated environmental cues: populations had either symmetric, identical environments (E_s condition) or asymmetric environments (E_a condition) mimicking their natural habitat of pine or deciduous forests. We also manipulated puzzle payoffs, where puzzle solutions offered either symmetric or asymmetric payoffs (Figure 1B). In the symmetric payoff condition (P_s), both solutions gave access to a high-value mealworm reward before and after immigration. In the asymmetric payoff condition (P_a), the tutor's solution gave access to medium-value buffalo worms, while the alternative solution gave access to low-value sunflower seeds. After the immigration event, the payoffs changed such that the immigrants' preferred solution would still give access to buffalo worms, but the resident's preferred solution would give access to mealworms. Thus, immigrants would either need to use social information, or use individual learning by sampling themselves to discover that changing preferences would yield a better payoff. We note that seeded traditions were balanced across the design to avoid any confound with a bias for a particular solution (which we did not find). Finally, our design meant that immigrants would change both physical and social environments, while residents would only change social environments. While this study is largely focused on the behavior of immigrants, residents provided valuable insight into behavioral changes caused by a change in social environment alone.

We hypothesized that immigrants would be most likely to adopt the resident solution using social learning under maximal spatial variability (E_a,P_a; see Figure 1C). We expected immigrants to adopt the resident solution more-so by individual learning in the E_s,P_a condition, as there would be no change in habitat cues to indicate a need to alter their behavior (comparable with the purely temporal variability tested in Aplin, Sheldon, and McElreath [32]). We

expected that immigrants might be somewhat influenced by residents in the E_a,P_s condition given the change in environmental cues, although there was no incentive to completely adopt the resident preference given that it provided the same reward. We expected immigrants would be least likely to switch preferences under minimal spatial variability (E_s,P_s). If social variability alone triggered social learning, we expected residents to be more likely to be influenced by immigrants in P_s conditions, since the mealworm reward would be more appealing that the buffalo worm reward obtained from the immigrant preference in P_a conditions.

To test these hypotheses, we recorded the solving behaviors produced by birds before and after immigration to determine whether immigrants adopted the resident behavior of their new population. We then used Bayesian dynamic learning models that could differentiate between social and individual learning to analyze the learning mechanisms responsible for changes to immigrant preferences.

Results

Before the experiment, we conducted pairwise food preference tests on a subset of birds (N = 21) to assess the relative value of the three food items used in our puzzles (sunflower seeds, buffalo worms, and mealworms). After 3 exposures to each food pair, birds chose buffalo worms over seeds roughly 75% of the time, and chose mealworms over buffalo worms roughly 93% of the time. A Bayesian inverse reinforcement learning model estimated that birds valued mealworms (estimated value Q=3.66) over buffalo worms (Q=1.72), and buffalo worms over seeds (Q=0.35). Food preference results are summarized in Table S1 and Figure S1).

We then introduced one automated puzzle box to each population. The solving behavior spread in 17 of 18 populations, with an median of 5 (range: 3−7) out of 7 non-tutor birds recorded as solving the puzzle in each population before the immigration event (total 78 birds). 8 of these birds were recorded as having fewer than 5 recorded solves, and were conservatively excluded from further analysis. The median latency to learn to solve the puzzle was 7.5 (range 1−31) days of exposure. In total, all solvers produced 200,109 recorded solutions, and non-tutor birds accounted for 145,426 of these. Solving frequency varied between birds, with non-tutor solvers producing a median of 1128 solutions (range: 5−8,677) over the course of the experiment. Tutors produced solutions about 5 times more frequently as non-tutors (tutors: median 126 solutions per day; non-tutors: 22.8).

Prior to the immigration event, non-tutor birds overwhelmingly preferred the solution demonstrated by the tutor, with 97.3% of non-tutor solutions being that of their tutor's. This preference was not significantly different between conditions, age and sex classes, or between birds that went on to become immigrants and residents (Table S2). Interestingly, but as expected, preference was estimated to be 3% lower in the symmetric payoff condition where both sides were equally rewarded with mealworms. Evidence that the behavior was socially learned was given by 1) the strong preference for the seeded solution in all populations that acquired the behavior, and 2) the 4 populations where the initial tutor did not solve also failed to innovate solving behavior and had to be supplied with tutors from other populations, or in the case of 1 more population, entirely excluded from the experiment.

Behavioral preferences after immigration

We then swapped two solving birds between each pair of populations to simulate an immigration event. Immigrants did not appear to exhibit stress responses to the immigration event, and there was no noticeable increase in antagonistic interactions towards them. Immigrants continued using the puzzle-box without interruption after immigration with a median delay of 0 days before starting to solve again. After the immigration, there were a median of 5 (range: 3 − 6) active solvers in each population, and a total of 33 immigrants were recorded as solvers (E_a,P_a = 9; E_s,P_a = 5; E_a,P_s = 11; E_s,P_s = 8). 29 of the 33 immigrants produced at least one resident side solution within the 14 days after immigration. Immigrants produced their first resident-side solution after a median of 2 solutions. All 4 immigrants that did not produce the resident side were in E_a,P_s condition in 4 separate populations.

Our hypothesis was generally supported when comparing the choices immediately preceding and following immigration (visualized in Figure 2), and over the longer term as the experiment progressed (Figure 3). Over the entire 14 day period following immigration, immigrants in the E_a,P_a condition produced the largest proportion of resident solutions (proportion per condition compared to the other conditions: E_a,P_a = .849, E_s,P_a = .676, E_a,P_s = .299, E_s,P_s = 0.014). This effect was observed whether we took the overall proportion of solutions (individual immigrants thus weighted by solution frequency), or allowed each solver to be weighted equally and took the mean (individual's mean proportion (SD) per condition: E_a,P_a = 0.891(0.129), E_s,P_a = 0.835(0.235), E_a,P_s = 0.269(0.422), E_s,P_s = 0.208(0.369)). Immigrants in the E_s,P_a condition also eventually adopted the resident solution, but with a delay relative to the E_a,P_a condition (Figure 2, Figure 3). This delay hinted at a difference in learning mechanism, which we return to in the following selection.

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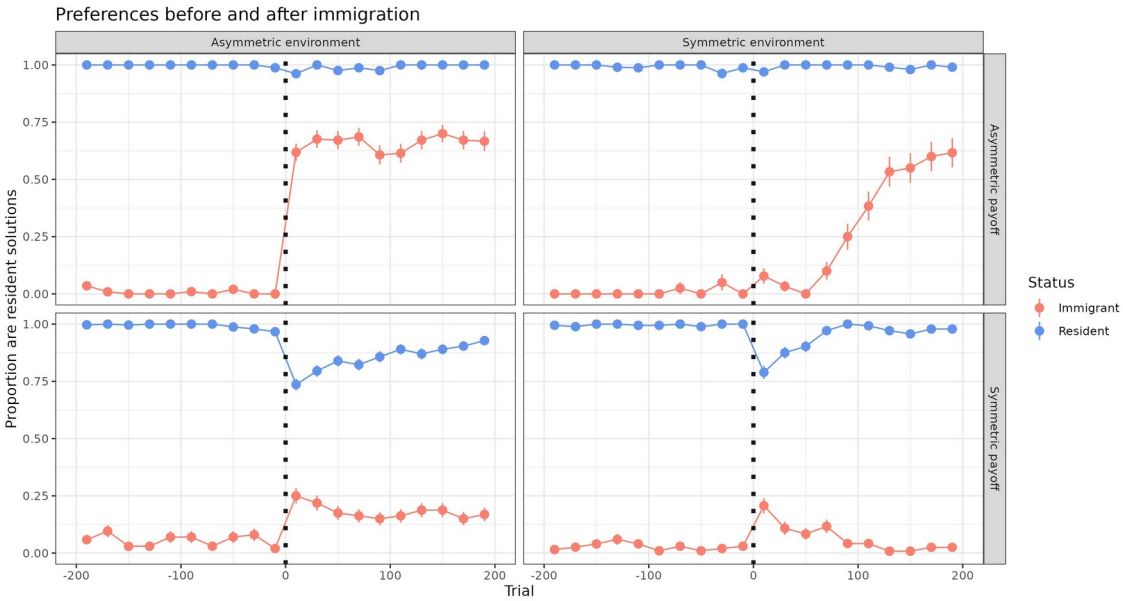

Figure 2: Behavioral preferences immediately before and after immigration. Mean, 95% CI of solutions produced by immigrants (blue) and residents (red) that were the resident preference in the destination population. Subset to the 200 choices before and after the simulated immigration event (dotted line). Prior to immigration, both immigrants and residents preferred the seeded solution in their respective populations. Following immigration, immigrants were most likely to adopt the resident solution when payoffs were asymmetric (P_a conditions). They adopted the resident solution fastest under E_a,P_a. Immigrants were least likely to adopt resident solutions under E_s,P_s, although more immigrants adopted the resident solution in E_a,P_s. The data underlying this figure can be found in our data and code repository [53].

We also found interesting perturbations in the preferences of immigrants and residents in the P_s conditions where both immigrants and residents appeared to be influenced by each other in the short term. Two immigrants came to prefer the resident preference (Figure 3 E_a,P_s condition), and surprisingly, nine residents used the immigrant preference more than 50% of the time (Figure S2 P_s conditions). Two of these had learned the puzzle after immigration, potentially socially learning from observations of immigrants. The commonality between the remaining seven were that they were very low-frequency solvers (range: 6-89 total solves) compared to the median (1128 total solves). We infer from this pattern that social variability can increase reliance on social information, as birds generally did not sample the opposing option prior to immigration. However, social influence was not generally strong enough to overcome the value of their original preference, gained through previous experience.

In order to understand how preferences changed over time, we conducted a logistic GLMM summarized in Table S3. On the first day after immigration, immigrants were most likely to produce the resident solution in the E_a,P_a condition (estimated $P = .896$). Immigrants in the E_s,P_a condition were significantly less likely to do so, with an estimated $P = .50$. Even less likely was the E_a,P_s condition at $P = 0.012$ and E_s,P_s condition at $P = 0.069$, although this was not estimated to be significantly different from E_a,P_s condition.

There was considerable variation in the solving experience of immigrants prior to the immigration event (median (Q1,Q3): 180 (7,1346) solutions), caused by variable solving rates (range: 1 to 260 solutions per day) or the latency to have learned to solve the puzzle. The amount of this prior experience negatively influenced the probability of producing the resident solution on the first day after immigration, although this did not meet our criterion for significance of $p < 0.05$ (GLMM; normalized experience - $\beta = -1.040$, $SE = 0.674$, $p = 0.124$). The interaction between experimental day and condition revealed that the probability of producing a resident solution significantly increased with each passing day in the both payoff asymmetric conditions (GLMM; day $\beta = 0.223$, $SE = 0.008$, $p < 0.001$, day : E_s condition - $\beta = 0.431$, $SE = 0.023$, $p < 0.001$). It significantly decreased in both environment symmetric conditions, more-so when the payoffs were also symmetric (GLMM; day : P_s condition - $\beta = -0.032$, $SE = 0.013$, $p = 0.015$, day : E_s condition : P_s condition - $\beta = -0.765$, $SE = 0.034$, $p < 0.001$). Age and sex did not significantly affect the probability of producing the resident solution, and were not included in the final model.

Learning models

Immigrants who began to prefer the resident-side solution could either have been influenced by social information provided by the residents, or could have independently decided to switch due to personal experience with the other solution. In order to better understand these potential mechanisms, we fit a set of 4 dynamic learning models, described in Materials and Methods, to the first 200 choices of all individuals after immigration. We were especially

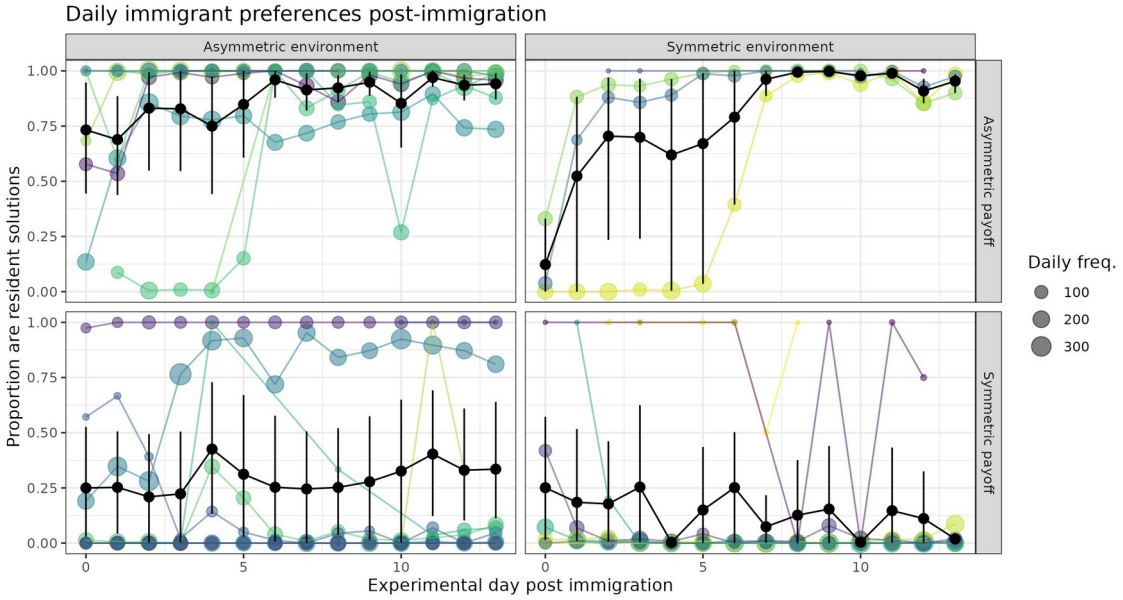

Figure 3: Daily preferences of immigrants after immigration. Proportion of immigrant solutions which were resident solutions (y-axis) over experimental day (x-axis). Colored lines are individual immigrants, with the daily solving frequency indicated (size). Black lines indicate mean, 95% CI. Immigrants were most likely to adopt the resident solution when payoffs were asymmetric. They adopted the resident solution faster when the environment was asymmetric, with a high adoption rate on day 0, compared to the symmetric environment condition. Immigrants were least likely to adopt when payoffs and environment were symmetric, although more immigrants adopted the resident solution when the environment was asymmetric. The data underlying this figure can be found in our data and code repository [53].

interested in the time-period immediately after immigration, as preferences stabilized after several days (Figure 3), and the acute effect that immigration might have on learning might dissipate as immigrants adjusted to the new environment. These models estimated learning parameters in each condition for both residents and immigrants (summarized in Tables S4, S5, S6, S7).

We found that all models which allowed individuals to be influenced by social information, rather than personal experience alone, predicted the data significantly better as measured by WAIC score, summarized in Figure S3. The lowest WAIC score was obtained by model SL3, which estimated a slope for the social influence parameter, a payoff bias and new associate bias parameters for social information (summarized in Figure 4, individual birds' point estimates in Figure S4). In all conditions, both residents and immigrants were estimated to be influenced by social information (although immigrants more-so), and this influence was estimated to decline over time in all conditions (Figure 4A). Importantly, the E_a,P_a condition was estimated to have the highest social influence immediately following immigration (σ(89% HPDI) = 0.49(0.18,0.81), Figure 4A), and immigrants were estimated to be disproportionately influenced by observations of the higher payoff solution (β_p= 0.75(−0.26,1.83), Figure 4B). When immigrants were socially influenced in the E_s,P_a condition, they were estimated to be more influenced by observations of the lower payoff solution by fellow immigrants (Figure 4B). Their eventual shift towards the residents' preference was thus more-so driven by individual learning, rather than social influence from residents.

Given that the payoff bias parameter's formalization required options with different payoffs, it was not informative for symmetric payoff conditions. However, SL3 also fit a new associate bias (B_n) to estimate whether immigrants and residents were more influenced by their new associates. We found a trend that residents in both symmetric payoff conditions were influenced by immigrant solutions (residents in E_a,P_s: β_n = 1.03(−0.03,1.95), E_s,P_s: β_n = 0.93(−0.67,2.45)), whereas posterior β_n distributions were centered around 0 in the P_a conditions, suggesting that residents were assessing the rewards and were not influenced by the lower-rewarded option (Figure S5). This bias explained the perturbation in residents preferences following immigration in Figure 2. Finally, we fit an ancillary model that estimated a tutor bias, but found no evidence for the disproportionate influence of tutors on immigrants (Figure S6).

When taken together with the general pattern in Figure 2, these mechanisms point to a clear behavioral difference between the E_a,P_a and E_s,P_a conditions: immigrants rapidly changed their preferences using social information when experiencing asymmetric environments, and were disproportionately influenced by the social observation of asymmetric payoffs. Meanwhile, when environments were symmetric, immigrants were less influenced by social information, and they did not disproportionately attend to the higher payoff solutions. Individual learning was the most likely mechanism behind their adoption of the resident preference.

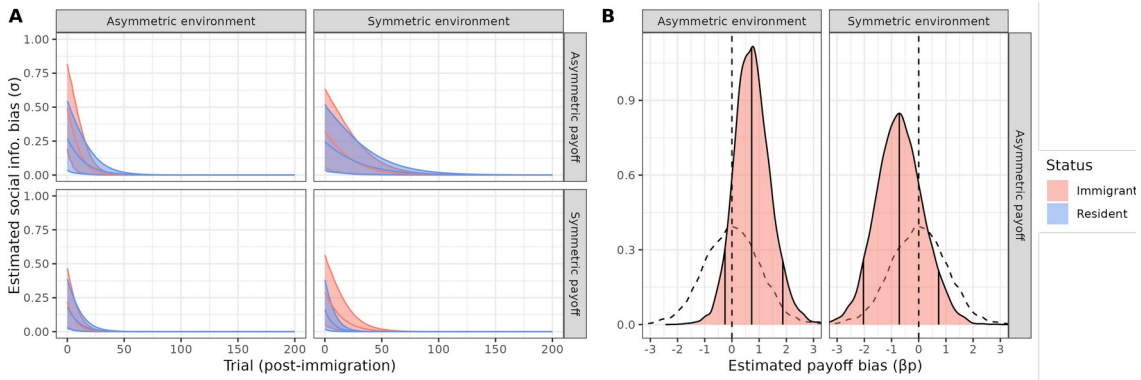

Figure 4: Learning parameter estimates related to social information for best fitting model SL3. A) Posterior distributions (mean, 89% HPDI) of social information bias (σ) over time since immigration. Individuals who immigrated to a different environment with different asymmetric payoffs were most immediately influenced by social information. B) Posterior distributions of estimated payoff bias (β_p) for conditions with asymmetric payoffs. Mean, 89% HPDI indicated by vertical lines. When birds immigrated to a novel environment, they strongly weighted observations of the higher-payoff solution.

Discussion

By simulating immigration events for individuals between groups with different traditions in different environments or different foraging pay-offs, we could disentangle flexibility in learning strategies associated with these two sources of variability. Our design also allowed us to test birds' responses to social variability alone. We found that immigrants were most likely to adopt the residents' preference when both environments and foraging payoffs differed, and relied more on social learning, likely with a pay-off bias. When environmental cues remained the same and only the payoff landscape changed, immigrants began to prefer the resident solution after a slight delay, more likely shifting due to individual learning. Immigrants were less likely to adopt the residents' preference under both symmetric payoff conditions, and least likely when environments and payoffs were symmetric. By contrast, residents, who only changed social partners and not locations, essentially never changed their preferences in the asymmetric payoff conditions, but did initially sample the immigrants' preference in the symmetric payoff conditions. These data suggest that residents were also able to perceive the rewards that others received at the puzzle-box, and that these observations initially influenced their choices immediately following immigration. Our results therefore generally supported our hypothesis with evidence for a stronger effect of spatial variability on behavioral responses.

The results of our experiment demonstrate that, in tits, social learning is not inflexible or unbiased, but rather can exhibit adaptive flexibility in response to environmental change or uncertainty [5, 12, 35, 13, 14, 36, 16]. Indeed, for over a century it has been recognized that phenotypic plasticity, or the expression of different phenotypes depending on environment, is crucial for success in adapting to novel environments [37, 38]. Our current study points to specific plasticity in learning strategy to changes in the environment. Our learning model analysis indicates the cognitive mechanism responsible for immigrants' rapid adoption of resident preferences in the E_a,P_a condition was the activation of a learning strategy where the rewards of others were accounted for when making future decisions. By inducing immigration events in controlled conditions, we further show that these changes in learning strategies, at least in great tits, are not due to underlying life-history state, e.g. tied to hormonal changes during dispersal [22]. Rather, they represent flexible shifts triggered by experience of new environments. However, we do not discount the role that hormonal changes may play in other contexts or species, and suggest that both mechanisms might operate in an additive effect.

In primates, immigrant individuals have been shown to conform to their new groups preferences [20], although this depended on behavioral context [21]. Specific reliance on a pay-off biased strategies by immigrants has been demonstrated in captive chimpanzees [39], and in male vervet monkeys, which are the dispersing sex [24]. The results of our experiment add to these findings, yet suggest that tits do not always adopt the preferences of their new group, but rather that this depends both on whether there is spatial variability in payoffs (in the sense that rewards of options has changed with physical location) and environmental cues. When uncertainty was high, either in the beginning of the experiment when birds were completely naive to the puzzle, or after immigration when payoffs and environmental cues changed, the tits relied on social information with a conformist bias in the first case (similar to initial acquisition in previous studies [29, 32]), and a payoff bias in the second case. Immigrants' retention of preferences in both P_s conditions, while conforming to theory, disagreed with anecdotal evidence from a limited number of birds suggesting that knowledgeable migrant birds adopt local preferences under symmetric payoffs [29]. However, unlike primates, tits likely do not use foraging behavior as a social identifier, and do not need to conform

to mitigate potential aggression [20]. Tits do not appear to conform for the sake of conformity, but rather need a good reason (i.e. better reward) to adopt resident preferences once having already learned how to use the puzzle.

Theory has suggested that payoff-biased learning should be favored in temporally varying environments [14], and evolves in spatially varying environments only if its cost is equal to or less than the cost of a conformist strategy [25]. We would suggest that a payoff bias is less costly than a conformist strategy for great tits, especially given their winter fission-fusion social system. Firstly, it may be difficult for immigrants to assess which of their group members are residents, as opposed to other immigrants from a third location. Secondly, the number of residents may be less than the number of immigrants, leading to a case where the frequencies of behaviors are not indicative of their adaptive value. This was also the case in our experiment, where residents varied substantially in their solving rate, leading to some replicates where the large majority of behavioral information was only available from one resident. Thirdly, we argue that payoff assessment is a cognitively straight-forward task in our design, since immigrant birds are already familiar with both buffalo worms and mealworms, and these food items are visually distinct with mealworms being about twice as large as buffalo worms. Birds carry the food items away from the puzzle in their bill before processing and eating them. Immigrants only had to attend to others' solutions and recognize the reward earned by the choice of a conspecific was a food item that they preferred more-so than the reward they had been earning from their own behavior. In open fission-fusion systems, the observation of payoff cues is therefore likely a more reliable means of identifying adaptive behavior. Thus, this is a case where theory and natural ecology of a species match to experiment.

Our experiment also highlights the distinction between transmission biases versus production biases. The birds in our study strongly preferred their tutor's seeded solution, with results in line with prior work on tits [29, 32]) that showed that great tits socially learn and acquire novel behaviors with a conformist transmission bias. The pay-off bias that we evidence after immigration is a bias in social influence, which acts on production, rather than a transmission bias (as emphasized by Chimento et al. [40]). Thus, while the prediction presented by Nakahashi et al. [25] that conformist transmission bias out-competes payoff transmission bias in spatially varying environments may be valid, it might not necessarily speak to the evolution of payoff-biased social influence on production, as would be the case for immigrants that held previous knowledge.

In most previous studies that rely on observations of natural immigration events [41, 29], it is impossible to distinguish between changes in social environments and changes in physical environments. In our study, changes in social environment alone did not trigger a payoff bias. This is perhaps to be expected, given that the tits exhibit fission fusion-foraging flocks during winter when their reliance on social information is highest [42]. Tits' associates may change within and between days, even though their home-range may only less than a square kilometer [43, 27], and likely not too spatially variable. However, tits can move several kilometers, and occasionally irrupt in response to environmental triggers, travelling hundreds of kilometers to take up residence in a novel environment [44]. Therefore, it is plausible that environmental variability, rather than social variability, would trigger payoff-biased social learning. A prior study on tit's response to purely temporal changes in payoffs found that birds relied more-so on individual learning rather than social information, with evidence for an ongoing conformist bias, but no evidence for a payoff-bias [32]. This finding is consistent with the results from our experiment in the E_s,P_a condition, where immigrants preferred the resident solution after a slight delay.

In summary, our results have shown that birds change their behavior most rapidly when immigrating to a novel environment, with behavior shifting to match the resident preferences. We further showed that this behavioral change was achieved through the use of payoff-biased social information. Our study therefore adds empirical support for the hypothesis that spatial variability can drive the evolution of flexible social learning strategies. Our results further suggest that, in tits, spatial variability is a stronger trigger for adaptive shifts in learning biases than temporal variability. Finally, we highlight that social learning strategies that act on production may not necessarily be the same as strategies that act on acquisition.

Materials and Methods

Our experiment consisted of 18 micro-populations of wild caught great tits (N = 144 birds), kept in outdoor aviaries of 3x4x3m volume, and given *ab libitum* access to water, a seed-based food mix, and a puzzle-box containing live food. Each population began with 8 birds, one of which was a "tutor" who had been previously trained to solve an automated puzzle-box using the training method described in Chimento, Alarcón-Nieto, and Aplin [33]. We balanced age and sex (77 males) to the best of our ability given the stochastic sampling of catching wild birds. Populations contained a mix of first-year and adult individuals (69 adults) and were caught from various sites within 10km of the Max Planck Institute of Animal Behavior (47.768064, 8.996331). The puzzle-box consisted of a sliding door that could be pushed left or right. Pushing in either direction was equally difficult, but the reward was side-specific: either mealworms, buffalo worms, or sunflower-seed, depending on the experimental conditions described below. Puzzle-boxes were automated, and used an RFID antenna to record identities of birds, the time at which they landed on the perch, the side which they pushed the door open (recorded by infrared sensors), and the time at which

they left the perch [29, 33, 45]. From this data, we could track the behavioral productions of each solving bird over the course of the experiment. Puzzle-boxes were placed in a corner facing the center of the room, allowing all birds in the room to potentially observe it.

The experiment took place over two time periods, from January to March in 2021 (N=48 birds) and 2022 (N=88 birds). The experiments were conducted during winter when tits are most tolerant of other birds and form foraging flocks. This is outside the main dispersal times in tits, which tend to occur during autumn or early spring, but flocks can roam extensively outside individuals' core home-range throughout winter [27]. The experiment began with a diffusion period lasting between 15-21 days to allow for the solving behavior to spread. Once the solving behavior was learned by three or more birds, the populations underwent an immigration event, where two non-tutor solvers from each population were exchanged with two non-tutor solvers from another population (henceforth immigrants). This was done in the night by moving nest boxes, such that birds went to sleep in their nest box in their source population, and woke up in their nest box in their destination population.

Importantly, immigration occurred between populations with opposing resident solutions. We attempted to balance immigrants based on sex (19 male), age (13 adult), and solving rate (17 with > 100 solutions prior to immigration). Two more non-solving birds were removed from each population at this point for ethical considerations, as non-solving birds were considered to be unlikely to learn the task. The experiment continued for 14 days following the immigration event. After the experiment ended, the birds were released back into the wild at the location where they were caught.

Populations were split into four conditions, in a 2x2 factorial design where we manipulated environmental conditions and payoff conditions. Aviaries contained foliage from one of two different environments that great tits are naturally found in: pine or deciduous forest. Additionally, the puzzle-box doors were also either blue or grey, depending on the environment type. In the symmetric environment (E_s) condition, immigrants moved to a population with an identical environment to their original population. In the asymmetric environment condition (E_a), immigrants moved to a population with a different environment.

In the symmetric payoff (P_s) condition, pushing from either side of the puzzle-box door gave access to a reservoir of mealworms, and the same was true after the immigration event. In the asymmetric payoff condition (P_a), populations began with a puzzle-box that gave either buffalo worms (the resident solution that the tutor had been trained on), or sunflower seeds (see Figure 1B). Buffalo worms are smaller than mealworms and less preferred by the tits (see section *Food item preference tests*). Both buffalo worms and mealworms are preferred to sunflower seeds [32]. After the immigration event, the food rewards were changed such that the resident solution gave access to mealworms, while the immigrant solution gave access to buffalo worms. Therefore, immigrants would not necessarily realize that the payoff structure had changed without using social information or sampling the other solution themselves.

Four of the E_a,P_s replicates were performed in 2021, with two more in 2022 to test for year effects. Two of the E_s,P_s replicates were performed in 2021, and two more were performed in 2022. All of the E_s,P_a and E_a,P_a replicates were performed in 2022. Altogether, E_s,P_s and E_a,P_a had four replicate populations, E_s,P_a had three replicates (due to the exclusion of one population where the solving behavior did not spread), while E_a,P_s had six. We also note that the tutors of 4 populations did not solve within the first 7 days, and were replaced with tutors trained on the same solution from another population.

Puzzle preference models

In order to assess non-tutor birds' preferences relative to the seeded solution in source populations prior to immigration we conducted a GLMM using the lme4 and lmerTest packages in R [46, 47, 48] where the dependent variable was a birds' proportion of solutions that were the seeded solution introduced by the tutor bird predicted by the age, sex, and a three-way interaction between immigrant status, payoff and environment conditions. Year was included as a random effect. Data was subset to only days prior to the immigration event.

In order to analyze how non-tutor birds' preferences changed over time after the immigration event, we used a logistic GLMM where the dependent variable was whether a solution was the seeded solution in the destination population, predicted by normalized experience, and a three way interaction between experimental day, environment and payoff conditions. ID nested within year was included as random effects. Data was subset to only days after the immigration event took place. Normalized experience was measured as the total number of solves minus the mean number of solves divided by its standard deviation. Experimental day 0 represented the day immediately following immigration. For both models, summary tables were created using the stargazer package [49].

Learning models

In order to understand the learning mechanisms by which immigrant birds' changed or kept their preferences, we analyzed the first 200 choices made immediately following immigration using Bayesian reinforcement learning models. Birds solved at variable rates, but these choices were generally made within the first few days following

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immigration. We first fit a model that only allowed for individual learning of preferences, and then fit decisionbiasing models, which estimate the degree to which social information influences preferences [10, 32, 50, 26]. These models assumed that individuals keep a memory of social observations (S) that were considered along with an expected value (Q) calculated from personal experience to influence choice probability. We compared models using the widely applicable information criterion (WAIC) scores.

Individual learning model (IL)

The simplest model estimated 2 parameters: a learning rate (ρ) and a temperature parameter (α). ρ is constrained between 0 and 1 and was estimated on a logit scale. *alpha* is constrained to be above zero and was estimated on a log scale. When a bird produced a solution k at the puzzle-box, its expected value for chosen option k, $Q_{k,t+1}$, was updated as a function of the reward (π_k) weighted by ρ:

$$Q_{k,t+1} = \rho\pi_k + (1-\rho)Q_{i,t}. \tag{1}$$

The un-chosen option was updated with $\pi_k = 0$. Expected values were transformed into an individual choice probability I in Equation 2 using a softmax function where repertoire Z_i was a vector of both behaviors and temperature parameter α controlled sensitivity to differences in expected values:

$$I_{i,k,t} = \frac{\alpha exp(Q_{k,t})}{\sum\limits_{k \in Z_i} \alpha exp(Q_{k,t})}. \tag{2}$$

When *alpha* > 1, individuals were more likely choose the option with a larger Q-value. When $\alpha = 1$, individuals were linearly sensitive to differences in Q values, and when $\alpha < 1$, they were less sensitive.

Social learning model (SL1)

The first social learning model estimated a learning rate (ρ), a risk-appetite parameter (α), and a social information bias (σ) with a frequency cue. *sigma* was estimated on a logit scale. Rather than relying on personal experience alone, socially observed solutions could bias individuals' final choice probabilities. Solutions k observed by individual i at time t were accounted for by frequency cue S:

$$S_{i,k,t} = \frac{\sum\limits_{t-15m}^{t} n_k}{\sum\limits_{k \in Z_i} \left(\sum\limits_{t-15m}^{t} n_k \right)}, \tag{3}$$

where the number of observations of solution k was summed over a period of 15 minutes prior to t, and was normalized by the sum of all solutions observed. This social information was combined with personal information into a probability of choice $P_{i,k}$. The relative importance of social information was determined by σ. Here a low value would mean agents were predominantly influenced by their personal experience, and a high value meant that they were predominantly influenced by their social observations.

$$P_{i,k,t+1} = (1-\sigma)I_{i,k,t} + \sigma S_{i,k,t} \tag{4}$$

The calculation of S required us to define which solutions could be observed by a focal bird. Given the position of the puzzle-box within the aviaries, all birds could potentially observe it, as well the rewards that birds carried away in their bills. We assumed that if solution k was produced by any other birds in the 15 minutes prior to the current solution, it was observed. 10 minutes, and 20 minutes were also tested, but resulted in similar estimates with poorer fits.

Social learning models with payoff and new associate biases (SL2)

In SL2, we implemented a payoff bias β_p and a new associate bias β_n in a log-linear term L:

$$L_k = \exp\left(\beta_p \bar{\pi}_k + \beta_n a_k\right). \tag{5}$$

Payoff cue $\bar{\pi}_k$ was the average reward observed for choice k. Thus, β_p estimated whether individuals were assessing the value of the food items obtained by others from either side of their puzzle, where $\beta_p = 0$ indicated that an individual was insensitive to observed payoffs, $\beta_p < 0$ indicated that they would be more influenced by behaviors

with relatively lower payoffs, and $\beta_p > 0$ indicated that they would be more influenced by behaviors with higher payoffs. Due to its formalization, this parameter could only be meaningfully estimated for asymmetric reward conditions. The new associate cue a_k represented the proportion of observed solutions k which had been performed by new associates. The log linear term was then included by modifying equation 3:

$$S_{i,k,t} = \frac{n_k L_k}{\sum_{k \in Z_i} (n_k L_k)}. \tag{6}$$

Social learning model with time-varying slopes (SL3)

We expected σ to potentially weaken over time, as evidenced in a previous experiment on human immigration [26]. We modified SL3 to include a slope parameter β_σ, allowing us to estimate whether social influence increased or decreased with each trial t:

$$logit(\sigma) \sim \mu_\sigma + \beta_\sigma t \tag{7}$$

The values of ρ, σ, β_p, β_n and β_σ were estimated within conditions C and immigrant status S, with random effects of individuals (e.g. $logit(\rho) \sim \alpha_{[ID]} + \mu_{\rho,[C,S]}$). We did not have any specific predictions about differences in α between conditions, and this was estimated as a grand mean with random effects of individuals. For all parameters except σ, we assumed weakly informative normal priors for means (e.g. $\mu_\rho \sim N(0,1)$), making our model skeptical of large effects. For σ, we conservatively assumed a lower prior ($\mu_\sigma \sim N(-1,1)$) based on estimated σ from a prior study [32]. We used non-centered varying effects with a Cholesky decomposition of the correlation matrix, following prior applications [50, 26]. We ensured model convergence using Gelman's statistic $\hat{r} < 1.01$ and visually confirmed that chains were well-mixed by using rank histograms. We validated models with simulated data using known parameter values to confirm that models could accurately recover values. Code for simulation is available at the link in the data availability section. All models were fit with 5 chains and 5000 iterations using R v. 4.0.2 [48] with Stan v. 2.27 [51] via Rstan v. 2.21.2 [52].

Food item preference tests and payoff coding

To determine how birds perceived the relative rewards of the different food items, we performed preference tests prior to the diffusion phase of the experiment. In these trials, open bowls of sunflower, mealworms and buffalo worms were provided in a table in the middle of 4 aviaries, and the choices by 21 individuals were recorded for 3 replicate trials in each aviary (summarized in Figure S1). We found that birds preferred mealworms over buffalo worms approximately 93% of the time, while buffalo worms were preferred over seeds. We conducted a Bayesian inverse reinforcement learning model to estimate the values of each food item (results reported in Table S1). We then used these point estimates to inform the rewards received in the learning models. We also used the values estimated by the inverse RL model to code birds initial knowledge state. Assigning $Q_{i,k,t=0} = 0$ for both solutions would be an unreasonable assumption that individuals have a 50% chance of producing either behavior immediately after immigration. All immigrants had a majority of their experience with the immigrantside solution (.97 of their solutions entire diffusion phase), and thus we coded $Q_{i,IM,t=0} = 1.72, Q_{i,RS,t=0} = 0$ in the asymmetric payoff condition, and $Q_{i,IM,t=0} = 3.66, Q_{i,RS,t=0} = 0$ in the symmetric payoff condition. This biased them towards their preferences upon immigration, yet assumed a non-zero probability that they might choose the alternative side.

Ethics Statement

All work was conducted by under a nature conservation permit and animal ethics permit from the Regierungsprasidium Freiburg, no.35-9185.81/G-20/100.

Data Availability

Code and data for statistical analyses, model validation and figures are available on Edmond [53].

Acknowledgements

M.C. and G.A.N. received funding from the International Max Planck Research School for Quantitative Biology, Ecology and Evolution (https://imprs-qbee.mpg.de/). L.M.A. was funded by a Max Planck Research Group Leader Fellowship (https://www.mpg.de/career/max-planck-research-groups). M.C. and L.M.A. were supported by the

Centre for the Advanced Study of Collective Behaviour, funded by the Deutsche Forschungsgemeinschaft (DFG) under Germany's Excellence Strategy (EXC 2117-422037984). (https://www.dfg.de/en/research-funding/funding-initiative/excellence-strategy). M.C. and L.M.A. were supported by the Swiss State Secretariat for Education, Research and Innovation (SERI) under contract number MB22.00056 (https://www.sbfi.admin.ch/sbfi/en/home.html). No funders played any role in the study.

Competing Interests

The authors declare no competing interests, financial or otherwise.

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