

Conformity does not perpetuate suboptimal traditions in a wild population of songbirds

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Social learning is important to the life history of many animals, helping individuals to acquire new adaptive behavior. However despite long-running debate, it remains an open question as to whether a reliance on social learning can also lead to mismatched or maladaptive behavior. In a previous study, we experimentally induced traditions for opening a bi-directional door puzzle-box in replicate sub-populations of great tits *Parus major*. Individuals were conformist social learners, resulting in stable cultural behaviors (Aplin LM et al. (2015) *Nature* 518: 539-541). Here, we vary the rewards gained by these techniques to ask to what extent established behaviors are flexible to changing conditions. When sub-populations with established foraging traditions for one technique were subjected to a reduced foraging pay-off, 49% of birds switched their behavior to a higher-payoff foraging technique after only 14 days, with younger individuals showing a faster rate of change. We elucidated the decision-making process for each individual using a mechanistic learning model (McElreath et al. (2005) *Evol. Human Behav.* 26: 483-508) to demonstrate that, perhaps surprisingly, this population-level change was achieved without significant asocial exploration and without any evidence for pay-off biased copying. Rather, by combining conformist social learning with payoff-sensitive individual reinforcement (updating of experience), individuals and populations could both acquire adaptive behavior and track environmental change.

Social learning | Animal Culture | Conformity | *Parus major*

Social learning, the acquisition of behavior by observation of, or interaction with, other individuals, is common to many animal species. It provides a relatively cheap way of acquiring valuable information, and shields naive individuals from the risks of engaging in trial and error learning. A range of studies have further highlighted the crucial role of social learning in promoting cultural behavior and shared traditions (1–4), and suggested that the cultural inheritance of information across generations may be an important component of the behavioral ecology of some animals (1, 5, 6). However social learning may also be disadvantageous, if copied information is outdated or mismatched to the observing individual. How individuals balance costs and benefits of social learning has therefore been the focus of much recent research aiming to understand how natural selection has shaped learning (7).

The use of social learning ‘strategies’ is one possible route by which animals can combine and filter different kinds of information to optimize learning outcomes (8–10). Here, individuals use social cues, often from multiple conspecifics, to bias learning in favor of better quality information. These include preferences to copy kin, more prestigious or older individuals, as well as conformist and pay-off biased social learning (11, 12). Such learning strategies also have implications for the spread and persistence of information in populations, and for cultural evolution more broadly (13, 14). For example, conformist

transmission, here defined as the disproportionate tendency to copy the most common behavioral variant (15, 16), may evolve as a means of providing naive individuals with a quick way of ascertaining locally adaptive information. However it may also have the outcome of maintaining group differences in behavior, with within-group traditions resilient to invasion by alternative variants.

Empirical evidence for conformity in non-human animals is currently limited, but hints at a wide taxonomic occurrence; with proposed cases in fish (17), birds (18), and primates (4, 19). Furthermore, theoretical modeling has suggested that conformist transmission should evolve under a wide range of conditions, and be particularly favored when environments are spatially heterogeneous (15, 20). Yet if individuals are exclusively conformist, then any new environmental change may result in a mismatch with the majority behavior, leading to a perpetuation of sub-optimal or maladaptive traditions over time (21), and exaggerating the disadvantages of social information use. Evolutionary modeling has gone as far as to suggest that in socially-learning animals, coupling of conformist learning with environmental change could lead to population collapse (22).

This apparent paradox of non-adaptive culture has thus been the subject of much debate (23–28), with two individual-level strategies proposed as a potential means of evading this evolutionary trap. First, individuals could switch from socially learnt behavior to engaging in asocial learning (individual innovation) when the rewards gained for performing the established tradition are less than previously (7, 12, 27, 29). Second, individuals could combine conformist tendencies with pay-off biased social learning, using a ‘behavioral toolbox’ of social learning strategies when choosing what behavior to adopt, thus integrating information about both the frequency of behavior and the relative reward gained by demonstrators (8, 30). Such a strategy has been observed in laboratory experiments in humans (8). However empirical tests for the occurrence or emergence of sub-optimal or maladaptive traditions in animals have been limited (31, 32).

In a previous study, we demonstrated an influence of conformist transmission on the social learning of novel foraging techniques in wild great tits (*Parus major*) (18). There, we trained two demonstrators in each of five sub-populations to one of two equal alternative solutions to a novel task, where food could be gained from a puzzle-box by pushing a bi-directional door to the right (technique A) or left (technique

LMA conceived of the study and the analysis, as well as designed and completed the experiments. RM coded and conducted the analysis. Both authors contributed equally to the manuscript. BCS conceived of the study, designed experiments and edited the manuscript.

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B). Using automated tracking of individuals and their choices, we then mapped the spread and establishment of these seeded behaviors through each sub-population. Results showed a sigmoidal relationship between a naive individual's probability of adopting one of the two techniques and its frequency in their foraging group, with birds disproportionately likely to learn the majority technique. Across each sub-population, the most common behavior therefore became increasingly prevalent over time (18). These strong preferences at the sub-population for one technique persisted over the two generations measured, suggesting that technique choice had become established as a stable cultural behavior.

Here, we vary the rewards gained by these techniques in order to investigate whether a reliance on conformist social learning will result in mismatched behavior after conditions change. First, in four sub-populations, two with established traditions for technique A ("left"), and two for technique B ("right"), we stocked all puzzle-boxes with a less preferred food reward over 2 days, so that solving using either technique was rewarded with a lower pay-off. This "equal low pay-offs" condition was designed to test whether individuals would explore alternative foraging behaviors when confronted with a lower pay-off from their previously learned behavior. Second, and immediately following this condition, all puzzle-boxes were stocked with unequal rewards for a period of 14 days. Solving using the established tradition was thus rewarded with this same less preferred food, but solving with the uncommon behavioral variant now resulted in a high pay-off. While most individuals had no experience of the uncommon solution, a small minority of individuals already preferred it, and so provided available social information for the new difference between the two techniques. Finally, all visits and behaviors at the puzzle-boxes were monitored using automated tracking. By quantifying the decision-making process for each individual's visit to the puzzle-box we then examined whether: 1) individuals switched from conformist to pay-off biased copying when observing others receiving variable rewards; 2) if individuals flexibly adjusted their behavior in response to learning about and gaining variable rewards; and 3) if this resulted in a population-level shift in behavior.

Results

Condition 1: Equal High Pay-offs. A tradition for pushing a bi-directional door either to the right (Variant A; T1-2) or left (Variant B, T3-4) was experimentally induced in 4 sub-populations of great tits (see Aplin et al. (18) for detailed methods), Fig. 1a. Either solving technique was rewarded with the same highly preferred food, a live mealworm. In all sub-populations, the large majority (87-98%) of solutions used the technique that had been introduced by the trained demonstrator at the beginning of each experiment, with the population-level bias to this technique becoming increasingly entrenched over time (18) (Fig. 1b).

Condition 2: Equal Low Pay-offs. For a two-day period following condition 1, three puzzle-boxes were distributed in each sub-population that rewarded both variant A and B with a less preferred food, sunflower seed (ESM Fig. 1) (18). Compared to condition 1, there was no change in the overall proportion of each solution performed in any sub-population (Welch two-sample test - T1: $t = 0.82$, $P = 0.42$; T2: $t = -0.16$, $P = 0.87$;

T3: $t = -0.57$, $P = 0.57$; T4: $t = 1.42$, $P = 0.16$), Fig. 1b. While these patterns may have differed over a longer time frame, these results suggest that, at least over two days (average no. solves per individual across replicates = 22(14-30)) birds did not change their sampling behavior in response to experiencing or observing lower rewards.

Condition 3: Unequal Pay-offs. Immediately following condition 2, puzzle-boxes with unequal rewards were installed at all sites/sub-populations over a period of 14 days. Here, solving using the established tradition was rewarded with this same less preferred food of sunflower seeds, while solving with the uncommon variant was rewarded with live mealworms. Overall, there were significantly more solutions of the alternative variant performance in condition 3 than in the previous conditions (Welch two-sample test, first vs. third condition - T1: $t = -5.28$, $P < 0.001$; T2: $t = -3.87$, $P < 0.001$; T3: $t = -3.75$, $P < 0.001$; T4: $t = -5.86$, $P < 0.001$), Fig. 1b. In the last part of condition 1, an average of 8(2-16)% of individuals showed either no preference, or preferred the alternative variant. For these individuals, their preference did not change in condition 3. By contrast, 49(33-71)% of other individuals had switched to change their variant preference by the end of the experimental period (proportion of all solves for each individual over last two days).

Similarly to Aplin et al. (18), we analyzed the change in individual and population preferences over time. First, as the data were clearly bi-modal (ESM Fig. 2), a longitudinal clustering algorithm was used to group individuals into two behavioral trajectories, with 48% (0.33-0.67%) of individuals falling into cluster 1. Clusters were then analyzed separately using a generalized estimating equation (GEE) model where the dependent variable was the proportion of solves using the established technique on each of 15 days and the explanatory variables were day, individuals weighted by their total number of solves, and sub-population (Fig. 2). There was strong evidence in cluster 1 that the preference for the established tradition decreased over time (pooled replicate data; coefficient \pm s.e.m. = -0.27 ± 0.02 , $P < 0.001$). Cluster 2 showed a significant but much lower decreasing preference for the established tradition (pooled replicate data; coefficient \pm s.e.m. = -0.13 ± 0.02 , $P < 0.001$); Fig. 2. This bimodality in the rate of change over time was related to age, with younger individuals more likely to fall into cluster 1 (GLMM: $z_{140} = -2.94$, $P = 0.003$). There was no relationship between cluster membership and any other measured variables (sex - GLMM: $z_{116} = 0.26$, $P = 0.79$; prior preference strength - GLMM: $z_{116} = -0.89$, $P = 0.37$; no. of solves in condition 1 - GLMM: $z_{116} = -0.89$, $P = 0.37$). Lastly, and in support of this result, there was a negative correlation between age and likelihood of preferring the high-payoff variant in the last two days of the experimental period (LMM: -0.07 ± 0.02 , $t = -3.83$, $P < 0.001$); Fig. S1.

Analysis of learning mechanisms. We next investigated the relative contribution of different learning mechanisms to the observed change in behavior during condition 3. To address these questions statistically, we used a sequential learning model of a form previously used to study the interaction of social and asocial learning (8, 33). This framework allows for individual choices to be modeled as products of time-varying interactions of different modes of learning. Specifically, each solution decision was modeled as a binary outcome in which

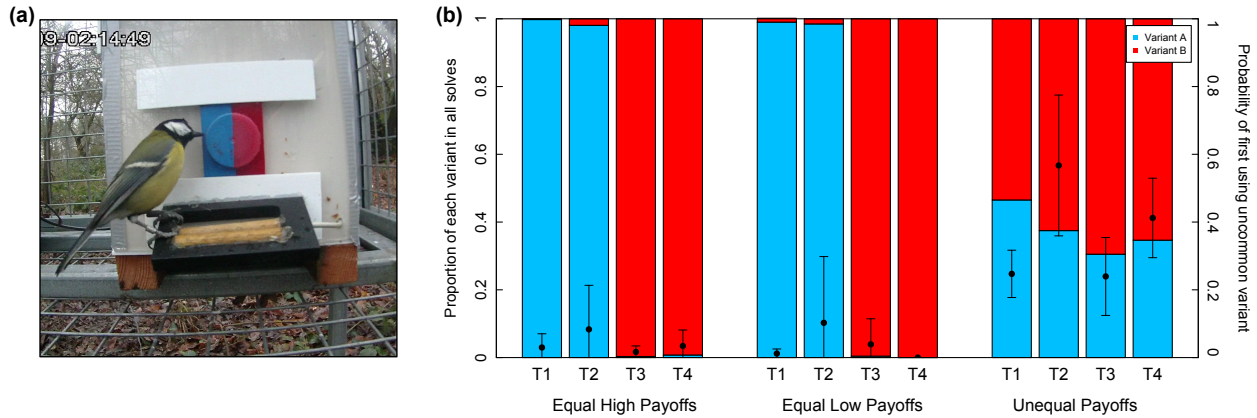


Fig. 1. (a) A puzzle-box where visiting individuals can slide the door open from either the blue/left side (variant A) or red/right side (variant B) in order to access a reward in a concealed feeder behind the door. The individual pictured is solving using variant A. Solving using either option can give the same (equal condition) or different (unequal condition) rewards. Puzzle boxes record identity, contact duration and solution choice, and reset after each visit. **(b)** Proportion of variant A or B used in each replicate (T1-4) in three sequential conditions after variant A (T1-2) or variant B (T3-4) had been initially introduced by a trained demonstrator: i) equally high pay-offs for each solving option, proportion for last 5 days shown; ii) equally low pay-offs for each solving option (2 days); and iii) unequal pay-offs, with the established tradition leading to a lower reward (14 days). Dots and error bars show mean and 95% CI of the probability of individuals' first solve in each condition being the uncommon variant.

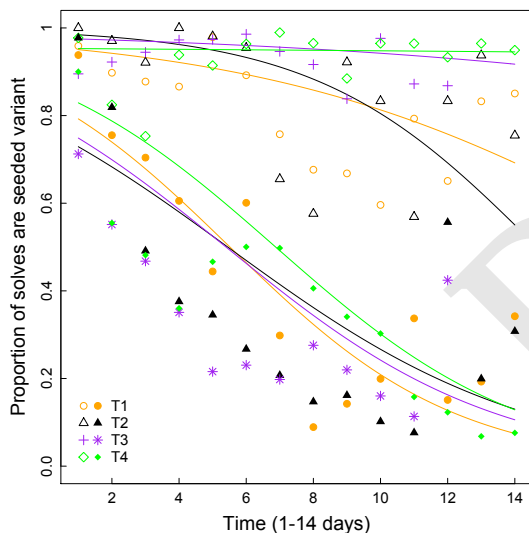


Fig. 2. The proportion of solutions using the seeded technique decreased over time in each replicate, with individuals moving towards preferring the previously uncommon technique. Each replicate is shown in a different color/shape, and filled and empty points represents the two distinct clusters of individuals identified in longitudinal clustering algorithm (filled points cluster 1, empty points cluster 2). Lines show the generalized estimating equation model fit for each cluster/replicate.

the probability of an individual choosing either option was a combination of both social cues and accumulated experience. Social cues included the frequencies of each behavior and the relative value of demonstrated rewards, and were calculated from activity immediately prior to a given solve at a given puzzle-box (18). Code sufficient to repeat our results is available as an R package, *wythamewa*, that contains the data, models, simulation code, as well as code for reproducing each figure to follow.

Four model parameters were considered: s , g , λ and y , representing respectively the influence of social cues on choice, the updating rate (how quickly individuals' attraction to an option responds to newly experienced payoffs), an individual's conformist exponent, and its pay-off social learning bias (population averages presented in table S1). There was little evidence for a pay-off social learning bias in individuals' behavior, with no individuals weighting this parameter higher than 0.1 (Fig. S2). All other parameters were more important, yet there was considerable individual variation in each (see ESM). Solving individuals ranged in their behavior from little use of social information to placing more than half of their decision-making weight on social cues (s). Similarly, the updating rate (g) ranged from nearly zero to over 0.8. Notably, these two parameters were correlated across individuals, indicating that birds that tended to learn socially also updated their personal information more quickly.

In contrast to pay-off social learning biases, the large majority of individuals had a conformity exponent (λ) above 1, indicating at least mild conformity in their use of social cues (above dotted line, Fig. 3a). However here was a strong negative correlation with overall reliance on social learning (s), such that birds who put lower weights on social learning were more strongly conformist (Fig. 3a). It is easier to understand the impact of these individual differences by translating the estimates for each individual into an implied social learning function, as defined by Expression 5. Panel (b) in Figure 3 shows these implied functions, plotted for the posterior mean of each individual. Here, an s-shaped curve corresponds to conformist learning. While a few birds appear slightly anti-

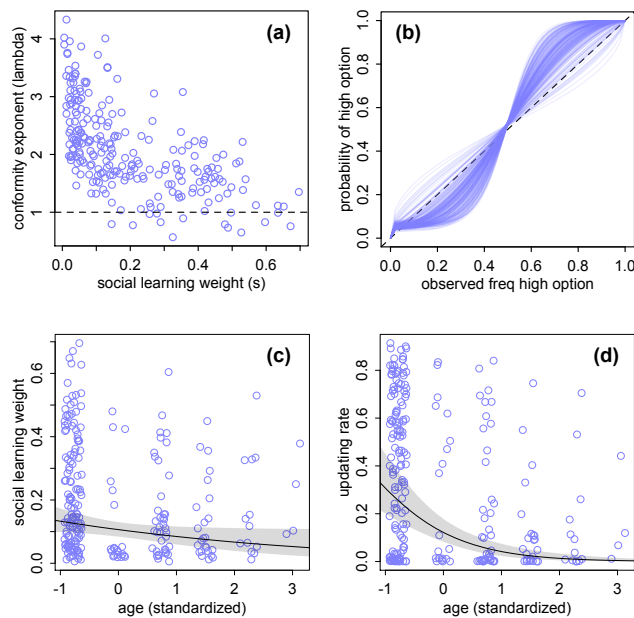


Fig. 3. Individual parameter estimates for mechanistic learning model. Each point represents the posterior mean for an individual bird. **(a)** Strength of conformity (λ) is negatively correlated with reliance on social learning (s), but most individuals show some conformist bias (exponent above 1). **(b)** Implied social learning influence functions (Expression 5). The diagonal line represents unbiased social learning. S-shaped curves are conformist individuals. The weak influence of payoff bias shifts these curves upwards in the lower-left corner. **(c)** Reliance on social cues tends to decline with age, explained mainly by the presence of large values of s in the youngest individuals. Individuals with low values are present at all ages. **(d)** Updating rate g tends to decline with age. The youngest individuals can be highly responsive to individual experience, while the oldest individuals change their attraction scores more slowly.

conformist, it must be noted that the figure shows posterior means, with considerable uncertainty about the exact function of any one individual. Inspecting individual functions with full uncertainty envelopes confirms that there is no strong evidence for anti-conformity in this population, only for a minority of individuals whose behavior is consistent with both weak anti-conformity and weak conformity.

There was a consistent negative impact of age on both weight given to social cues (s) and updating rate (g). In contrast, there were no consistent or strong effects of age on conformity (λ) nor on payoff-bias (y). These relationships are shown in Figure 3c and d, and suggest that older individuals were much less influenced by social cues and also changed their behavior more slowly in response to changes in personal experience. This is in agreement with the descriptive results: older individuals switched to the high-payoff variant more slowly. Younger individuals, in contrast, adapted more quickly; these "adaptor" individuals showed the strongest use of social information and simultaneously tended to be less conformist, yet also tended update their own attraction scores more quickly in response to new personal experience.

Modeling the link between individual behavior and population-level patterns. The results in the previous section suggest a combination of conformist social learning and payoff-sensitive individual reinforcement (updating) in the population, with individual variation in all measures. Surprisingly, given our initial hypotheses, we found no evidence of individual explo-

ration or payoff-biased social learning of sufficient strength to explain the patterns of behavior change. Therefore, does the conformity present in the population slow the rate of switching; or does it rather help both individuals and the population show adaptive responses to environmental change?

To test this, we used the same learning model as for data analysis and used it as a forward evolutionary simulation. We simulated groups of individuals learning together, with parameters for the weight of social cues, strength of conformity, and updating rate. We first used these simulations to validate our data analysis code, and then explored the population dynamics arising from different parameter settings. Finally, we computed selection gradients on the parameters.

First, we consider three examples to show the role of conformist social learning (Fig. 4). Each plot shows the time series of a simulated group of 10 learners, where pay-offs switch for the variants at turn 1 and again at turn 30, with groups starting by preferring the low variant. Only conformist strength λ is varied, with other parameters held at $s = 0.5$, $g = 0.6$, and $y = 0$ (representative of the posterior distribution in the fit model). When conformity is turned off ($\lambda = 1$), individuals take a long time to stabilize on the high-payoff variant and are slow switch back when the environment changes again (Fig. 4a). Similarly, when conformity is set very high ($\lambda = 10$) adaptive learning is very slow, and most individuals fail to establish on the high-payoff variant at all before the environment switches (Fig. 4b). However when conformity is set to a moderately high value ($\lambda = 5$), all individuals stabilize on the high-payoff variant before turn 30, and quickly switch back after the variants switch again (Fig. 4c).

Second, we ran a simulation using parameter values for 10 birds sampled from the posterior distribution deduced from the experimental data (Fig. 4d). The simulation shown here is representative, and if anything, the birds showed less conformity than is optimal in this setting. Nevertheless, the amount of conformity that is present, combined with payoff-sensitive updating, allows individuals to track changes in behavioral variants.

Finally, selection gradients for social learning weight (s) and conformity strength (λ) were used to determine whether selection favors larger or smaller values of each parameter, conditional on the value of the other. We calculated the selection gradients by conducting 20,000 simulations at each of 63 combinations of s and λ (for a total of 1,260,000 simulations) to compute the selection differential of a mutant (Fig. 5). In each simulation, we considered the difference in total payoffs between a mutant individual with parameters $s + \delta_s$ or $\lambda + \delta_\lambda$ and an average common-type individual with parameters s and λ . This difference defines a numerical estimate of the selection gradient for an invader. The parameters g and y were again fixed at 0.6 and 0. We display the results in Fig. 5 as a vector field. Selection adjusts combinations on s and λ in the directions indicated by the arrows, with longer arrows indicating stronger selection. The red dashed contour are the combinations of s and λ at which selection on conformity is neutral. Selection increases conformity below this contour. The blue dashed contour are the combinations where selection on s is neutral. Selection increases s above this contour. Therefore selection favors more conformity for most of the gradient space, only becoming disadvantageous at high weights of social learning. Social learning weight increases above and

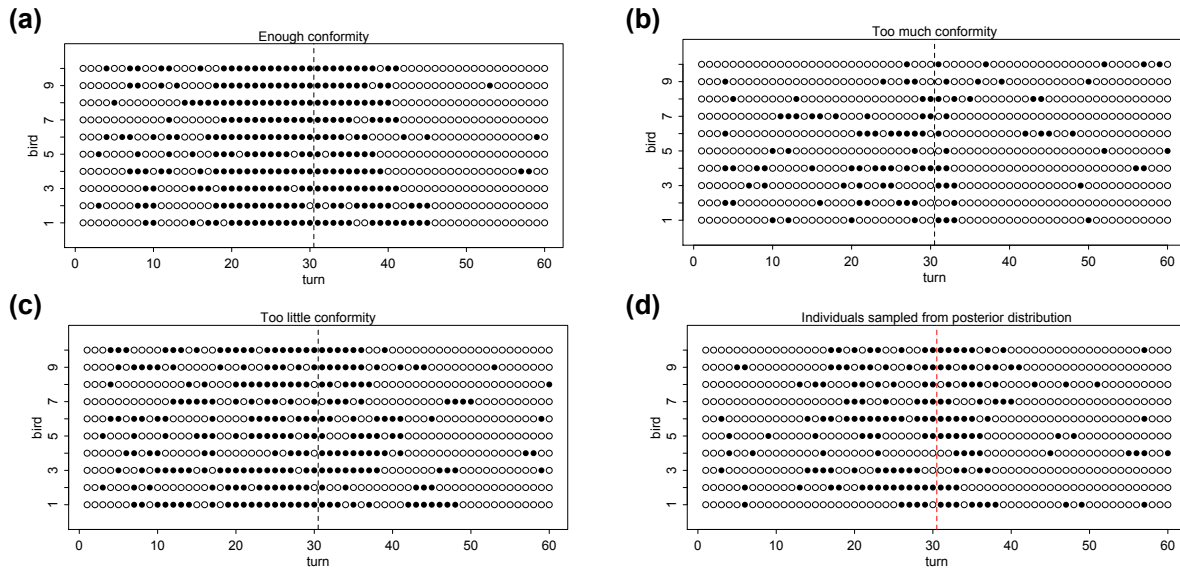


Fig. 4. Simulations of the population consequences of mixes of conformist social learning and individual reinforcement. In each plot, each row is an individual agent and each column is a time period. Open and closed circles represent alternative behavior. Before the vertical dashed line at turn 30, closed is adaptive. After turn 30, open is adaptive. All groups of learners initialized with non-adaptive attraction scores, $s = 0.5$, $g = 0.6$, and $y = 0$. (a) $\lambda = 1$, no conformity. (b) $\lambda = 10$, high conformity. (c) $\lambda = 5$, intermediate conformity. (d) 10 birds sampled from posterior distribution of the fit model.

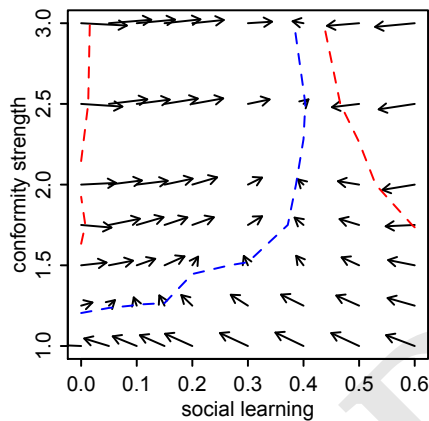


Fig. 5. Selection gradient on social learning weight and conformity, represented as vector field for social learning weight (horizontal axis) and conformity (vertical axis). Selection increases conformity below the outer red contours. Selection increases social learning above and left of the central blue contour. For these parameter values, selection does not favor much social learning, unless social learning is also conformist.

left of the blue contour. Here, social learning weight cannot increase from zero unless social learning is slightly conformist (above the central blue contour), however once conformity is above a threshold value, higher social learning weight is favored only up to a point. These processes combine to produce evolutionary dynamics that favor conformity combined with an intermediate weighting of social learning (Fig. 5).

In summary, the birds in the experiment obviously did not evolve in the experiment, and we do not expect them to be precisely adapted to it. Nevertheless, these simulations help us to understand why conformist social learning, in combination with payoff-sensitive individual reinforcement, facilitates the ability of individuals and groups to track environmental change.

Discussion

Our experiment reveals that socially learned foraging traditions in great tits are flexible in response to environmental change. Indeed when sub-populations with strongly established foraging traditions for a single behavioral variant were subjected to a change in foraging pay-offs, after just 14 days 49% of birds had switched their behavior to prefer an alternative higher pay-off variant, with almost all individuals sampling this option. By modeling the decision-making process for each individual we show that, perhaps surprisingly, this population-level flexibility was achieved without significant asocial sampling and despite an ongoing bias for conformity at the individual level. Instead, switching depended on two factors. First, there was an interaction between social information and personal experience, with individuals that had experienced the higher pay-off behavior having a strong preference for that variant in future solves. Second, there was extensive individual variation, with those individuals that relied more on social information showing a weaker conformist bias. These factors allowed some individuals to switch once fortuitously exposed to, and experiencing, the high pay-off variant. These individuals then provided the correct social information for others, leading to a positive feedback loop and eventual population-level turnover.

There has been extensive speculation about whether a reliance on social learning can lead to mismatched or out of date behavior (23, 25). Conformity has been thought to potentially exacerbate this process, as conformist individuals rely on an indirect cue of information quality (the proportion of individuals exhibiting a behavior) rather than assessing the value of the information itself (21, 22). However there has been a paucity of empirical evidence in non-human animals. In the only prior study, guppies (*Poecilia reticulata*) were trained on a longer, sub-optimal route to reach a feeding station. This route preference transmitted and persisted over several days before eroding towards a faster route (31). It

was assumed that this erosion was associated with asocial learning, but this was not tested. The learning mechanisms that individuals may be using to optimally exploit variable environments were more explicitly tested in Rendell, et al. (7), where a computer tournament was used to compete different sets of learning strategies. Winning strategies invested in social learning over asocial learning, learned most when individuals experienced a reduced pay-off, and relied on recently acquired information. Most interestingly, strategies did not benefit in variable environments by using either conformist learning or by preferentially copying high payoffs.

Our experiment supports the findings from Rendell, et al. (7) in two main ways. First, we found no evidence that individuals used asocial sampling to change established behavior. This is contrary to previous theory, which had suggested that individuals should use 'critical social learning', switching to individual innovation under reduced pay-offs (27, 34). In Rendell, et al. (7), indiscriminate social learning was adaptive because other agents were 'rational', that is, they reliably demonstrated the highest pay-off behavior in their repertoire. Again, our results reflect this finding; individuals exhibited a clear pay-off bias in their personal experience, preferring to use the high pay-off technique once experiencing both possible options. Second, we found no evidence that individuals were incorporating information about the differences in pay-offs achieved by different observed demonstrators. Thus our results, along with (7), suggest that the evolution of adaptive social learning strategies like 'copy the high-payoff' may not be necessary for individuals and populations to cope with temporally variable environments.

Our results differ in one major respect to (7); individuals exhibited a conformist bias in their social information use. This agrees with our previous experiment conducted under stable pay-off conditions, where individuals were also conformist in their social learning (18). This conformity did not prevent the population from tracking environmental change. Rather our simulations demonstrated that the combination of conformist social learning with the pay-off sensitive individual reinforcement we observed allowed individuals to acquire adaptive when naive, and actually promoted their ability to switch behavior once conditions changed. However, our simulations found that evolutionary dynamics favored conformity only under intermediate social learning. This reflects the model in Kandler and Laland (35) which also suggested that conformity bias should be associated with a weaker influence for social learning (also see (20, 21)).

Interestingly, we also found considerable individual variation in these parameters, with individuals that used most social information also generally being less conformist. The role that this between-individual variation plays in mediating population-level outcomes merits more investigation. Additionally, future research should investigate whether these underlying individual differences in learning behavior are consistent across contexts, and whether they relate to other correlates of behavior, for example differences in personality or in developmental conditions (36, 37).

Our simulations of model parameters therefore suggest that a mix of conformist social learning and individual reinforcement is sufficient to result in population-level switches in groups of free-mixing individuals. However it is interesting to consider how social structure might have additionally

influenced this process in the wild population. Great tits show a fission-fusion social structure, with extensive mixing and remixing of small foraging flocks (38, 39) and with social information moving between individuals via these foraging associations (18, 40). It seems likely that this social system might have acted to increase the rate at which the population could flexibly adjust. That is, if individuals occur in small groups that frequently fission, then if there is any behavioral heterogeneity within the population, then even as conformist learners, they will likely have some opportunity to acquire this alternative information. In species with highly modular networks, by contrast, social structure could rather act to slow the rate at which individuals and populations could flexibly adjust their socially learned behavior, with individuals repeatedly exposed to the same mix of potential demonstrators when copying.

In addition to social structure, population demography could also influence the speed at which populations can flexibly adjust socially learned behavior in a variable environment. While we found no sex differences in learning, unlike in (41, 42), younger individuals in our population tended to show a faster move away from the established low pay-off technique than older individuals, and had a higher probability of preferring the high pay-off technique by the end of the experiment. All individuals had equal opportunity in condition 1 to learn and practice the established behavior, and this result was unrelated to previous experience. Rather it appears that younger birds were generally more likely than older individuals to use social information, and once having experienced the high pay-off technique, were also more able to flexibly adjust their behavior. As younger individuals are often also more likely to disperse, such flexibility in behavior could be an advantageous when moving between new habitats (41). More broadly, future work should model the effects of population demography and social network structure on the ability of socially learning populations to track environmental change. Indeed, both population demography and social structure could also potentially be manipulated, and their effect experimentally tested.

In conclusion, we show that socially learned traditions in wild populations of great tits will track environmental change. We further find that populations can track pay-offs while individuals remain conformist social learners, and use simulations to elucidate the mechanisms by which this counter-intuitive outcome occurs. Indeed, our results suggest that conformist social learning actually helps the population adapt to and retain high-payoff behavior, provided it is not too strong. This adds further weight to arguments that social learning will be adaptive in a wide range of environments and contexts (7, 12). It is intriguing to consider what circumstances might therefore promote the perpetuation of maladaptive traditions. One possibility is that some kinds of socially learned information might be more vulnerable to this; for example where matching group patterns is more important than the absolute adaptive value of a behavior, or where the adaptive value of a behavior is obtuse or delayed. Future work should continue to investigate how general these findings are to other species, including humans, and explore their possible implications for the adaptive significance of animal culture.

Materials and Methods

Study System. The study was conducted in a population of great tits (*Parus major*) at Wytham Woods (51° 46' N, 01° 20' W; 385ha). This population has been the subject of a long-term study; all resident great tits were caught as chicks or adults and fitted with a British Trust for Ornithology metal leg ring and a plastic leg ring encasing an passive integrated transponder (PIT) tag (IB Technology, Glenfield, U.K.). In addition to this main marking scheme, regular mist netting targeted individuals immigrating into the population, and was also used to age and sex birds (by plumage). Immigrants could only be classed as first year or older on plumage, however as most individuals disperse as relatively young individuals, in all analysis they were assigned as their youngest possible age based on first capture date. From autumn to winter, birds form loose flocks of unrelated individuals (38, 39) with groups aggregating to exploit patchy food sources. In spring and summer, great tits prefer insect prey, but switch to a seed-based diet in winter when insects are less available (e.g. beech mast, *Fagus sylvatica* (40)). All experiments mimicked this diet, using live mealworms, unhusked sunflower seeds and peanut granules; previous work has established that mealworms are a highly preferred food type, and sunflower seed is preferred to peanut granules (18).

Experimental Apparatus. The social learning task consisted of a plastic box containing a feeder that was accessed by sliding a bi-directional door either to left or right. The left side of this door was colored blue and right side red, and it had a raised front section to allow an easier grip. A perch in front in the door functioned as an RFID antenna registering the identity, visit duration and action of each visiting individual; this was recorded and controlled by a printed circuit board (Stickman Technology, Southampton, U.K.) inside the box. One second after a bird was recorded as departed from the antenna, the door reset back to the middle. When installed in the woodland, each puzzle-box was surrounded by a 1x1m cage with a 5x5cm mesh to prevent access by larger species, and a freely accessible bird feeder providing peanut granules was provided at 1m distance.

In experimental condition 1, the puzzle-box feeder contained live mealworms. However for experimental condition 2 and 3, the puzzle-box was modified to provide two different rewards depending on the solving technique. This modification involved widening the door by approximately 1.5cm, however no other changes were made to the puzzle-box interface.

Experimental Design. A social learning and foraging experiment was conducted in four relatively isolated sub-populations across the woodland, in 4-week periods between December 2013 – January 2014 (Treatment 1, Treatment 3-4) and in a 4-week period in January 2013 for Treatment 2. First, two males were caught from each sub-population and trained in captivity to solve a novel puzzle-box: in two sub-populations (T1-2), they were trained to solve using variant A (solving pushing right from blue side), while in T3 and T4) they were trained to solve using variant B (solving pushing left from red side), Fig. 1a. All birds were then released to act as the initial demonstrators for this behavior, and three such puzzle-boxes were installed 250m apart in each sub-population. These then continuously operated from dawn on Monday to dusk on Friday for a total of 20 days [18]. In all areas the solving behavior

spread rapidly, with 68%-83% (n=37-96 per sub-population) of resident individuals solving either variant at least once. Puzzle-boxes were used frequently, with 7945-12411 rewarded visits per sub-population; for more detail see (18).

In January-February 2014, these four replicates were then exposed to a modified puzzle-box providing changed rewards. In condition 2 (2 days), this modified puzzle-box provided sunflower seeds as a reward for solving using either technique. This was followed by condition 3 (14 days): here the behavioral variant introduced in initial experiment was rewarded with sunflower seed, while the alternative technique was rewarded with live mealworms. In three replicates, these conditions occurred immediately following the initial experiment. In T2, the experiment occurred a year later, however the population was given 15 days of exposure to the puzzle-box immediately prior to condition 2, with 73% of resident individuals solving the task (either variant) in this period. The results from this replicate were similar to the three other replicates.

Statistical Analysis. To analyze the change over time in individual and population level preferences in condition 3, we used a generalized estimating equation model (GEE) where the dependent variable was the proportion of solves using the established tradition and explanatory variables were day, replicate and individuals, weighted by their total number of solves per day. As the data distribution was bi-modal, we first divided the data into two clusters using a longitudinal clustering algorithm that fit the data for the relative proportion of events that were variant A for individuals over cumulative 2 hour time periods. This method was implemented using the R-package *km13d*.

Learning mechanisms underlying individual changes in behavior were analyzed using a sequential learning model that modeled individual choices as products of time-varying interactions of different modes of learning. The foundation of this framework is the experience-weighted attraction learning model (43), but with additional terms that allow behavior to be guided by social cues. Specifically, we assume that the probability of observing a choice k at time t by individual i is given by:

$$p_{kit} = (1 - s_i)I_{kit} + s_iS_{kit} \quad [1]$$

where s_i is the influence of social cues on choice, I_{kit} the probability of choice k according only to accumulative individual attraction, and S_{kit} the probability of k according only to social cues. The individual attractions are modeled as ordinary experience-weighted attractions with a simple reinforcement model, such that the attraction score for an option k at time t and individual i is given by:

$$A_{ki,t} = (1 - g_i)A_{ki,t-1} + g_i\pi_k \quad [2]$$

where g_i is the importance of newly experienced payoff π_k . Therefore $g_i = 1$ when there is no influence of past experience. Here we estimate both g_i for each individual i and the unobservable payoff π_k to each option k . Attraction scores at time t imply choice probability by means of a softmax choice rule:

$$I_{kit} = \frac{\exp(A_{kit})}{\sum_n \exp(A_{nit})} \quad [3]$$

In fitting the model, we set the initial attraction scores at time $t = 0$ for each individual to the empirical preferences

from the first condition. This accounts for the fact that most individuals begin the second condition with strong preferences for the formerly-high option.

Social cues at time t can influence choice by changing the probability S_{kit} . In the simplest example, conformist learning is modeled as:

$$S_{kit} = \frac{n_{kt}^\lambda}{\sum_m n_{mt}^\lambda} \quad [4]$$

where n_{kt} is the frequency of choice k among social cues at time t and $\lambda = \lambda_i$ is individual i 's conformist exponent. When this exponent is 1, social learning is unbiased by frequency and behavior is sampled merely in proportion to its occurrence among cues. When however the exponent exceeds 1, social learning is conformist. In this study, we consider also payoff-biased social learning, which favors the highest payoff choice among choices observed at time t . Specifically, we construct a convex combination of conformist and payoff-bias terms:

$$S_{kit} = (1 - y_i) \frac{n_{kt}^\lambda}{\sum_m n_{mt}^\lambda} + y_i(1) \quad [5]$$

where y_i is individual i 's reliance on payoff-bias. When there is no variation in social cues, we assume that $y_i = 0$, which means that payoff-bias is only active when observed payoffs vary.

We allow learning strategy to vary at the individual level, estimating s_i , g_i , λ_i , and y_i for each individual i in the sample. In each case, we construct each parameter such that its log-odds are a linear combination of an individual random effect and an age-specific offset. For example, the sub-model for s_i is:

$$\text{logit}(s_i) = a_{i,1} + b_s x_i \quad [6]$$

where x_i is the standardized age of individual i and a_i is a vector of individual random effects, one for each parameter s , g , λ , and y . The conformity exponent λ is given a log rather than logit link.

Model fitting was performed using Hamiltonian Monte Carlo, as implemented in version 2.12 of Stan (44), to draw samples from the posterior distribution. We assessed convergence by inspection of the trace plots, Gelman-Rubin \hat{R} , and an estimate of the effective number of samples. Finally, model priors were defined to be weakly informative and conservative, so that estimated effects and correlations were shrunk slightly towards zero. Specifically, the averages for s , g , λ , and y were assigned Normal(0,1) priors on the latent scale. The standard deviations of each random effect were assigned Exponential(2) priors, also on the latent scale. For the correlation matrix of random effects, we used the LKJ family of distributions of matrices and assigned $\eta = 3$, which shrinks correlations away from extreme values near -1 or $+1$ and towards zero. For the unobserved payoff advantage of the high-payoff option, we assigned a Cauchy(0,1) prior, which is essentially uninformative. See ?ewadef for details. Code sufficient to repeat our results is available as an R package, **wythamewa**, that contains the data, models and simulation code.

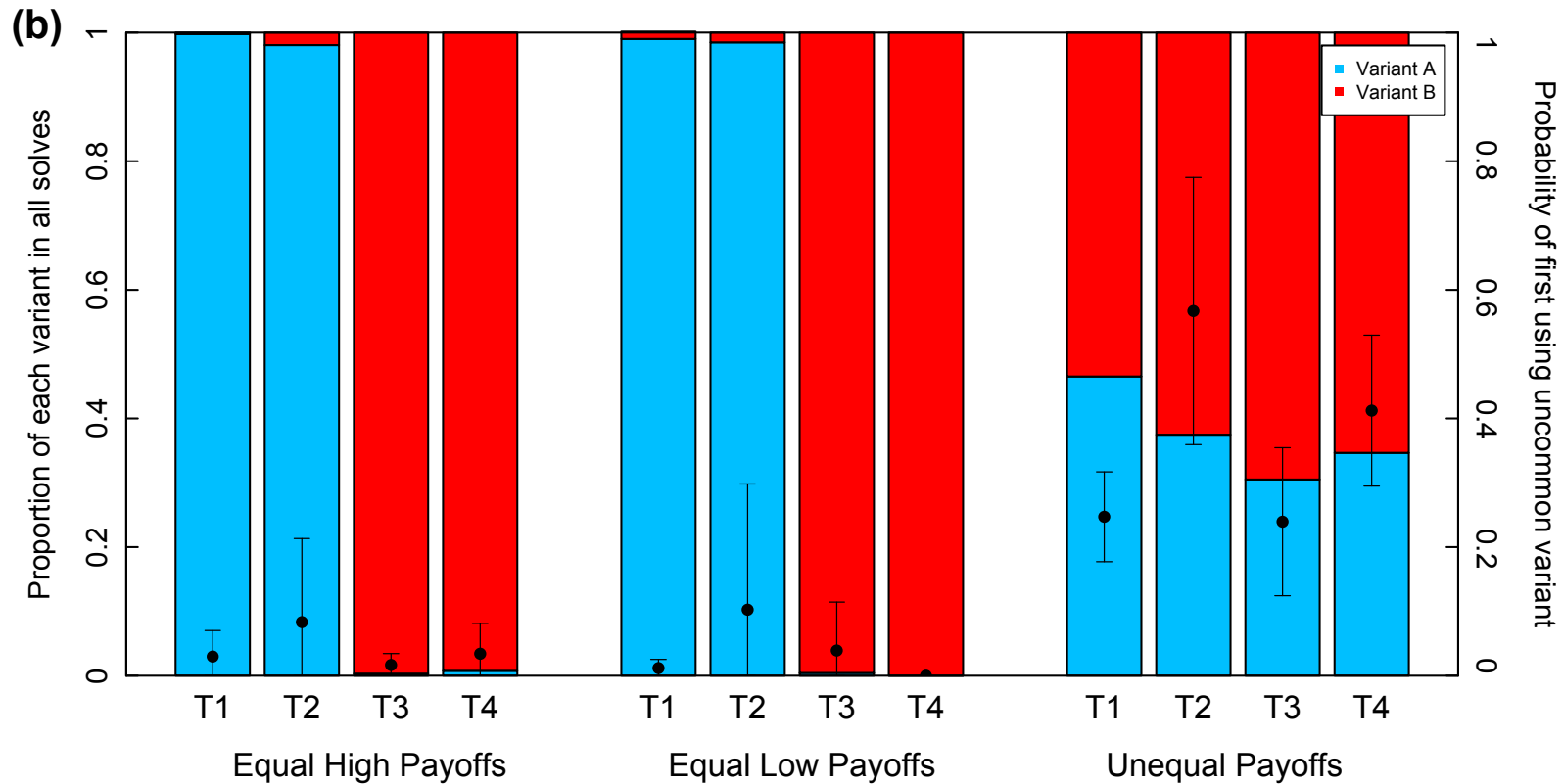
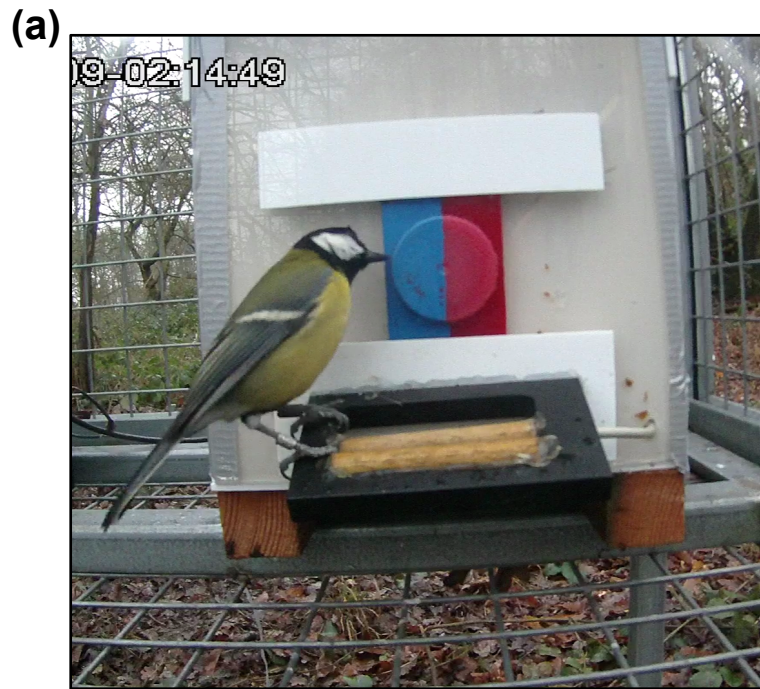
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Proportion of solves are seeded variant

