

# Population turnover facilitates cultural selection for efficiency

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## Abstract

Selection for more efficient socially learned behaviors over alternatives is crucial for cumulative cultural evolution, yet our understanding of such cultural selection in animals is limited. We performed a cultural diffusion experiment using 18 populations of wild-caught great tits (*Parus major*) to ask whether more efficient foraging traditions are selected for, and whether this process is affected by turnover. We show that gradual replacement of individuals greatly increases the probability that a more efficient behavior will invade a population's cultural repertoire, out-competing an established inefficient behavior. Turnover does not increase innovation rates, but instead increases adoption rates, as immigrants are more susceptible to novel, efficient behaviors. An agent based model further supported our results by demonstrating that this effect holds across populations of different types of learners. Altogether, these results provide strong evidence for cultural selection for efficiency in animals, and highlight the importance of population turnover for this process.

## 1 Introduction

Culture, here defined as socially transmitted information and behaviors that are shared in groups and persist over time, is increasingly accepted to occur across wide range of taxa and behavioral domains [1]. While persistent, cultural traits are not necessarily static, and their distribution can change in frequency and type in response to selective pressures, analogous to that of genetic alleles. This has led to the treatment of culture as an evolutionary process, with cultural evolutionary theory arguing that culture exhibits the three fundamental components of Darwinian evolution: variation, competition, and inheritance [2, 3, 4, 5]. Beyond genes, culture offers a secondary inheritance system that provides an alternative pathway to adaptive plasticity [6, 7]. Humans have undoubtedly leveraged this to its fullest extent by accumulating and recombining a wealth of cultural behaviors and artifacts into evermore efficient complexes in a process termed cumulative cultural evolution (CCE) [8]. Yet despite its potential importance for broader evolutionary theory, cultural evolution is understudied in non-human animals (outside of birdsong, see [9, 10] for recent reviews). It remains an open question to identify and describe processes of cultural evolution in non-human species, including potential precursors to CCE, and the social factors that may affect these evolutionary dynamics.

Culture exists on the substrate of the social network [11]. It follows that cultural evolution should be responsive to network properties such as population size, structure and dynamic turnover in various ways [12, 13, 14, 15, 4, 16, 17]. Notably, larger population sizes have been linked to the generation and maintenance of cultural diversity in humans, with larger populations having an elevated probability of both innovation and faithful cultural transmission [12, 18, 19, 20, 21]. Conversely, population decline and fragmentation can result in loss of diversity and simplification of traits, as observed in bird song [22, 23, 24]. Population turnover, caused by immigration and emigration or births and deaths, could affect cultural evolution by elevating innovation probabilities as incoming individuals could introduce new innovations or increase 'behavioral noise' [25]. Alternatively, naive individuals might be able to better re-sample the behavioral space, leading to more adaptive cultural outcomes [26]. Yet while population turnover is a fundamental demographic process in populations of any species, its effect on cultural evolution is poorly understood. Linear transmission chains provide an approximation of turnover, but it has not been well explored using populations of socially learning animals, and there are no clear predictions about how turnover might influence the tempo and mode of cultural evolution.

One potentially important process in cultural evolution is selection for efficiency. Recent discussions have proposed that repeated instances of cultural selection for efficiency in a singular cultural trait may represent

48 a potential precursor to more complex forms of CCE unique to humans [25, 27]. While claims of CCE in  
49 non-human animals are controversial [28, 29], cases of increases in efficiency have recently been identified in  
50 several animals. Reintroduced storks and ungulates refine migration routes over several generations [30, 31],  
51 and in homing pigeons, transmission chains refined routes beyond improvement achieved by single individual  
52 [25]. There is much less evidence for the cultural evolution of efficiency outside of movement, although wild  
53 chimpanzees' adoption of moss-sponges over leaf-sponges suggests that they may be able to select tool material  
54 based on efficiency [32]. Working against any type of selection for efficiency is behavioral conservatism, or a  
55 low probability of sampling behavioral variants beyond those already produced. The inability to adopt more  
56 profitable alternatives is well documented in studies on chimpanzees [33, 34, 35], but less studied in other  
57 taxa (but see [36]).

58 Great tits (*Parus major*), a common passerine bird species, are a useful study system for investigating how  
59 population turnover might affect cultural evolution. Tits spontaneously innovate new behavior at high rates  
60 [37], and are well known for the social transmission of foraging behavior, such as the spread across Great  
61 Britain of a new innovation - piercing milk bottle caps to access cream [38, 39]. Experimental studies have  
62 provided strong evidence for the social learning of foraging behavior and establishment of new traditions in  
63 tits [40, 41, 36]. In these studies, birds exhibited a conformist bias, in that they disproportionately learned the  
64 most commonly demonstrated variants, and maintained stable foraging traditions over multiple generations  
65 [41]. Further, turnover within and between generations is a pertinent feature of great tit social systems.  
66 Roughly 50% of breeders are newly arrived immigrants each year, and the mean lifespan of breeders is only 2  
67 years [42, 43]. During winter, birds exhibit fission-fusion dynamics in larger social networks [44], with local  
68 foraging flock membership varying throughout a single day depending on density and location of birds [45].

69 To study the effect of population turnover on cultural selection for efficiency, we conducted a large-scale  
70 cultural diffusion and evolution experiment on 18 artificial populations of wild-caught great tits ( $n = 181$ ,  
71 over 40 days). Each population had a membership of 6 birds, the size of a small winter foraging flock [46, 47].  
72 The study consisted of two phases: 1) an initial diffusion period (12 days), and 2) a subsequent experimental  
73 period in which population turnover was manipulated (28 days). During the diffusion period, a foraging  
74 tradition to access food by pushing on a bidirectional door of an automated puzzle box was established using  
75 a 'tutor' bird trained on the inefficient solution (Fig. 1A). This set all populations to the same initial,  
76 inefficient cultural state prior to the experimental manipulation. In the experimental period, birds could either  
77 improve their speed at the established foraging tradition, or potentially innovate an alternative solution that  
78 was on average about .5s faster (Fig. 1C). This solution offered a greater payoff for the solver, as they could  
79 receive the same reward for less time investment. In 9 populations (hereafter turnover populations), turnover  
80 was simulated by replacing 2 birds with new, wild-caught birds in the first turnover event (T1). Turnover  
81 events then occurred every subsequent week (T2-T4) for the remainder of the experimental period. Another 9  
82 populations maintained stable membership for the duration of the experiment (hereafter static populations).  
83 We predicted that turnover populations would be more likely than static populations to innovate and adopt  
84 the alternative, more efficient solution. We further hypothesised this might be occur through one of two  
85 mechanisms: incoming naive birds might be more likely 1) to innovate the efficient solution, or 2) to adopt  
86 the efficient solution once innovated. Finally, we supported our results using a complementary agent-based-  
87 model that replicated the design of the experiment and allowed us to test the effect of turnover while varying  
88 relevant individual learning parameters.

## 89 2 Results

90 In order to establish a foraging tradition in all populations, the first 12 experimental days were designated as a  
91 diffusion period, with one knowledgeable bird in each population trained to the inefficient solution. During the  
92 diffusion period, this behaviour spread in 17 of 18 populations, with 83 of 163 naive birds eventually learning  
93 to solve. While only the inefficient solution was available to learn during this period, evidence that solving  
94 behavior was socially learned is threefold: 1) outside of the diffusion period, 87% of birds first solved using  
95 the most predominant solution in their population, 2) the puzzle was difficult to individually learn (tutors  
96 took anywhere from 1 to 2 weeks of incremental training to learn to solve) and 3) the behavior failed to be  
97 re-innovated in a population where the solving behavior went extinct.

98 Overall, populations produced an average of 9,719 total solutions (range: 1,494–17,208), and solvers  
99 produced an overall average of 1,803 solutions (range: 20–6,612), and a daily average of 89 solutions. Tutors  
100 produced 47,000 total solutions, with a daily average of 100 solutions. Naive birds produced 127,939 total  
101 solutions, with a daily average of 86. Altogether, solvers produced a total of 174,393 recorded solutions,  
102 with 89% (156,487) of those with measurable time-to-solve (TTS). Birds that learned to solve the puzzle



Figure 1: Diagram of puzzle box alongside a photograph of a great tit at the puzzle, and average time-to-solve for pushing the door one way or the other (tutors excluded; efficient:  $n = 44$  birds, 34,444 solutions; inefficient:  $n = 50$  birds, 78,616 solutions). Open circles are from first quartile of solutions produced by an individual, and closed circles are second-fourth quartile of solutions. **A)** Each population was provided with one puzzle box that had a 4 cm wide door which gave access to a silo of mealworms. The access point was offset from the center of the door by .5 cm, such that pushing from the left (red) side is more efficient. A microcomputer recorded identity (RFID and video), and solution type and automatically closed the door after each solve. **B)** The black perch below the door contained an RFID antenna to record identities from the unique transponder (PIT) tags on birds, and a camera above recorded identity from barcodes placed on the backs of birds. Both systems allowed calculation of time-to-solve. **C)** The shorter travel of the efficient solution made it significantly faster to solve both for inexperienced (closed circles) and experienced (open circles) birds. We observed a general process of refinement within solutions independent of social influence.

103 became significantly faster at solving with experience, reducing their TTS by about 3% with every standard  
 104 deviation of solutions produced, suggesting that a process of reinforcement learning was leading to continuous  
 105 improvements in efficiency (Linear Mixed Model (LMM), solution index (z-scaled):  $\beta = -0.027 \pm 0.002$ ,  
 106  $t = -11.975$ ,  $P < 0.001$ ; Table S1A).

## 107 2.1 Turnover facilitates cultural selection for efficiency

108 After the diffusion period, both solutions were available in all populations, and populations were either left  
 109 as static, or underwent gradual turnover. The efficient solution was significantly faster than the inefficient  
 110 solution. When controlling for experience, as well as differences between populations and individual solvers,  
 111 the average TTS for the efficient solution of a bird with average experience was significantly faster than  
 112 the inefficient solution (LMM, solution type (efficient):  $\beta = -0.395 \pm 0.051$ ,  $t = -7.787$ ,  $P < 0.001$ ;  
 113 LMM, intercept (inefficient):  $\beta = 0.925 \pm 0.215$ ,  $t = 4.299$ ,  $P < 0.001$ ; Table S1A; Fig 1C). The same  
 114 relative amount of solving experience obtained a lower average TTS with the efficient solution compared  
 115 to the inefficient solution (LMM, solution type (efficient)\*solution index (z-scaled):  $\beta = -0.117 \pm 0.006$ ,  
 116  $t = -18.102$ ,  $p < 0.001$ ). The efficient solution therefore offered a greater payoff on average, as the solver  
 117 received the same reward for less time investment.

118 Individual populations displayed a variety of dynamics and outcomes, visualized in Fig. 2 (see Fig. S1  
 119 for a detailed view of all populations). Both conditions innovated the efficient solution shortly after the  
 120 diffusion period. However, turnover populations were clearly more likely to select for the efficient solution  
 121 as the experiment progressed (Fig. 2A,B; Fig.3A). To quantify selection for efficiency, we used a logistic  
 122 GLMM to predict the likelihood of producing the efficient solution using a full interaction between condition  
 123 and experimental day. Immediately following the diffusion period, any given bird in either condition was  
 124 initially unlikely to produce an efficient behavior (GLMM, intercept:  $\alpha = -10.853 \pm 1.088$ ,  $Z = -9.974$ ,  
 125  $P < 0.001$ ; turnover condition:  $\beta = -2.169 \pm 1.700$ ,  $Z = -1.276$ ,  $P = 0.203$ ; Table S1C). With each  
 126 passing day, there was an increasing probability of producing efficient solutions in both conditions (GLMM,  
 127 exp. day:  $\beta = 0.291 \pm 0.010$ ,  $Z = 28.986$ ,  $P < 0.001$ ). However birds from the turnover condition  
 128 became significantly more likely to produce efficient solves compared to the static condition (GLMM, exp.  
 129 day\*turnover:  $\beta = 0.603 \pm 0.016$ ,  $Z = 38.713$ ,  $P < 0.001$ ).

130 By the end of the experiment, turnover populations had produced 44,703 inefficient solutions and 39,815  
 131 efficient solutions, while static populations had produced 88,829 inefficient solutions and only 1,592 efficient  
 132 solutions. Overall, 7/9 turnover populations selected for and switched to the efficient solution. Interestingly,  
 133 in one of the two turnover populations that did not select for the efficient solution, the solving behavior went

134 completely extinct due to turnover of all knowledgeable individuals. By contrast, only one static population  
 135 selected for the efficient solution after it was innovated. This population accounted for most of the efficient  
 136 solutions in the static condition (1,466), while all other static populations produced the efficient solution only  
 137 a handful of times, if at all (range: 0-28).

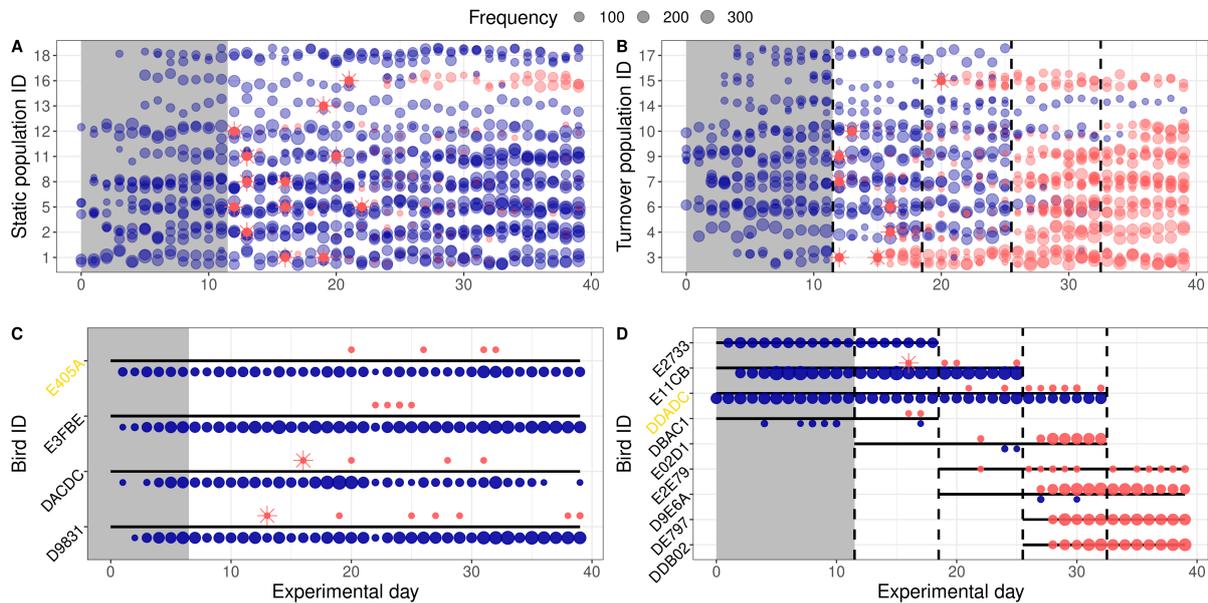


Figure 2: Overview of behavioral frequency data over experimental day from static (A) and turnover (B) conditions, and behavioral data from individual birds over experimental day from two exemplar static (C) and turnover (D) populations. Type (color), frequency (size), innovation events (asterisk circle, see Methods for definition), tutors (gold text), diffusion period (grey background), and duration of individuals (black lines) are marked. **A)** Despite nearly all static populations innovating the efficient solution, it only invaded one population from this condition ( $n = 29$  birds, 90,421 solutions). **B)** Nearly all of the turnover populations innovated the efficient solution, but there was a latency period between its innovation and its uptake, as adopters were primarily naive individuals ( $n = 70$  birds, 84,518 solutions). **C)** A static population in which two birds independently innovated the efficient solution, and it is produced in low frequency, yet it fails to invade the cultural repertoire. ( $n = 4$  birds, 14,483 solutions) **D)** A turnover population that selected for the efficient solution. An experienced bird innovated on day 11, and efficient solution was produced by several birds at low frequency until it was widely adopted by naive immigrants after the third turnover ( $n = 9$  birds, 16,616 solutions).

## 138 2.2 Cultural selection generates population-level differences in performance

139 While both conditions had a decreasing TTS as the experiment went on, (LMM, exp. day (scaled between  
 140 -1 and 1):  $\beta = -0.048 \pm 0.005$ ,  $t = -9.885$ ,  $P < 0.001$ ; Table S1b), on average, turnover populations  
 141 had a significantly steeper reduction their TTS than static populations (LMM, exp. day (scaled)\*condition  
 142 (turnover):  $\beta = -0.077 \pm 0.010$ ,  $t = -7.832$ ,  $P < 0.001$ ; Fig. 3B). Turnover populations were slower than  
 143 static populations through the first two turnover events, suggesting that the loss of knowledgeable birds may  
 144 have initially hindered the accumulation of expertise at the inefficient solution. However, by the final week of  
 145 the experiment, birds in turnover populations were solving faster than static populations, despite individuals  
 146 having less experience with either solution ( $M_t = 1.66s$ ,  $M_s = 1.96s$ ). This was a result of the increasing  
 147 frequency of the efficient solution as the dominant solving behavior, which allowed turnover populations to  
 148 achieve a lower TTS.

## 149 2.3 Mechanisms producing cultural outcomes: do innovation rates differ between 150 conditions?

151 Innovators were classified as either the first to have produced the efficient solution in a population, or birds  
 152 that produced the efficient solution without having seen it demonstrated (given the amount of time elapsed

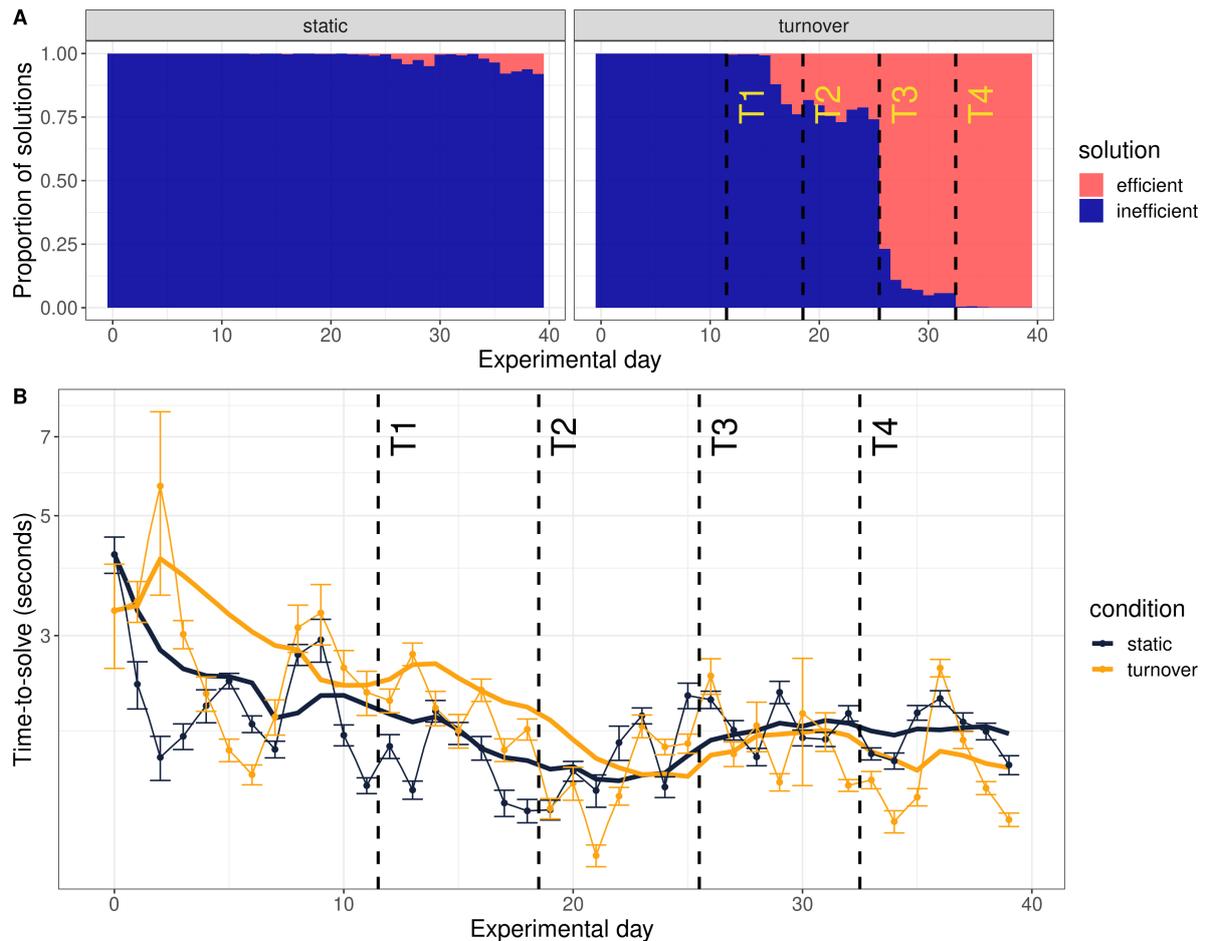


Figure 3: Above, the proportion of solution types faceted by condition, and below, daily average time-to-solve over experimental day for each condition. **A)** The proportion of solutions that are inefficient or efficient in all populations on a given experimental day (static:  $n = 28$  birds, total solutions = 88,224; turnover:  $n = 70$  birds, total solutions = 84,518). All populations started by producing inefficient solutions. Static populations produced mostly inefficient solutions for the majority of the experiment. In contrast, efficient solutions fully invaded the cultural repertoire of nearly all turnover populations by the end of the experiment. **B)** Mean time-to-solve for static and turnover conditions over experimental day (thin lines with 95% SE). Thick lines are right-aligned 7 day moving average. Y-axis log2 coord. transformed for visualization, and vertical dashed lines show turnover events (T1-T4). In the last two weeks of the experiment, turnover populations were on average solving faster than static populations. This increase in efficiency was driven by the widespread cultural selection for the efficient solution. (static:  $n = 21$  birds, total solutions = 52,458; turnover:  $n = 61$ , total solutions = 60,735).

153 since the prior efficient solution, see Methods for details). In total, 21 birds were innovators (static: 13,  
 154 turnover: 8). Innovators were almost equally split between age (10 juveniles, 11 adults) and sex (10 female,  
 155 11 male), and were typically experienced, knowledgeable solvers.

156 To test whether turnover increased the probability of innovation, we compared the timing of innovation  
 157 events between both conditions in several ways: 1) days solving before innovation, 2) exposure time before  
 158 innovation and 3) experimental day of innovation (Fig. S2). Exposure time before innovation ( $M_t = 14.1$ ,  
 159  $M_s = 15.5$ ) and experimental day of innovation ( $M_t = 14.5$ ,  $M_s = 16.3$ ) were not significantly different  
 160 between conditions (Table S2B, S2C). Innovators in the turnover condition did have a significantly shorter  
 161 period of days solving before innovation ( $M_t = 8.88$ ,  $M_s = 13.8$ ; GLM condition (static):  $\beta = 5.772 \pm 1.918$ ,  
 162  $t = 3.009$ ,  $P = 0.008$ ; Table S2A), although this difference was driven by only 2 data points (Fig. S2). These  
 163 results, along with the fact that static populations innovated more often during the experiment, suggest  
 164 that innovation probabilities were comparable between conditions. Surprisingly, only 5 of the 21 innovators  
 165 permanently adopted the efficient solution after innovation, hinting at some level of behavioral conservatism.

## 166 2.4 Mechanisms producing cultural outcomes: do birds exhibit behavioral conser- 167 vatism?

168 Most learners held a strong preference for one solution, and relatively few birds were observed producing large  
169 amounts of both solution types. Out of 53 birds that produced both solutions, 36 failed to adopt the more  
170 efficient solution. This suggests that behavioural conservatism could have either been the effect of experience  
171 (e.g. habit formation) or conformity. To test their relative importance, we analyzed the probability of failure to  
172 adopt the efficient solution in the subset of birds which had produced both solutions using a logistic regression  
173 against predictor variables that included experience (days producing the inefficient solution before producing  
174 their first efficient solution) and conformity (proportion of socially observed inefficient solutions on day of  
175 first efficient solution). Birds were very likely to adopt the efficient solution if they experienced an efficient  
176 solution on the first day of solving (GLMM, intercept:  $\alpha = -3.421 \pm 1.977$ ,  $Z = -1.730$ ,  $P = 0.084$ ; Table  
177 S3). However, each day of experience with the inefficient solution had a significant positive effect on failure  
178 (GLMM, days solving:  $\beta = 0.364 \pm 0.132$ ,  $Z = 2.761$ ,  $P = 0.006$ ). Conformity had a non-significant effect  
179 on failure, and age and sex did not significantly predict failure to adopt. This suggests that experience was  
180 the more important factor in conservatism.

## 181 2.5 Hypothesis verification via agent based model

182 In order to test the robustness of the observed patterns, we reproduced the experimental design in an agent  
183 based model. Birds were represented by agents who socially learned to solve the puzzle with an estimated  
184 conditional probability of learning derived from the experimental data. Following the experimental design, each  
185 simulated population was initialized with one agent that was "trained" on the inefficient solution, although  
186 not programmed to exclusively produce this solution, and simulations ran for 35 time-steps. Agents made  
187 behavioral decisions based on both individual and social information using a modified experience weighted  
188 attraction (EWA) model (previously used in similar cultural studies [36, 48, 49, 50]). Three individual-level  
189 parameters of interest were systematically varied: 1) sensitivity to social cues, 2) sensitivity to the current  
190 payoff versus their memory of payoffs, and 3) level of behavioral conservatism, or sensitivity to differences in  
191 attraction scores. 500 simulations were run at each point within this parameter space using homogeneous  
192 populations with a medium-level conformity value (but see Fig S3, S4 for exploration of conformity and payoff  
193 parameters). To quantify selection for efficiency, we used the same measure as the experiment—the proportion  
194 of efficient versus inefficient solutions produced by agents was measured at the final time-step such that a  
195 value of 1 indicates a full invasion of the efficient behavior.

196 Our model showed that, on average, population turnover increased selection for efficiency across all three  
197 relevant parameters, resulting in a higher average proportion of efficient solutions in the final time-step (Fig.  
198 4). This was not deterministic, as simulation variance generated a variety of overlapping outcomes between  
199 conditions on a simulation by simulation level. Further, the behavior went extinct in approximately 1/3 of the  
200 turnover simulations, following the expected probability of extinction due to stochastic turnover.

201 As agents' sensitivity to the current payoff against previous payoffs increased, so did the average proportion  
202 of efficient solutions, as agents heavily weighted higher payoffs received from producing the efficient solution  
203 in their following decision. As social cue bias increased, the proportion of efficient solves decreased in both  
204 conditions. Indeed, conditions performed most similarly at extremely high parameter values of social cue  
205 bias (Fig. 4C; wall of blue Fig. 4A and Fig. 4b), as social information nearly always trumped individual  
206 feedback. As agent's conservatism (sensitivity to differences in attraction) increased, selection for efficiency  
207 also weakened. Both conditions responded similarly to the changes in all three parameters, but turnover  
208 populations consistently produced more efficient solutions in the final time-step. Finally, while this model  
209 used a conditional probability of socially learning that was calculated from experimental data, these results  
210 were robust even when the probability function was reversed (Fig S5). These results provide important  
211 evidence that population turnover expands the parameter space in which cultural selection for efficiency may  
212 occur. The effect of turnover is realized across populations composed of a variety of types of individuals, with  
213 minimal assumptions about the learning process. Whatever the true values of these parameters were in the  
214 populations of tits in the current study, turnover would have produced the effect we observed.

## 215 3 Discussion

216 Our results illustrate a striking positive relationship between population turnover and cultural evolution.  
217 The emigration and immigration of individuals allow populations to shift away from an established foraging  
218 tradition towards more efficient alternatives in a process of cultural selection for efficiency. This was not as

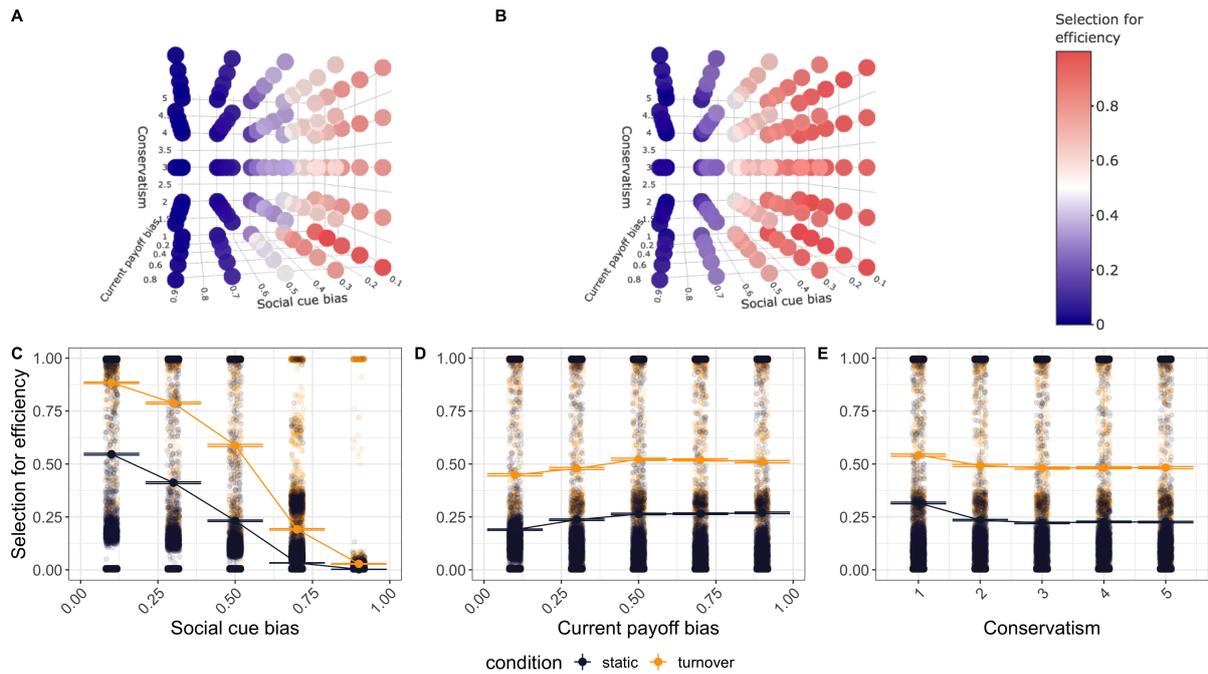


Figure 4: Above: Agent based model results showing average selection for efficiency (red strongest, blue weakest; measured as the proportion of efficient behaviors in the final time step of the simulation) visualized in a parameter space for (A) static and (B) turnover populations. Below: average selection for efficiency with 95% SE and points representing the result of an individual simulation, marginalized over the same three parameters of interest. **A)** Average selection for efficiency at different combinations of parameter values for static populations ( $n = 62,500$ ; 500 sims per point in parameter space). **B)** Average selection for efficiency within the same parameter space for turnover populations ( $n = 42,202$ ; 20,298 sims excluded due to behavioral extinction). Compared to the parameter space of the static condition, the diminished dark-blue area indicates there are more valid combinations of parameter values under turnover which can produce higher frequencies of efficient behaviors. **C)** Increased social cue bias decreases selection for efficiency, as the initial tutor agent's preference is more influential. Turnover is more likely to have a higher proportion of efficient solutions in the final time step, even in populations that heavily weight social information. **D)** Current payoff bias generally increases selection for efficiency. **E)** Behavioral conservatism (agents' sensitivity to differences in attraction score) generally decreases selection for efficiency. Turnover mitigates this effect by introducing new agents who do not already have attraction scores for either solution.

219 a result of innovation or noise introduced by immigrants; rather older, knowledgeable residents more often  
 220 innovated efficient behaviors, which were then more often adopted by immigrants. This pattern contrasts  
 221 with the repeated failure of the efficient behavior to invade the cultural repertoire of static populations,  
 222 despite it having been regularly innovated. The widespread adoption of the efficient solution mitigated the  
 223 effects of reduced opportunity for development of expertise in turnover populations. They exhibited a faster  
 224 time to solve at the foraging puzzle by the end of the experiment, despite individuals having less overall  
 225 contact time with the puzzle. In sum, we conclude that turnover provides a mechanism that facilitates  
 226 cultural selection for efficiency by providing a path to adaptive plasticity that navigates around individual-level  
 227 behavioral conservatism. Our results point to one further piece of the puzzle of cultural evolution, which is  
 228 the essential role that inexperienced individuals play not as innovators, but as susceptible adopters of more  
 229 optimal cultural variants.

230 The only other direct experimental test of cultural evolution for efficiency was in homing pigeons [25],  
 231 where pairs of birds developed relatively more direct, efficient homing routes over time when one of the pair  
 232 was repeatedly replaced in a chain design. In this case, the authors hypothesised an alternative mechanism  
 233 for this result - that the naive individuals might be producing behavioural variation on which cultural selection  
 234 could act. However their behaviour was a continuously measured variable (flight straightness), and they could  
 235 not directly observe or measure innovations. Our study expands and extends this work in several important  
 236 ways. First, we conduct turnover in groups, mimicking realistic fission-fusion dynamics and natural flock sizes  
 237 for this species. Second, we test this process in a foraging context; most theoretical and observational work,

238 particularly in humans and non-human primates, has focused on foraging - our work gives new insights into  
239 this key behavioural domain. Finally, our experimental design allowed for a directly quantifiable step-change in  
240 efficiency (alternative solving techniques), as well as continuous (reducing in time to solve). This allowed us  
241 to identify innovation events and their effect on population-level behaviour, thus revealing underlying drivers  
242 of the relationship between turnover and efficiency.

243 Our results suggest a near inversion of the hypothesis from [25]— experienced resident individuals innovated,  
244 while naive immigrant individuals adopted. This contrast may be a direct result of the differences  
245 between the the continuous spectrum of efficiency in the context of movement [25, 30, 31], and the the  
246 discrete difference in foraging efficiencies often associated with foraging behaviour. In a continuous, dynamic  
247 behavior such as flight, noise might be more easily generated by naive individuals, and then edited by experienced  
248 individuals. In the current study, experience was clearly needed to be able to innovate the efficient  
249 solution in the first place. In natural populations that experience regular turnover, both cultural evolutionary  
250 mechanisms may be active as immigrants either innovate themselves, or successfully resample the behavioral  
251 space, and adopt more beneficial, but less frequently produced alternatives. The dominant mechanism  
252 through which turnover acts on culture might likely be determined by the ease with which innovations can  
253 occur. Future research should seek to identify both processes in their analysis of how populations navigate  
254 the payoff landscape of culturally transmitted behaviors.

255 Overall, birds were behaviorally conservative throughout the experiment; continuing to produce the inefficient  
256 solution even after having performed the efficient solution. The role of expertise in suppressing any  
257 motivation to adopt alternative behaviors, previously observed in primate studies [34] may explain our finding,  
258 as behavioral conservatism was best predicted by time spent solving before sampling the efficient solution.  
259 Birds which mastered the inefficient solution could perform it within the same recorded time as the efficient  
260 solution, although ostensibly by applying slightly more force to move the door. The perception of this difference  
261 in force may have become negligible with practice. Further, a conformist bias might also account for the  
262 resistance to switch in some birds, but not all. This accords with a previous study that inferred variable  
263 estimates of individual great tits' conformity levels [36].

264 Behavioral conservatism is cited as a primary reason for the lack of observed CCE in animal species [51].  
265 Such resistance to switching behaviors is also one of the key reasons why population turnover is vital to  
266 the evolution of efficiency in a cultural system. Turnover alters the memory structure of the population  
267 by effectively wiping a portion of the populations' slate clean and allowing for re-sampling of the behavior  
268 space. Perhaps the most intriguing suggestion of this effect of turnover on cultural inertia comes from  
269 translocation studies of blue-headed wrasse, a fish that maintains spawning sites through cultural inheritance.  
270 When all members of a wrasse population were replaced with naive individuals, they resampled the set of  
271 potential spawning sites and selected different mating sites from the original population [26]. A second  
272 new replacement population selected the same sites, leading the author to suggest that turnover resulted in  
273 more optimal sampling [52]. This particular experiment was designed to test whether spawning sites were  
274 culturally inherited, so the entire population was turned over at once. Although, the successful resampling of  
275 sites by naive fish appears analogous to that observed in immigrant tits. Given we find this similar example  
276 from a species whose last common ancestor with the great tit was 430 mya, and that the effect of turnover  
277 is replicated across learning parameter values *in silico*, we propose that population turnover might provide  
278 a broad, substrate independent mechanism for resampling socially transmitted information and potentially  
279 moving populations towards more adaptive local optima.

280 The cultural evolution of more refined, efficient, behaviors has been considered as a precursor to more  
281 complex, human-like forms of cumulative culture [27]. While we do not argue that this experiment demonstrates  
282 CCE in tits, our results add to the growing evidence that cultural evolution of efficiency is possible  
283 in animals, and extend this to a new behavior domain (foraging behavior). This small passerine species is  
284 capable of moving the cultural ratchet forward by one tick, fulfilling a key description of CCE: a behavior  
285 innovated by an individual spreads within a group, and stays in place until future individuals make further  
286 modifications that are more efficient, which then spread and supplant the previous behavior [8]. The design  
287 of the puzzle box made it such that the birds could not innovate and spread an improvement more than  
288 once. However, it is not a far leap to imagine that this process of cultural selection for efficiency might have  
289 repeated itself in an extended experiment. In the wild, great tits form fission-fusion foraging flocks, whose  
290 membership is constantly changing. Perhaps this demographic churn facilitates rapid cultural evolution of  
291 locally adaptive behavior. Indeed, the conservatism evidenced in the current study may be surprising in light  
292 of a prior study which found that 49% of great tits were capable of switching to a higher payoff solution when  
293 the payoff structure of a puzzle box was altered [36]. However, these birds were part of free-mixing, wild  
294 flocks that underwent regular turnover, lending further support for the facilitating role of population turnover  
295 in the cultural evolution of efficiency.

296 Still, it remains an open question as to why repeated instances of selection for efficiency are so rarely  
297 observed in non-human species in the field. Our results suggest this is not due to an inability to select for  
298 more efficient variants; rather behavioral conservatism can be mitigated by population turnover. Yet turnover  
299 also presents a real cost: memory loss through turnover may be detrimental to the population depending  
300 on their knowledge state. One turnover population exhibited a complete extinction of the solving behavior,  
301 and approximately one third of our simulations ended in cultural extinction, suggesting that cultural benefits  
302 of turnover may also carry a corresponding risk of the potential loss of all knowledgeable individuals and  
303 subsequent extinction of cultural traits. This effect could be exacerbated if the underlying resource the  
304 cultural behavior is exploiting is ephemeral and inter-generational turnover is particularly high.

305 This paper illustrates how dynamic populations are more likely to select for efficient cultural behaviors,  
306 and details an overlooked mechanism: naive immigrants are more successful at adopting more optimal cultural  
307 behaviors that were originally innovated by more experienced residents. This mechanism provides a pathway  
308 towards the evolution of efficient, locally adaptive cultural behaviors in populations of behaviorally conservative  
309 individuals. If a particular population of animals is capable of maintaining cultural traditions, we might well  
310 expect to find an effect of turnover rate on their cultural state.

## 311 4 Materials and Methods

### 312 4.1 Study design

313 The objective of this study was to determine how population turnover might affect the cultural evolution of  
314 efficiency: the innovation and spread of an efficient tradition in populations that have an already established  
315 inefficient cultural tradition. We began the experiment with the hypothesis that naive individuals might be  
316 more likely to innovate the efficient solution. However, during data analysis we found evidence to support the  
317 hypothesis that naive individuals were adopters, and not necessarily innovators.

318 To test this hypothesis, we used 18 captive populations of wild-caught great tits—a small passerine bird  
319 that is widely distributed across Europe. This experiment attempted to recreate natural foraging flocks by  
320 using micro-populations consisting of 6 individuals, each housed in aviaries with dimensions of 4m\*4m\*3m.  
321 This group size falls within the range of natural foraging flocks, and meets ethical criteria for the confinement  
322 of passerines within aviaries of this size. Sex was balanced (94 female, 87 male), however age was not (118  
323 juveniles, 63 adults) due to unpredictable variation in the week-to-week catching of wild birds. A total of  
324 181 tits were used in the experiment, with 54 participating in the static condition, and 127 in the turnover  
325 condition. The extra bird in the turnover condition was a replacement for a bird which had died during the  
326 diffusion period. Tits were caught using mist nets at 7 different sites, all within a range of 10 km from The  
327 Max Planck Institute of Animal Behavior. When caught, birds were fitted with a metal identification ring,  
328 as well a passive integrated transponder (PIT) tag (IB Technology). Birds were aged and sexed by plumage.  
329 Birds were released back into the wild at the location where they were captured. All work adhered to relevant  
330 ethics approval by Regierungspraesidium Freiburg (35-9185.81/G-17/168).

#### 331 4.1.1 Experimental apparatus

332 The foraging puzzle box consisted of an acrylic box with a bidirectional sliding door. The door (4 × 6-cm)  
333 could be slid to the left or right to reveal a 1-cm hole through which the bird could access a reservoir of  
334 meal worms. The hole was off-center by .5-cm, such that pushing the red side of the door would be more  
335 efficient (1-cm from door-edge to hole) than pushing the blue side (2-cm to hole). This difference provided a  
336 significant challenge, given the tit's size. Average solve speed confirms that it was faster to use the red side  
337 of the door.

338 The puzzle-boxes were fully automated to minimize disturbance of the birds during the experiment. Puzzle  
339 boxes included a micro-computer, a stepper motor to automate the door return mechanism, and an external  
340 printed circuit board to handle RFID reading (PriorityOne). An RFID antenna mounted under the perch  
341 recorded identities of birds from their PIT tag, as well as their arrival and departure times.

342 Movement of the door was measured using sensors, which were triggered once the door moved past a  
343 position that would allow the bird to access the hole. Once a sensor was triggered and the solving bird left,  
344 the door would automatically close either after 3 scrounge attempts, or after 3 seconds, whichever came first.  
345 In the 2020 field season (accounting for 12 of 18 total populations), the puzzle also recorded video of the  
346 visiting birds, from which identities could be resolved using a bar-code attached to the bird using leg loops  
347 [53]. Bar-code data was used 1) to resolve identities of solves without a positive identity from RFID data,  
348 2) to measure TTS. Solvers were defined as birds who had  $\geq 20$  recorded solutions in all of the following

349 analyses. Since data was collected using an automated system, this minimum was a conservative way to filter  
350 noise to ensure that the birds were indeed solvers, and also allowed for mixed effects models to converge with  
351 ID as a random effect.

#### 352 4.1.2 Experimental design

353 One experimental population was considered a replicate, with 9 replicates for each condition. Each population  
354 was supplied with 1 tutor that had been trained to produce the inefficient solution. During training, tutors  
355 interacted with the puzzle with door open, and then we progressively closed the door in subsequent trials until  
356 they had learned the full solving behavior. Populations were given a diffusion period of 12 days before the first  
357 turnover event to allow the inefficient tradition to become established (by the end of 12 days, the behavior  
358 had diffused to 1 or more birds in all populations, excluding population 13). During the diffusion period, the  
359 efficient solution was blocked to promote uptake of only the inefficient solution into the population before  
360 the experimental manipulation of population turnover began. Therefore, in their initial state, populations  
361 were intended to represent a wild foraging flock that exclusively used an established foraging tradition before  
362 another variant became available. 52 birds learned to solve the puzzle box during the diffusion period, however  
363 there was no evidence that this treatment influenced the probability that birds would sample the alternative  
364 solution once unblocked (Table S4). Further, almost all of the innovators of the efficient solution were birds  
365 which had experienced this treatment (Results 2.3). Tutors from two populations were re-used as tutors in 2  
366 separate populations, as tutors in these populations failed to produce the inefficient solution.

367 For the 28 days following the diffusion period, populations were either *static*, where the population con-  
368 sisted of the same set of 6 birds, or *turnover*, where 2 birds within generation were randomly replaced with  
369 new, naive birds every 7 days. The initial 6 members of a population were considered Generation 1, with  
370 incoming birds considered as Generation 2. This stochastic, within generation turnover was meant to repli-  
371 cate conditions similar to turnover of foraging flock composition, rather than generational turnover. 28 days  
372 allowed for a total of 4 turnover events (T1-T4). The experiment was concluded after 28 days because of  
373 the ethical consideration that the tits be released by the beginning of the breeding season beginning in early  
374 March. Data collection took place over two field seasons (Jan-March 2019, Jan-March 2020).

## 375 4.2 Statistical Analyses

### 376 4.2.1 Individual-level improvement in performance

377 TTS for solutions were calculated similarly to [41], as the time difference between a bird's arrival (recovered  
378 from RFID data and QR data) and the time when the door is detected as open (recovered from sensor  
379 data). Both RFID and QR reads of birds were noisy and subject to error, so TTS was the average of both  
380 measurements for cases when both RFID and QR data were available for a particular solution.

381 To assess differences in solving performance over time within individuals, data was subset to solvers, non-  
382 tutors and  $TTS < 60s$ . 59 solutions longer than 60 seconds were excluded, and 18,534 were excluded due to  
383 unrecorded solve speeds. We then used a Linear Mixed Effects model in which  $\log(TTS + 1)$  was predicted  
384 by age, sex and a full interaction between Z-scaled trial number and solution type, and population, ID and  
385 year controlled for as nested random effects. TTS was logged to account for non-normality of residuals, with  
386 1 added since the shortest TTS value was 0. Experimental day was not included, as it was collinear with trial  
387 number.

388 To visualize the difference between inexperienced and experienced solvers in 1C, within each bird the data  
389 was divided into the first 25% of solutions produced and the remaining 75% of solutions produced. Changing  
390 the values of this division do not invert either the relationship between solutions, or between inexperienced  
391 and experienced TTS.

### 392 4.2.2 Condition-level differences in solving

393 To analyze how much each condition had improved over the course of the experiment data was subset to  
394 solutions produced by solvers with  $TTS < 60s$ , tutors excluded. We ran a LMM [54, 55] in which  $\log(TTS + 1)$   
395 was predicted by age, sex, and experimental day\*condition interaction. ID, population and year were included  
396 as nested random effects, and solution type was included as another random effect. Trial number was not  
397 included, as it was collinear with experimental day.

398 To quantify the difference in selection for efficiency between conditions, we first subset the data to solvers  
399 only, and experimental day  $\geq 6$ . We then used a logistic GLMM with the probability of producing an  
400 efficient solve regressed on age, sex, and an interaction between experimental day and condition. Population

401 and year were included as nested random intercepts. Individual birds were not included as random intercepts,  
402 since the intercept value represented experimental day 7 (first day after turnover). Since many of the birds in  
403 the turnover condition were not present on this day, a random intercept would be creating estimates for large  
404 proportions of data which didn't exist.

### 405 4.2.3 Innovation

406 Comparing a true innovation rates proved difficult, as once an innovation is adopted by a population and  
407 produced with any frequency, subsequent true innovation events would be masked due to the assumption that  
408 a frequently produced solution would be observed by all birds. Innovators were therefore defined in two possible  
409 ways. 1) Innovators were birds who were the very first to produce the efficient solution within a population. 2)  
410 We calculated the distribution of time between efficient solves ( $\Delta t$ ), Innovators were also defined as birds who  
411 produced the efficient solution with an outlier  $\Delta t$  ( $>63$  hours), as we deemed it unlikely that the innovator  
412 had observed the previous efficient solution. We analyzed differences in innovation timing between conditions  
413 using three GLMS in which sex, age and condition predicted 1) days solving before innovation, 2) days of  
414 exposure to puzzle before innovation, 3) total elapsed experimental days before innovation.

### 415 4.2.4 Behavioral conservatism

416 To test whether experience or conformity played a more relevant role in the failure of birds to switch from  
417 inefficient to efficient we subset to solvers that had produced both solutions. If inefficient solutions outnumbered  
418 efficient solutions in the last 10% of their solves, then that bird was marked as failed to switch (given  
419 the average of 1,795 solutions per solver, this 10% conservatively covers the last hundred or so behavioral  
420 productions of a solver before they were removed from the experiment). Experience was calculated as days  
421 solving before experiencing the efficient solution. To measure conformity, we measured the proportion of  
422 socially observed inefficient solutions of all solutions produced the day that bird first produced the efficient  
423 solve. We used a GLMM to control for population and year level differences, in which failure to switch was  
424 predicted by experience with the inefficient solution prior to sampling the efficient, and the proportion of  
425 socially observed inefficient solutions.

## 426 4.3 Agent Based Model

427 Due to the practical limitations of replicating treatments with wild-caught birds, an agent based model was  
428 used to 1) test the verbal hypothesis relating demographic features to cultural outcomes, and 2) provide  
429 virtual power to the experiment. Simulations were run across parameter space under these conditions to test  
430 the hypothesis that population turnover would increase the area of parameter space in which populations of  
431 agents would converge on a more efficient solution to solve a foraging puzzle.

432 The model is comprised of agents capable of learning and producing foraging behaviors. Agents learned  
433 both through observation and personal experience, updating their probabilities of producing either solution  
434 according to a modified experience-weighted attraction (EWA) learning model [56, 50, 36, 48, 49]. In terms  
435 of temporal scale, the time-step approximates one experimental day. The simulation lasts for 35 time-steps,  
436 simulating the 5 weeks of the experiment. Each time step, agents interacted with, and observed others  
437 produce behaviors. There were two possible behaviors, with agents receiving scalar payoffs of 10 and 20  
438 for each solution respectively (see Fig. S4 for other payoff values.) The behavior with the higher reward  
439 signal represented the efficient solution in the experiment. To imitate the blocked efficient solution for the  
440 establishment period, payoffs were set as efficient: 0, inefficient: 10 for the first 7 time steps. Turnover  
441 occurred every 7 time-steps in the same manner as the experiment.

442 Agents could be in 1 of 2 states: knowledgeable or naive. If knowledgeable, agents produced solution  
443 behaviors. If naive, agents simply observed others' solutions, and this information was recorded in their  
444 social memory, influencing behavioral decisions after an agent became knowledgeable in proportion to how  
445 much agents would weight social information (see parameters below). Possible transition from naive to  
446 knowledgeable states occurred once per time-step according to the conditional probability of learning function.

447 The values for the conditional probability of learning function were determined using latency-to-learn data  
448 gathered from the experiment. Data was subset to solvers and non-tutors, and right censored for individuals  
449 that never learned. A log-normal parametric survival analyses was performed in R using the rms package [55,  
450 57] with only the intercept as a predictor, such that a hazard function considering all birds was estimated (log-  
451 normal model had a higher log-likelihood than a Weibull model). From this hazard function the conditional  
452 probability of learning was estimated. Agents each had a count variable  $t$  to keep track of how many time-  
453 steps each bird had been exposed to the puzzle, used to return the probability of transitioning from naive

454 to knowledgeable state  $R(t)$ . This function produces the probability that an individual would acquire the  
 455 behavior within the interval  $[t, t + 1]$  given that it had not acquired it previously. The shape of this probability  
 456 curve approximates the hazard rate, and was calculated as

$$p(\text{learn}|\text{not learned yet}) = \frac{(R(t) - R(t + 1))}{R(t)} \quad (1)$$

457 where  $R(t)$  is the survival function. To test whether this particular function was an important mechanism  
 458 for the effect of turnover, we re-ran the sensitivity analysis with the reverse of this function, such that  
 459 probability of learning increased with time. We found no major differences.

460 This model allows for variation of the four following learning parameters within each agent:

- 461 •  $g_i$ : current payoff bias (weight given to most recently received payoff vs. previous payoffs). Values  
 462 could range from  $[0,1]$ . We chose to test a range from  $[0.1, 0.9]$  at increments of 0.2.
- 463 •  $s_i$ : social cue bias (weight given to social information vs. personal information). Values could range  
 464 from  $[0,1]$ . We chose to test a range from  $[0.1, 0.9]$  at increments of 0.2.
- 465 •  $\tau$ : conservatism (sensitivity to differences in attraction scores). A value of 1 indicates choice is in  
 466 proportion to the difference in attraction, and increasing values will increase the probability that an  
 467 agent will stick with a previously produced, well sampled behavior even after sampling a different,  
 468 higher payoff behavior. We chose to test a range from  $[1, 5]$  at increments of 1, as tits were observed  
 469 to be behaviorally conservative, rarely alternating between choices.
- 470 •  $\lambda$ : conformity (sensitivity to the most frequently observed behavior): A value of 1 indicates linear  
 471 sensitivity to social cues (no effect), values less than 1 are anti-conformist, and values greater than  
 472 1 are conformist. We chose to set the value at 5 for medium-level conformity, following a previous  
 473 convention for this type of model [36]. See Fig. S3 for results from populations of non-conformists and  
 474 extreme-conformists.

475 These parameters are used in four equations that shape how an agent learns through individual and social  
 476 experience. The attraction score equation:

$$A_{kt} = g_i \pi_k + (1 - g_i) A_{k,t-1} \quad (2)$$

477 These raw attraction scores over set of behaviors  $m$  must be converted into probabilities  $I_{kt}$  for a behavioral  
 478 choice  $k$  at time  $t$ , which is done using a soft-max choice rule given in the equation below:

$$I_{kt} = \frac{\exp(\tau A_{kt})}{\sum_m \exp(\tau A_{mt})} \quad (3)$$

479 The  $\tau$  parameter determines the sensitivity to differences in attraction scores, with large values of  $\tau$   
 480 ensuring that the behavior with the largest attraction score will be chosen.

481 Socially observed information is given a weight according to the following equation

$$S_{kit} = \frac{n_{kt}^\lambda}{\sum_m^K n_{mt}^\lambda} \quad (4)$$

482 Personal and social information is combined into a probability of choice using this final equation.

$$P_{kit} = (1 - s_i) I_{kit} + s_i S_{kit} \quad (5)$$

483 For each point in the parameter space described above, data was recorded from 500 simulations per  
 484 condition. In each simulation, agents were initialized with identical parameter values. One agent was the  
 485 designated "tutor", and was programmed with a high attraction score for the inefficient solution.

486 Within one time-step, each knowledgeable individual would produce 100 behaviors, which approximated  
 487 the real average from the experiment. The order of individuals was not randomized, as social information  
 488 was not processed until the end of a time step. When a knowledgeable individual produced a solution, they  
 489 received a payoff. Next, they updated their attraction scores, and finally updated the probabilities for their  
 490 next choice of solution. At the end of each time-step, the following data was recorded: time-step, condition,  
 491 mean values of parameters, frequency of solves of each type, and number of solvers. Also, the social cue  
 492 matrices were updated for all agents using the frequencies of behaviors produced within that time-step. Their  
 493 choice probabilities were then updated to reflect this new social information. If there were still naive agents in  
 494 the population, each naive agent could transition to a knowledgeable state according to  $R(t)$ . The remaining  
 495 naive agents update their acquisition probabilities for the next time-step. If the simulation was in the turnover  
 496 condition, then every 7 time-steps there was a turnover event.

## 5 Data Availability

Code and data for statistical analyses and main text figures, as well as code to replicate the agent based model is available at <https://github.com/michaelchimento/DemographicTurnoverEfficiency>.

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## 7 Author Contributions

MC and LA designed the experiment. MC and GAN designed the automated data capture system. MC performed the experiment with support from GAN and LA. MC designed, coded the agent based model. MC analyzed the data with support from LA. MC wrote the first draft of the manuscript, and all authors edited, commented and added to it.

## 8 Competing Interests

The authors declare no competing interests, financial or otherwise.

## 9 Materials & Correspondence

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