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Population turnover facilitates cultural selection for efficiency in birds

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Summary

Culture, defined as socially transmitted information and behaviors that are shared in groups and persist over time, is increasingly accepted to occur across a wide range of taxa and behavioral domains¹. 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^{2–5}. Selection for more efficient behaviors over alternatives is a crucial component of cumulative cultural evolution⁶, yet our understanding of how and when such cultural selection occurs in non-human animals is limited. We performed a cultural diffusion experiment using 18 captive 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 a fundamental demographic process—population turnover. Our results showed that gradual replacement of individuals with naive immigrants greatly increased the probability that a more efficient behavior invaded a population’s cultural repertoire and out-competed an established inefficient behavior. Fine-scale, automated behavioral tracking revealed that turnover did not increase innovation rates, but instead acted on adoption rates, as immigrants disproportionately sampled novel, efficient behaviors relative to available social information. These results provide strong evidence for cultural selection for efficiency in animals, and highlight the mechanism that links population turnover to this process.

Keywords: cultural evolution, cultural selection, efficiency, population turnover, *Parus major*

1 Results and discussion

2 Beyond genes, culture offers a secondary inheritance system that provides an alternative pathway to
3 adaptive plasticity^{7,8}. Humans have leveraged this to its fullest extent, accumulating and recombining
4 cultural behaviors into evermore efficient complexes in a process termed cumulative cultural evolution
5 (CCE)⁹. Simpler forms of cultural evolution are also likely to be widespread in non-human animals⁷,
6 although this remains understudied (but see^{10,11} for recent reviews). While claims of cumulative cul-
7 ture in non-human animals are controversial^{12,13}, increases in cultural efficiency have been identified in
8 movement behavior of storks, pigeons and ungulates^{14–16}. Recent discussions have proposed that such
9 repeated instances of cultural selection for efficiency in a singular cultural trait represent a precursor
10 to the more complex forms of CCE unique to humans^{6,16}. Given its importance for a broader evolu-
11 tionary account of culture, it is critical to identify and describe cultural selection for efficiency and its
12 mechanisms in non-human species.

13 Culture exists on the social network¹⁷, and cultural evolution should be responsive to network prop-
14 erties such as population size, structure and dynamic turnover^{4,18–22}. Larger population sizes have been
15 linked to elevated cultural diversity, innovation and faithful transmission^{18,23–26}. Conversely, popula-
16 tion decline and fragmentation can reduce trait diversity and complexity, as observed in bird song^{27–29}.
17 Population turnover, caused by immigration, emigration, births and deaths, is a universal demographic
18 process, yet its effect on cultural evolution is poorly understood³⁰. It could lead to adaptive cultural

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19 outcomes if incoming individuals introduce new innovations¹⁶. Alternatively, naive individuals might
20 better re-sample the behavioral space because they are less behaviorally conservative, or less subject to
21 factors such as conformity³¹.

22 To study the effect of population turnover on cultural selection for efficiency, we conducted a cul-
23 tural evolution experiment in a common passerine bird, the great tit (*Parus major*). Inter- and intra-
24 generational turnover are key features of their social system³²⁻³⁵, and they are an established study
25 system for innovation and animal culture³⁶⁻⁴¹. We created 18 artificial populations of wild-caught great
26 tits with a membership of 6 birds each, the average size found in winter foraging flocks of great tits³⁵.
27 The study then consisted of two phases: 1) a diffusion period (12 days), and 2) a subsequent experi-
28 mental period (28 days) in which population turnover was manipulated. During the diffusion period,
29 a foraging tradition to access food by pushing on a bidirectional door of an automated puzzle box was
30 established in each population using a tutor bird trained on the inefficient solution (Figure 1). This set all
31 populations to the same initial, inefficient cultural state prior to the experimental manipulation. In the
32 experimental period, turnover was simulated in 9 populations by replacing 2 randomly selected birds with
33 new, wild-caught birds in the first turnover event (T1). Turnover events then occurred every subsequent
34 week (T2-T4) for the remainder of the experimental period. Another 9 populations maintained stable
35 membership for the duration of the experiment (static populations). Birds could improve their speed
36 at the established foraging tradition, or potentially innovate an alternative, more efficient solution. We
37 predicted that turnover populations would be more likely to innovate and adopt the alternative solution,
38 either because incoming naive birds might be more likely 1) to innovate the efficient solution, or 2) to
39 adopt the efficient solution once innovated.

40 *Social learning lead to established traditions*

41 During the diffusion period, the solving behavior spread in 17 of 18 populations, with 46 of 90
42 naive residents learning to solve. During the experimental period, 37 of 73 immigrants also learned to
43 solve. There were no significant differences between age or sex classes in latency to learn (Figure S1).
44 Evidence that solving was socially learned is: 1) outside of the diffusion period, 87% of birds first solved
45 using the most predominant solution in their population, 2) the puzzle was difficult to individually
46 learn (tutors took anywhere from 1 to 2 weeks of incremental training to learn) and 3) the behavior
47 failed to be re-innovated in a population where the behavior went extinct. Over the course of the entire
48 experiment, birds that learned to solve the puzzle (solvers) produced a total of 174,393 recorded solutions
49 (average 9719 per population, range: 1,494–17,208), with 89% of those with measurable time-to-solve
50 (TTS). Tutors accounted for 47,000 of all solutions, with a daily average of 100 solutions. New learners
51 accounted for 127,939 solutions, with a daily average of 86. Altogether, solvers produced an average of
52 1,803 solutions (range: 20–6,612), and a daily average of 89 solutions.

53 Solvers became significantly faster with experience, reducing their TTS by about 3% with every stan-
54 dard deviation of solutions produced, suggesting that reinforcement learning was leading to improvements
55 in efficiency (Linear Mixed Model (LMM), solution index (scaled): $\beta = -0.027 \pm 0.002$, $t = -11.975$,
56 $P < 0.001$; Table S1A). The efficient solution was significantly faster than the inefficient solution when
57 controlling for experience, between populations and individual solvers (LMM, solution type (efficient):
58 $\beta = -0.395 \pm 0.051$, $t = -7.787$, $P < 0.001$; LMM, intercept (inefficient): $\beta = 0.925 \pm 0.215$, $t = 4.299$,
59 $P < 0.001$; Table S1A; Figure 1C). The same amount of solving experience with the efficient solution ob-
60 tained a lower average TTS compared to the inefficient solution (LMM, solution type (efficient):solution
61 index (scaled): $\beta = -0.117 \pm 0.006$, $t = -18.102$, $p < 0.001$). The efficient solution therefore offered a
62 greater payoff as solvers tended to receive the same reward in less time.

63 *Turnover facilitated cultural selection for efficiency*

64 Following the diffusion period, populations were either left as static, or underwent gradual turnover
65 throughout the experimental period. Initially, birds in either condition were unlikely to produce the
66 efficient solution (GLMM, intercept: $\alpha = -10.853 \pm 1.088$, $Z = -9.974$, $P < 0.001$; turnover condition:
67 $\beta = -2.169 \pm 1.700$, $Z = -1.276$, $P = 0.203$; Table S1C). With each passing day, there was an increasing
68 probability of producing efficient solutions in both conditions (GLMM, exp. day: $\beta = 0.291 \pm 0.010$,
69 $Z = 28.986$, $P < 0.001$). However birds from the turnover condition became significantly more likely
70 to produce efficient solutions compared to the static condition over time (GLMM, exp. day:condition
71 (turnover): $\beta = 0.603 \pm 0.016$, $Z = 38.713$, $P < 0.001$) (Figure 2A, 2B; Figure 3A). Overall, turnover
72 populations produced 44,703 inefficient and 39,815 efficient solutions, while static populations produced
73 88,829 inefficient and only 1,592 efficient solutions.

74 Social information available about the efficient solution predicted the extent to which individuals
75 sampled the solution (LMM, efficient social information, $\beta = 0.285 \pm 0.023$, $t = 12.417$, $P < 0.001$).
76 Importantly, immigrants were more likely than residents to sample the efficient solution, even given rela-
77 tively little available social information. They continued to sample the efficient solution more frequently
78 than residents as social information increased (LMM, intercept (immigrant): $\beta = 0.578 \pm 0.071$, $t = 8.110$,
79 $P < 0.001$; resident: $\beta = -0.401 \pm 0.063$, $t = -6.393$, $P < 0.001$; efficient social information:resident :
80 $\beta = -0.153 \pm 0.043$, $t = -3.586$, $P < 0.001$ Table S2). This suggests that, unlike residents, immigrants
81 were amplifying social information about the efficient solution through their own productions, and that
82 the evolution of solution frequencies at the population-level was caused by selection, rather than drift.

83 *Cultural selection generated population-level differences in performance*

84 While individual populations displayed a variety of dynamics (Figure 2; Figure S2 for all populations)
85 and both conditions innovated the efficient solution, turnover populations were much more likely to adopt
86 the efficient behavior. In total, 7/9 turnover populations selected for and adopted the efficient solution
87 as the majority solution. By contrast, only one static population selected for the efficient solution. This
88 population accounted for most of the efficient solutions in the static condition (1,466), while all other
89 static populations only produced the efficient solution a handful of times, if at all (range: 0-28).

90 Both conditions exhibited a decreasing trend in TTS, (LMM, exp. day (scaled): $\beta = -0.048 \pm 0.005$,
91 $t = -9.885$, $P < 0.001$; Table S1b). Yet on average, turnover populations had a significantly steeper
92 reduction their TTS than static populations (LMM, exp. day (scaled):condition (turnover): $\beta = -0.077 \pm$
93 0.010 , $t = -7.832$, $P < 0.001$; Figure 3B). Turnover populations were slower than static populations
94 through the first two turnover events, suggesting that the loss of knowledgeable birds may have initially
95 hindered the accumulation of expertise in the inefficient solution. However, by the final week after T4,
96 birds in turnover populations were solving faster than static populations ($M_t = 1.66s$, $M_s = 1.96s$). The
97 increasing dominance of the efficient solution therefore allowed turnover populations to achieve a lower
98 TTS despite having less experience solving than individuals in the static condition.

99 *Innovation rates were not the mechanism behind differences in cultural outcomes*

100 Innovators were classified as birds which produced the first efficient solution in a population, or
101 produced the efficient solution without having seen it demonstrated given the amount of time elapsed
102 since a prior innovation (see Methods). In total, 21 birds innovated (static: 13, turnover: 8). Innovators
103 were almost equally split between age (10 juveniles, 11 adults) and sex (10 female, 11 male), and were
104 generally experienced solvers.

105 To test whether turnover increased the probability of innovation, we compared 1) days solving before
106 innovation, 2) exposure time to the puzzle before innovation and 3) experimental day of innovation
107 between both conditions (Figure 4). Exposure time before innovation ($M_t = 14.1$, $M_s = 15.5$) and
108 experimental day of innovation ($M_t = 14.5$, $M_s = 16.3$) were not significantly different between conditions
109 (Table S3). Innovators in the turnover condition had a significantly shorter period of days solving
110 before innovation ($M_t = 8.88$, $M_s = 13.8$; GLM condition (static): $\beta = 5.772 \pm 1.918$, $t = 3.009$,
111 $P = 0.008$), but this difference was driven by only 2 data points. These results, along with the fact
112 that static populations innovated more often, suggest that innovation probabilities were comparable
113 between conditions. Surprisingly, only 5 of 21 innovators permanently adopted the efficient solution
114 after innovation, hinting at some level of behavioral conservatism.

115 *Turnover allowed populations to overcome individual-level behavioral conservatism*

116 Relatively few birds were observed producing large amounts of both solution types—most learners
117 strongly preferred one solution. Out of 53 birds that sampled both solutions, 36 failed to adopt the
118 efficient solution. The effect of experience (habit formation) or conformity could contribute to this
119 behavioral conservatism. We found that birds were very likely to adopt the efficient solution if they
120 experienced an efficient solution on the first day of solving (GLMM, intercept: $\alpha = -3.421 \pm 1.977$,
121 $Z = -1.730$, $P = 0.084$; Table S4). However, each day of experience with the inefficient solution
122 significantly increased the probability an individual wouldn't adopt the efficient solution (GLMM, days
123 experience: $\beta = 0.364 \pm 0.132$, $Z = 2.761$, $P = 0.006$). Conformity, as well as age and sex, were not
124 significant predictors. This suggests that increasing experience reinforced behavioral conservatism, and
125 that the introduction of naive individuals via turnover allowed populations to overcome this inertia.

127 Turnover allowed populations to shift from an established foraging tradition towards a more efficient
128 alternative. This was not a result of innovation or noise introduced by immigrants; rather knowledgeable
129 residents more often innovated efficient behaviors, which were then more often adopted by immigrants.
130 The widespread adoption of the efficient solution mitigated the effect of reduced opportunity for develop-
131 ment of expertise, leading to a faster overall time-to-solve. This pattern of cultural outcomes contrasted
132 with the absence of selection for the efficient behavior by birds in static populations, despite its regular
133 innovation. We conclude that turnover can be a mechanism that facilitates cultural selection for efficiency
134 by providing a pathway to adaptive plasticity that navigates individual-level behavioral conservatism.

135 The only other direct experimental test of cultural evolution of efficiency in birds was in homing
136 pigeons¹⁶, where pairs of birds developed more direct, efficient homing routes over time when one of the
137 pair was repeatedly replaced in a chain design. An alternative mechanism was proposed—that naive
138 individuals might produce behavioral variation on which cultural selection could act. However, flight
139 behavior was a continuously measured variable (straightness), and the authors could not directly quantify
140 innovation events. Our study extends this work in several important ways. First, we conduct turnover in
141 groups, mimicking realistic fission-fusion dynamics and natural flock sizes. Second, we test this process in
142 a foraging context; most work related to this topic in non-human primates has focused on foraging^{42–44},
143 and our work gives new insights into this key behavioral domain. Finally, our experimental design allowed
144 for a discrete step-change in efficiency (alternative solution variants), as well as continuous (time-
145 to-solve). We could identify discrete innovation events and their effect on continuous population-level
146 behavior, revealing the mechanism mediating the relationship between turnover and efficiency.

147 Our results suggest a near inversion of the aforementioned hypothesis¹⁶—experienced residents
148 innovated, while naive immigrants adopted. This contrast may result from the differences between the
149 the continuous spectrum of efficiency in the context of movement^{14–16}, and the discrete differences in
150 efficiency often associated with foraging behavior. In a continuous, dynamic behavior such as flight,
151 noise might be more easily generated by naive individuals, and then edited by experienced individuals.
152 In the current study, by contrast, experience aided innovation. In natural populations, both cultural
153 evolutionary mechanisms may be active. Immigrants may either innovate themselves, or successfully
154 resample the behavioral space, and adopt more beneficial, but less frequently produced alternatives. The
155 dominant mechanism through which turnover acts on culture might likely be determined by the ease of
156 producing innovations. Future research should seek to identify both processes when investigating cultural
157 evolutionary dynamics.

158 Behavioral conservatism is identified as a primary reason for the lack of observed CCE in animal
159 species⁴⁵, yet may be a key reason why population turnover is vital to the evolution of efficiency. Memory
160 loss through the replacement of individuals creates opportunities for unbiased re-sampling of behavioral
161 payoffs. A suggestion of this effect of turnover on cultural inertia comes from translocation studies
162 of blue-headed wrasse, a fish that culturally inherits spawning sites. When all members of a wrasse
163 population were replaced, naive fish resampled the set of potential spawning sites and selected different
164 mating sites from the original population³¹. A second replacement population selected the same sites,
165 suggesting that turnover resulted in more optimal sampling⁴⁶. The successful resampling by naive fish
166 appears analogous to that observed in immigrant tits. Population turnover might therefore provide a
167 broad mechanism for resampling socially transmitted information and potentially moving populations
168 towards more adaptive local optima.

169 The cultural evolution of refined, efficient, behaviors has been considered a precursor to more complex,
170 human-like forms of cumulative culture⁶. While we do not argue that our results demonstrate CCE, they
171 add to the growing evidence that cultural evolution of efficiency is possible in animals, and extend this to
172 foraging behavior. This small passerine species is capable of moving the cultural ratchet one tick forward,
173 fulfilling a key description of CCE: a behavior innovated by an individual spreads within a group, and
174 persists until future individuals make efficient modifications, which then spread and supplant the previous
175 behavior⁹. Yet it remains an open question as to why repeated instances of selection for efficiency are so
176 rarely observed in the field. Our results suggest this is not due to an inability to select for more efficient
177 variants; rather population turnover can mitigate behavioral conservatism. The conservatism identified
178 in our study may be surprising given a prior finding that 49% of great tits could switch solutions when
179 the payoff structure of a puzzle box was altered⁴⁰. However, those were free-mixing, wild flocks, further
180 supporting a facilitating role of demographic churn on behavioral flexibility. However, the benefits of
181 turnover carry a risk: the potential loss of knowledgeable individuals and extinction of cultural traits.
182 One turnover population exhibited a complete extinction of the solving behavior. Future work should
183 further explore how varying turnover rate and scale influences cultural dynamics.

184 This study illustrates how dynamic populations are more likely to select for efficient cultural be-
185 haviors, and details an overlooked mechanism: naive immigrants are more successful at adopting more
186 optimal cultural behaviors that were originally innovated by more experienced residents. This provides
187 a pathway towards the evolution of efficient, locally adaptive cultural behaviors in populations of behav-
188 iorally conservative individuals. If a particular population of animals is capable of maintaining cultural
189 traditions, we might well expect to find an effect of turnover on their cultural state.

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197 Author Contributions

198 Conceptualization, M.C., L.A.; Methodology, M.C., G.A.N., L.A.; Software, M.C.; Formal Analysis,
199 M.C.; Investigation, M.C., G.A.N., L.A.; Resources, M.C., G.A.N., L.A.; Writing—Original Draft, M.C.,
200 Writing—Review and Editing, M.C., G.A.N., L.A.; Visualization, M.C.; Supervision, L.A.

201 Declaration of Interests

202 The authors declare no competing interests.

203 Main text figure/table legends

204 **Figure 1: Automated foraging puzzle with solutions of differing efficiency. A)** Populations
205 were provided one puzzle box with a 4 cm wide door which gave access to mealworms. The access point
206 was offset from the center by .5 cm, such that pushing from the left (red) side was more efficient. A
207 microcomputer recorded identity and solution type using **B)** an RFID antenna in the perch to record
208 identities from unique transponder tags on birds, and a camera above recorded identity from barcodes
209 placed on the backs of birds. Both systems allowed calculation of ‘time-to-solve’ TTS. **C)** Birds improved
210 with experience, but the efficient solution was significantly faster to solve (mean±SE, tutors excluded;
211 efficient: n = 44 birds, 34,444 solutions; inefficient: n = 50 birds, 78,616 solutions). See also Table S1.

212 **Figure 2: Overview of behavioral frequency data between conditions and within exem-**
213 **plar populations. A)** Each point represents the daily solutions of a unique bird in that population.
214 Type (color), frequency (size), innovation events (triangle shape, see Methods for definition), tutors
215 (gold text), diffusion period (grey background), and duration of individuals (black lines) are marked.
216 Despite nearly all static populations innovating the efficient solution, only one population selected for
217 it (n = 29 birds, 90,421 solutions). **B)** Almost all turnover populations innovated and selected for the
218 efficient solution, and adopters were primarily naive individuals (n = 70 birds, 84,518 solutions). **C)**
219 A static population in which two birds independently innovated the efficient solution, produced it with
220 low frequency, yet failed to select for it (n = 4 birds, 14,483 solutions). **D)** A turnover population that
221 selected for the efficient solution. An experienced bird innovated on day 11, and the efficient solution
222 was produced at low frequency until it was widely adopted by immigrants after the third turnover (n =
223 9 birds, 16,616 solutions). See Figure S2 for all populations.

224 **Figure 3: The link between cultural evolution and efficiency. A)** The daily proportion of
225 solutions by type from all populations (static: n = 28 birds, total solutions = 88,224; turnover: n = 70
226 birds, total solutions = 84,518). Static populations produced inefficient solutions for the majority of the
227 experiment. In contrast, efficient solutions fully invaded the cultural repertoire of nearly all turnover
228 populations by the end of the experiment. **B)** Daily time-to-solve for non-tutors in static and turnover
229 conditions (thin lines with 95% SE), along with a right-aligned 7 day moving average (thicker lines). Y-
230 axis log2 coord. transformed for visualization, and vertical dashed lines show turnover events (T1-T4). In
231 the last two weeks of the experiment, turnover populations were solving faster than static populations on
232 average. This increase in efficiency was driven by widespread cultural selection for the efficient solution
233 (static: n = 21 birds, 52,458 solutions; turnover: n = 61 birds, 60,735). See also Table S1.

234 **Figure 4. Innovation timing between conditions.** A) Days exposure to the task before inno-
235 vation and experimental day was not found to be significantly different between conditions (static: dark
236 blue, turnover: yellow; $n = 21$ innovation events). B) Days solving before innovation was significantly
237 lower in the turnover condition, however two data points drove this difference. C) Experimental days
238 before innovation was not found to be significantly different between the two conditions. From this data,
239 we suggest the difference in innovation between conditions was not primarily responsible for the strong
240 selection for efficiency in the turnover condition. See also Table S3.

241 STAR Methods

242 *Resource Availability*

243 *Lead Contact*

244 Further information and requests should be directed to and will be fulfilled by the Lead Contact,
245 Michael Chimento (mchimento@ab.mpg.de).

246 *Materials Availability*

247 This study did not generate new unique materials.

248 *Data and Code Availability*

249 The datasets and code generated during this study are available at Github: [https://github.com/
250 michaelchimento/PopulationTurnoverEfficiency](https://github.com/michaelchimento/PopulationTurnoverEfficiency).

251 *Experimental Model and Subject Details*

252 Our study used 18 captive populations of wild-caught great tits—a small passerine bird that is widely
253 distributed across Europe. Artificial populations consisted of 6 individuals, each housed in aviaries with
254 dimensions of 4m x 4m x 3m. This group size falls within the range of natural foraging flocks, and meets
255 ethical criteria for the confinement of passerines within aviaries of this size. Sex was balanced (94 female,
256 87 male) but age was not (118 juveniles, 63 adults). This imbalance may have been due to unpredictable
257 variation in capture rates but may have also represented the structure of the local population. A total
258 of 181 tits were used in the experiment, with 54 participating in the static condition, and 127 in the
259 turnover condition. The extra bird in the turnover condition was a replacement for a bird which had died
260 during the diffusion period. Tits were caught using mist nets at 7 different sites, all within a range of 10
261 km from The Max Planck Institute of Animal Behavior. When caught, birds were fitted with a metal
262 identification ring, as well a passive integrated transponder (PIT) tag, and aged and sexed by plumage.
263 Birds were released back into the wild at the location where they were captured. All work was conducted
264 by under a nature conservation permit and animal ethics permit from the Regierungspräsidium Freiburg,
265 no.35-9185.81/G-17/168.

266 *Method Details*

267 *Experimental apparatus*

268 The foraging puzzle box consisted of an acrylic box with a bidirectional sliding door. The door (4cm
269 x 6cm x .3cm) could be slid to the left or right to reveal a 1-cm hole through which the bird could access
270 a reservoir of meal worms. The hole was off-center by .5-cm, such that pushing the red side of the door
271 would be more efficient (1-cm from door-edge to hole) than pushing the blue side (2-cm to hole). This
272 difference provided a significant challenge, given the tit’s size. Average time-to-solve (TTS) confirmed
273 that it was faster to use the red side of the door.

274 The puzzle-boxes were fully automated to minimize disturbance to the birds during the experiment.
275 Puzzle boxes included a Raspberry Pi micro-computer, infrared sensors, a stepper motor to automate
276 the door return mechanism, and an external printed circuit board for RFID data logging (Priority1).
277 They operated using custom software written in Python⁴⁷. An RFID antenna mounted under the perch
278 recorded identities of birds from their PIT tag, as well as their arrival and departure times. Movement of
279 the door was measured using infrared sensors, which were triggered once the door moved past a position
280 that would allow the bird to access the hole. Once an sensor was triggered and the solving bird left, the
281 door would automatically close either after 3 scrounge attempts, or after 3 seconds, whichever came first.
282 In the second field season (accounting for 12 of 18 total populations), the puzzle also recorded video of
283 the visiting birds, from which identities could be resolved using a bar-code attached to the bird using
284 leg loops and a customized implementation of Pinpoint software⁴⁸. Bar-code data was used 1) to resolve

285 identities of solves without a positive identity from RFID data, 2) to measure TTS. Solvers were defined
286 as birds who had ≥ 20 recorded solutions in all of the following analyses. Since data was collected
287 using an automated system, this minimum was a conservative way to ensure that the birds were indeed
288 solvers, and also allowed for mixed effects models to converge with ID as a random effect.

289 *Experimental design*

290 One experimental population was considered a replicate, with 9 replicates for each condition. Each
291 population was supplied with 1 tutor that had been trained to produce the inefficient solution. During
292 training, tutors interacted with the puzzle with door open, and then we progressively closed the door
293 in subsequent trials until they had learned the full solving behavior. Populations were given a diffusion
294 period of 12 days before the first turnover event to allow the inefficient tradition to become established
295 (by the end of 12 days, the behavior had diffused to 1 or more birds in all populations, excluding one
296 static population). In their initial state, populations were intended to represent a wild foraging flock that
297 exclusively used an established foraging tradition before another variant became available. To ensure this
298 state prior to the experimental manipulation of population turnover began, during the diffusion period,
299 the efficient solution was blocked to promote uptake of only the inefficient solution into the population.
300 There was no evidence that this treatment decreased the probability that birds who learned to solve
301 during this period would sample the alternative solution once unblocked (Table S5). In fact, almost all
302 of the innovators of the efficient solution were birds which had experienced this treatment. Tutors from
303 two turnover populations were re-used as tutors in 2 static populations, as tutors in those populations
304 failed to produce the solving behavior within the diffusion period.

305 For the 28 days following the diffusion period, populations were either *static*, where the population
306 consisted of the same set of 6 birds, or *turnover*, where 2 birds within a generation were randomly replaced
307 with new, naive birds every 7 days. The initial 6 members of a population were considered Generation
308 1, with incoming birds considered as Generation 2. This stochastic, within generation turnover was
309 meant to replicate conditions similar to turnover of foraging flock composition, rather than generational
310 turnover. 28 days allowed for a total of 4 turnover events (T1-T4). The experiment was concluded after
311 28 days because of the ethical consideration that the tits be released by the beginning of the breeding
312 season beginning in early March. Data collection took place over two field seasons (Jan-March 2019,
313 Jan-March 2020).

314 *Quantification and Statistical Analysis*

315 *Individual-level learning and improvement in performance*

316 To compare differences in learning rates between age and sex classes, we used a non-parametric
317 Kaplan-Meier survival analysis⁴⁹ (Figure S1), in which an individual's latency to produce their first
318 solution of either type was predicted by an interaction between age (juvenile, adult) and sex. Survival
319 analysis is appropriate for time-to-event data, usually death. In this case, the event was learning to solve
320 the puzzle box.

321 TTS for solutions were calculated as the time difference between a bird's arrival and the time when
322 the door is detected as open. Both RFID and QR reads of birds were noisy and subject to error, so
323 TTS was the average of both measurements for cases when both RFID and QR data were available for
324 a particular solution.

325 To assess differences in solving performance over time within individuals, data was subset to solvers,
326 non-tutors and $TTS < 60s$. 59 solutions longer than 60 seconds were excluded, and 18,534 were excluded
327 due to unrecorded solve speeds. We then used a Linear Mixed Effects model in which $\log(TTS + 1)$
328 was predicted by age, sex and a full interaction between Z-scaled solution index and solution type, and
329 population, ID and year controlled for as nested random effects (Table S1). TTS was logged to account
330 for non-normality of residuals, with 1 added since the shortest TTS value was 0. Experimental day was
331 not included, as it was collinear with solution index.

332 *Condition-level differences in solving*

333 To analyze how much each condition had improved over the course of the experiment, data was
334 subset to solutions produced by solvers with $TTS < 60s$, tutors excluded. We ran a LMM^{50,51} in which
335 $\log(TTS + 1)$ was predicted by age, sex, and experimental day*condition interaction (Table S1). ID,
336 population and year were included as nested random effects, and solution type was included as another
337 random effect. Solution index was not included, as it was collinear with experimental day.

338 To quantify the difference in selection for efficiency between conditions, we first subset the data to
339 solvers during the experimental period only. We then used a logistic GLMM with the probability of

340 producing an efficient solve regressed on age, sex, and an interaction between experimental day and
341 condition (Table S1). Population and year were included as nested random intercepts. Individual birds
342 were not included as random intercepts, since the intercept value represented the first experimental day.
343 Since many of the birds in the turnover condition were not present on this day, a random intercept would
344 be creating estimates for large proportions of data which didn't exist.

345 To answer whether the immigrant birds were disproportionately sampling the efficient solution relative
346 to social information, we performed a LMM in which the daily proportion of efficient solutions produced
347 by a given solver was predicted by an interaction between whether they were an original resident (presence
348 on experimental day 0) and the proportion of social information they could potentially observe about
349 the efficient solution on that given day (Table S2). Data was subset to non-tutor solvers during the
350 experimental period only. ID nested in population were included as random effects.

351 *Innovation*

352 Measuring true innovation rates is difficult, as once an innovation is adopted by a population and
353 produced with any frequency, subsequent innovation events might be masked due to the assumption of
354 social information use. Innovators were therefore defined in two possible ways. 1) Innovators were birds
355 that were the first to produce the efficient solution within a population. 2) Innovators were also defined
356 as birds who produced their first efficient solution as an outlier in time Δt (>63 hours). This time period
357 was chosen we deemed it unlikely that the innovator had socially learned the efficient solution if they
358 had not observed or exhibited the behavior in this time. We analyzed differences in innovation timing
359 between conditions using three GLMS in which sex, age and condition predicted 1) days solving before
360 innovation, 2) days of exposure to puzzle before innovation, 3) total elapsed experimental days before
361 innovation (Table S3, Figure S2).

362 *Behavioral conservatism*

363 To test whether experience or conformity played a more relevant role in the failure of birds to switch
364 from inefficient to efficient, we first subset data to solvers that had produced both solutions. If inefficient
365 solutions outnumbered efficient solutions in the last 10% of their solves, then that bird was marked as
366 failed to switch. Given the average of 1,795 solutions per solver, this 10% conservatively covered the last
367 hundred or so behavioral productions of a solver before they were removed from the experiment. Expe-
368 rience was calculated as days solving before experiencing the efficient solution. To measure conformity,
369 we measured the proportion of socially observed inefficient solutions out of all solutions produced on the
370 day that bird first produced the efficient solve. We used a GLMM to control for population and year
371 level differences, in which failure to switch was predicted by experience with the inefficient solution prior
372 to sampling the efficient, and the proportion of socially observed inefficient solutions (Table S4).

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Figures

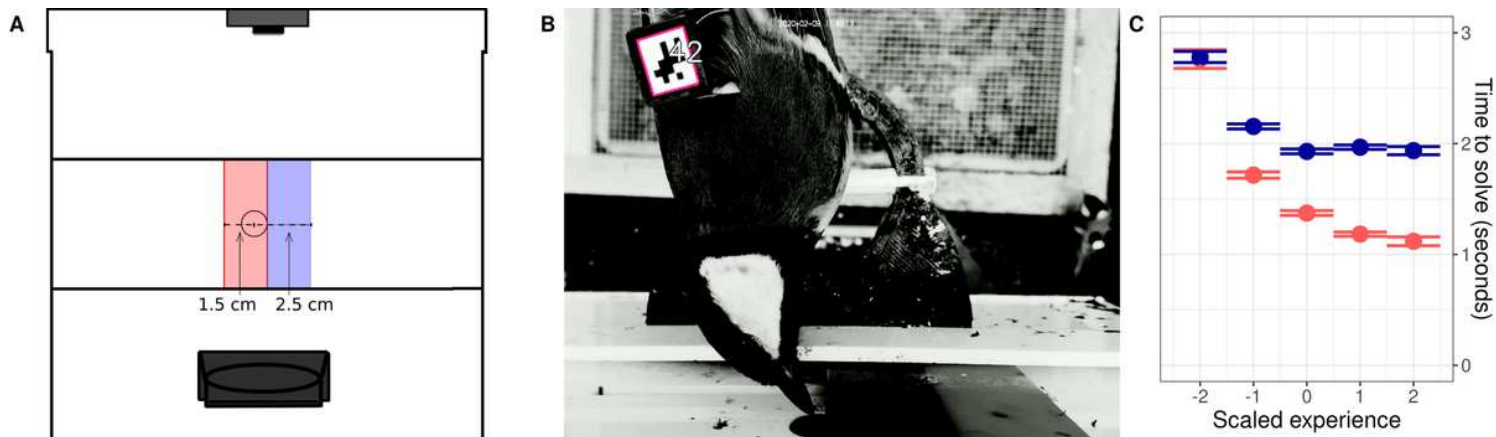


Figure 1

Automated foraging puzzle with solutions of differing efficiency. A) Populations were provided one puzzle box with a 4 cm wide door which gave access to mealworms. The access point was offset from the center by .5 cm, such that pushing from the left (red) side was more efficient. A microcomputer recorded identity and solution type using B) an RFID antenna in the perch to record identities from unique transponder 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' TTS. C) Birds improved with experience, but the efficient solution was significantly faster to solve (mean \pm SE, tutors excluded; efficient: n = 44 birds, 34,444 solutions; inefficient: n = 50 birds, 78,616 solutions). See also Table S1.

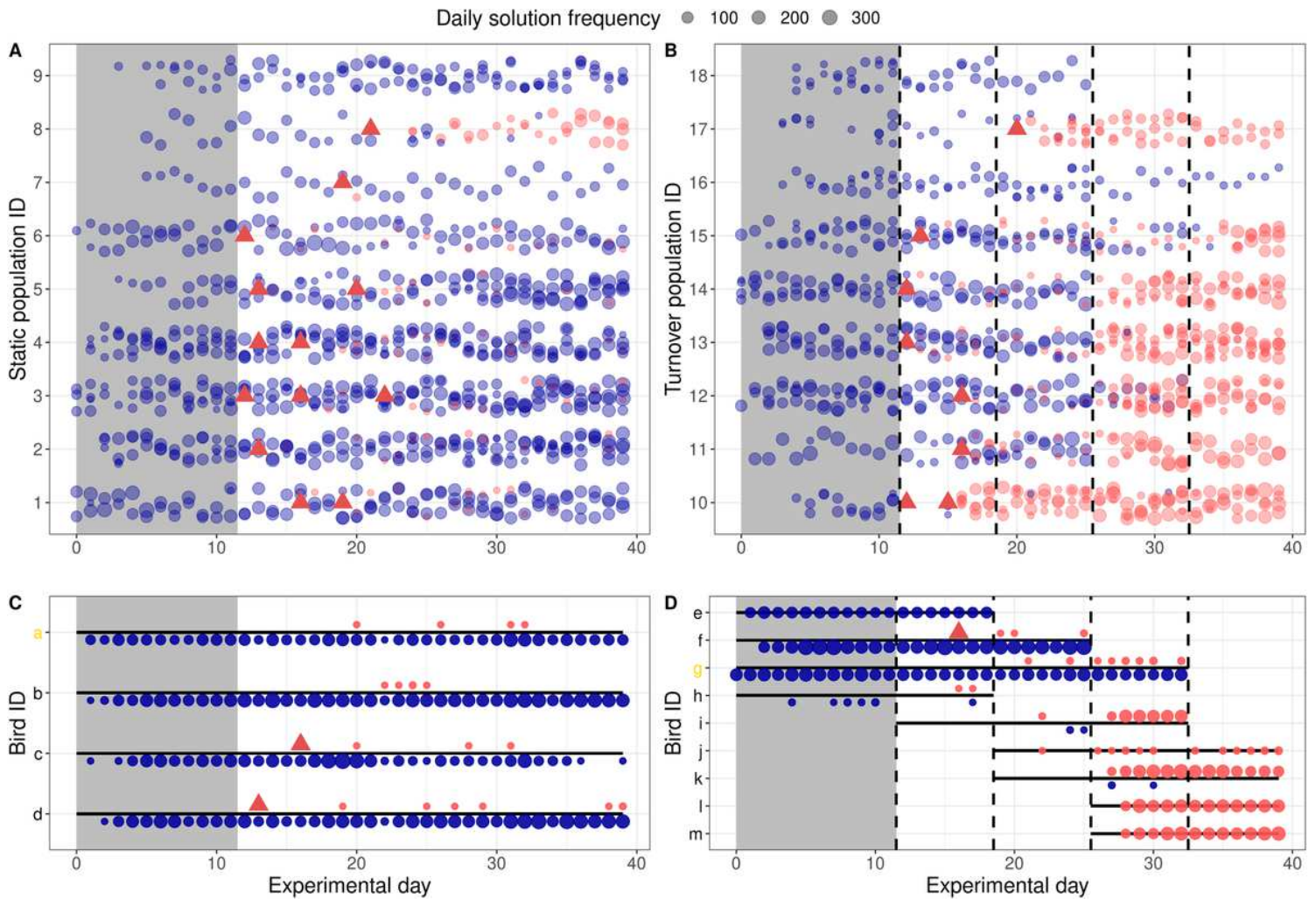


Figure 2

Overview of behavioral frequency data between conditions and within exemplar populations. A) Each point represents the daily solutions of a unique bird in that population. Type (color), frequency (size), innovation events (triangle shape, see Methods for definition), tutors (gold text), diffusion period (grey background), and duration of individuals (black lines) are marked. Despite nearly all static populations innovating the efficient solution, only one population selected for it ($n = 29$ birds, 90,421 solutions). B) Almost all turnover populations innovated and selected for the efficient solution, and adopters were primarily naive individuals ($n = 70$ birds, 84,518 solutions). C) A static population in which two birds independently innovated the efficient solution, produced it with low frequency, yet failed to select for it ($n = 4$ birds, 14,483 solutions). D) A turnover population that selected for the efficient solution. An experienced bird innovated on day 11, and the efficient solution was produced at low frequency until it was widely adopted by immigrants after the third turnover ($n = 9$ birds, 16,616 solutions). See Figure S2 for all populations.

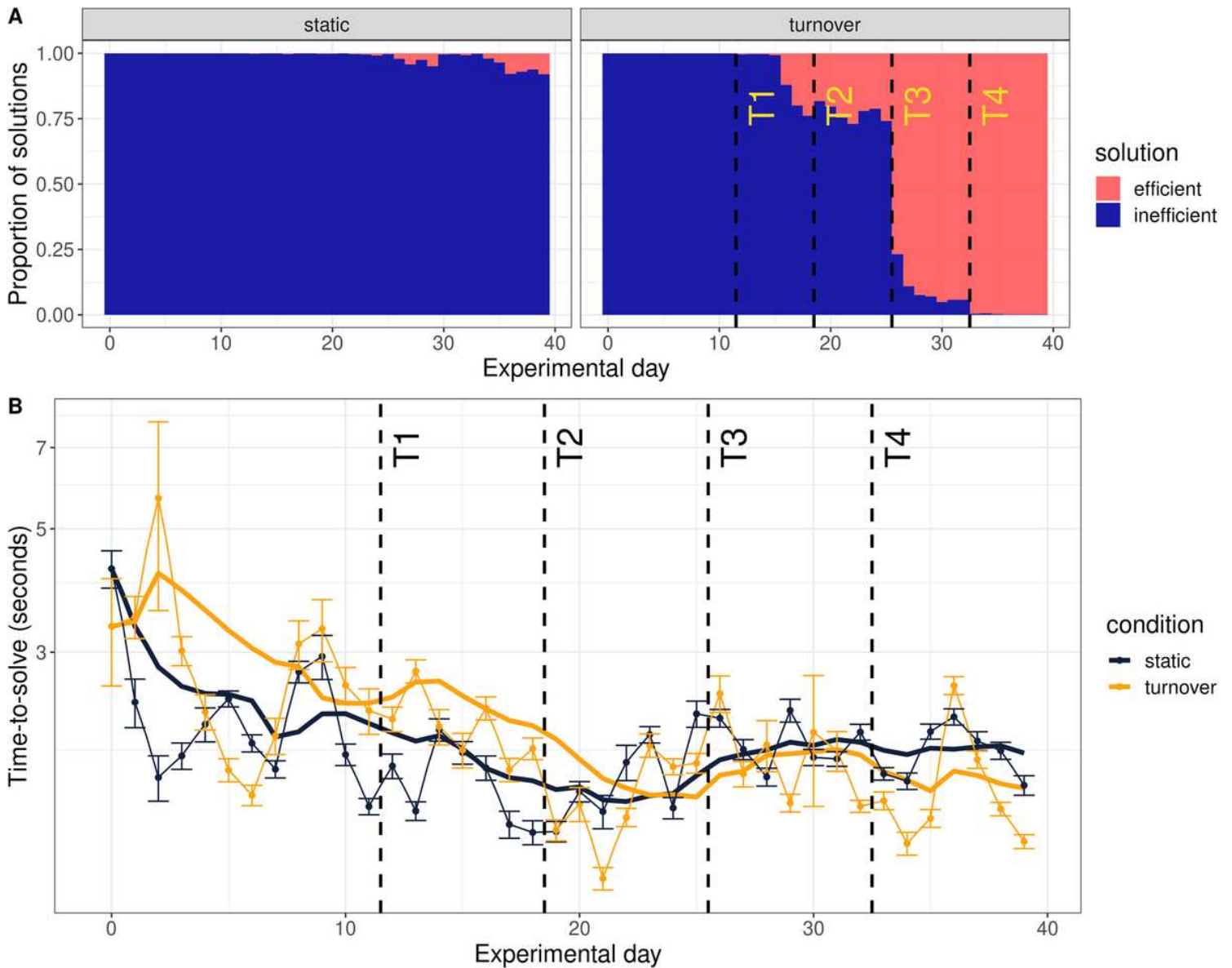


Figure 3

The link between cultural evolution and efficiency. A) The daily proportion of solutions by type from all populations (static: $n = 28$ birds, total solutions = 88,224; turnover: $n = 70$ birds, total solutions = 84,518). Static populations produced 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) Daily time-to-solve for non-tutors in static and turnover conditions (thin lines with 95% SE), along with a right-aligned 7 day moving average (thicker lines). Y axis \log_2 coord. transformed for visualization, and vertical dashed lines show turnover events (T1-T4). In the last two weeks of the experiment, turnover populations were solving faster than static populations on average. This increase in efficiency was driven by widespread cultural selection for the efficient solution (static: $n = 21$ birds, 52,458 solutions; turnover: $n = 61$ birds, 60,735). See also Table S1.

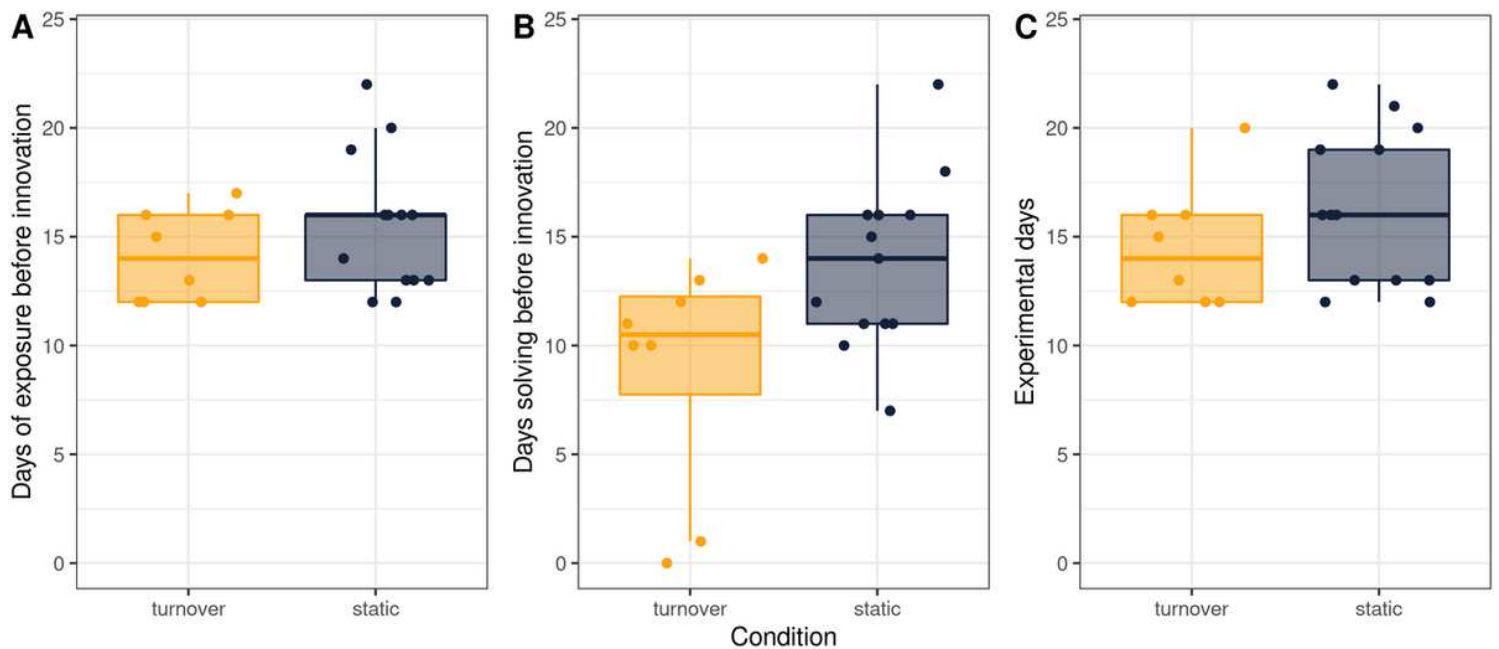


Figure 4

Innovation timing between conditions. A) Days exposure to the task before innovation and experimental day was not found to be significantly different between conditions (static: dark blue, turnover: yellow; $n = 21$ innovation events). B) Days solving before innovation was significantly lower in the turnover condition, however two data points drove this difference. C) Experimental days before innovation was not found to be significantly different between the two conditions. From this data, we suggest the difference in innovation between conditions was not primarily responsible for the strong selection for efficiency in the turnover condition. See also Table S3.

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