Current Biology

Report

Population turnover facilitates cultural selection for efficiency in birds

Highlights

- We conducted a cultural evolution experiment using captive great tits
- Gradual replacement of individuals promoted the spread of efficient cultural variants
- Immigrants played a role as adopters rather than innovators of efficient variants
- Turnover might be a general mechanism in the cultural evolution of efficiency

Authors

Michael Chimento,
Gustavo Alarcón-Nieto, Lucy M. Aplin

Correspondence

mchimento@ab.mpg.de

In brief

In a cultural evolution experiment on great tits, Chimento et al. demonstrate the importance of population turnover for the evolution of efficiency. Populations in which residents are gradually replaced select for a more efficient foraging behavior. Naive immigrants function as adopters of more optimal innovations by knowledgeable residents.

Chimento et al., 2021, Current Biology *31*, 2477–2483
June 7, 2021
https://doi.org/10.1016/j.cub.2021.03.057

Current Biology

CellPress
OPEN ACCESS

Report

Population turnover facilitates cultural selection for efficiency in birds

Michael Chimento,[1,2,3,4,5,*] Gustavo Alarcón-Nieto,[1] and Lucy M. Aplin[1,2]
[1]Cognitive and Cultural Ecology Lab, Max Planck Institute of Animal Behavior, Am Obstberg 1, 78315 Radolfzell, Germany
[2]Centre for the Advanced Study of Collective Behaviour, Konstanz University, Universitätsstraße 10, 78464 Konstanz, Germany
[3]Department of Biology, University of Konstanz, Universitätsstraße 10, 78464 Konstanz, Germany
[4]Twitter: @evogom
[5]Lead contact
*Correspondence: mchimento@ab.mpg.de
https://doi.org/10.1016/j.cub.2021.03.057

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 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.[2–5] Selection for more efficient behaviors over alternatives is a crucial component of cumulative cultural evolution,[6] 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 outcompeted 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.

RESULTS AND DISCUSSION

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

Culture exists on the social network,[17] and cultural evolution should be responsive to network properties such as population size, structure, and dynamic turnover.[4,18–22] Larger population sizes have been linked to elevated cultural diversity, innovation, and faithful transmission.[18,23–26] Conversely, population decline and fragmentation can reduce trait diversity and complexity, as observed in bird song.[27–29] Population turnover, caused by immigration, emigration, births, and deaths, is a universal demographic process, yet its effect on cultural evolution is poorly understood.[30] It could lead to adaptive cultural outcomes if incoming individuals introduce new innovations.[16] Alternatively, naive individuals might better re-sample the behavioral space because they are less behaviorally conservative, or less subject to factors such as conformity.[31]

To study the effect of population turnover on cultural selection for efficiency, we conducted a cultural evolution experiment in a common passerine bird, the great tit (*Parus major*). Inter- and intra-generational turnover are key features of their social system,[32–35] and they are an established study system for innovation and animal culture.[36–41] We created 18 artificial populations of wild-caught great tits with a membership of 6 birds each, the average size found in winter foraging flocks of great tits.[35] The study then consisted of two phases: (1) a diffusion period (12 days), and (2) a subsequent experimental period (28 days)

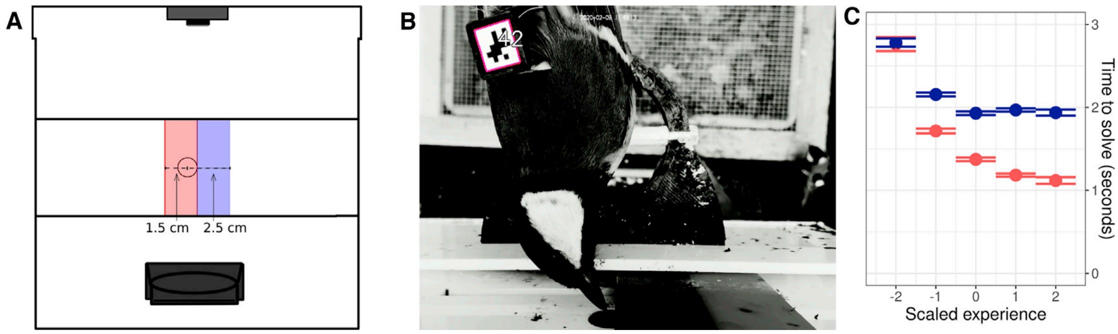

Figure 1. Automated foraging puzzle with solutions of differing efficiency

(A) Populations were provided one puzzle box with a 4 cm wide door that gave access to mealworms. The access point was offset from the center by 0.5 cm, such that pushing from the left (red) side was more efficient.

(B) A microcomputer recorded identity and solution type using 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 ± 95% SE, tutors excluded; efficient, n = 44 birds, 34,444 solutions; inefficient, n = 50 birds, 78,616 solutions).

See also Table S1.

in which population turnover was manipulated. During the diffusion period, a foraging tradition to access food by pushing on a bidirectional door of an automated puzzle box was established in each population using a tutor bird trained on the inefficient solution (Figure 1). This set all populations to the same initial, inefficient cultural state prior to the experimental manipulation. In the experimental period, turnover was simulated in 9 populations by replacing 2 randomly selected birds with new, wild-caught birds in the first turnover event (T1). Turnover events then occurred every subsequent week (T2–T4) for the remainder of the experimental period. Another 9 populations maintained stable membership for the duration of the experiment (static populations). Birds could improve their speed at the established foraging tradition, or potentially innovate an alternative, more efficient solution. We predicted that turnover populations would be more likely to innovate and adopt the alternative solution, because incoming naive birds might be more likely to either (1) innovate the efficient solution or (2) adopt the efficient solution once innovated.

Social learning leads to established traditions

During the diffusion period, the solving behavior spread in 17 of 18 populations, with 46 of 90 naive residents learning to solve. During the experimental period, 37 of 73 immigrants also learned to solve. There were no significant differences between age or sex classes in latency to learn (Figure S1). Evidence that solving was socially learned is as follows: (1) outside of the diffusion period, 87% of birds first solved using the most predominant solution in their population; (2) the puzzle was difficult to individually learn (tutors took anywhere from 1 to 2 weeks of incremental training to learn); and (3) the behavior failed to be re-innovated in a population where the behavior went extinct. Over the course of the entire experiment, birds that learned to solve the puzzle (solvers) produced a total of 174,393 recorded solutions (average 9,719 per population, range: 1,494–17,208), with 89% of those with measurable time-to-solve (TTS). Tutors accounted for 47,000 of all solutions, with a daily average of 100 solutions. New learners accounted for 127,939 solutions, with a daily average of 86. Altogether, solvers produced an average of 1,803 solutions (range: 20–6,612) and a daily average of 89 solutions.

Solvers became significantly faster with experience, reducing their TTS by about 3% with every standard deviation of solutions produced, suggesting that reinforcement learning was leading to improvements in efficiency (linear mixed model [LMM], solution index [scaled]: $\beta = -0.027 \pm 0.002$, $t = -11.975$, $p < 0.001$; Table S1A). The efficient solution was significantly faster than the inefficient solution when controlling for experience, between populations and individual solvers (LMM, solution type [efficient]: $\beta = -0.395 \pm 0.051$, $t = -7.787$, $p < 0.001$; LMM, intercept [inefficient]: $\beta = 0.925 \pm 0.215$, $t = 4.299$, $p < 0.001$; Table S1A; Figure 1C). The same amount of solving experience with the efficient solution obtained a lower average TTS compared to the inefficient solution (LMM, solution type [efficient]: solution index [scaled]: $\beta = -0.117 \pm 0.006$, $t = -18.102$, $p < 0.001$). The efficient solution therefore offered a greater payoff as solvers tended to receive the same reward in less time.

Turnover facilitated cultural selection for efficiency

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

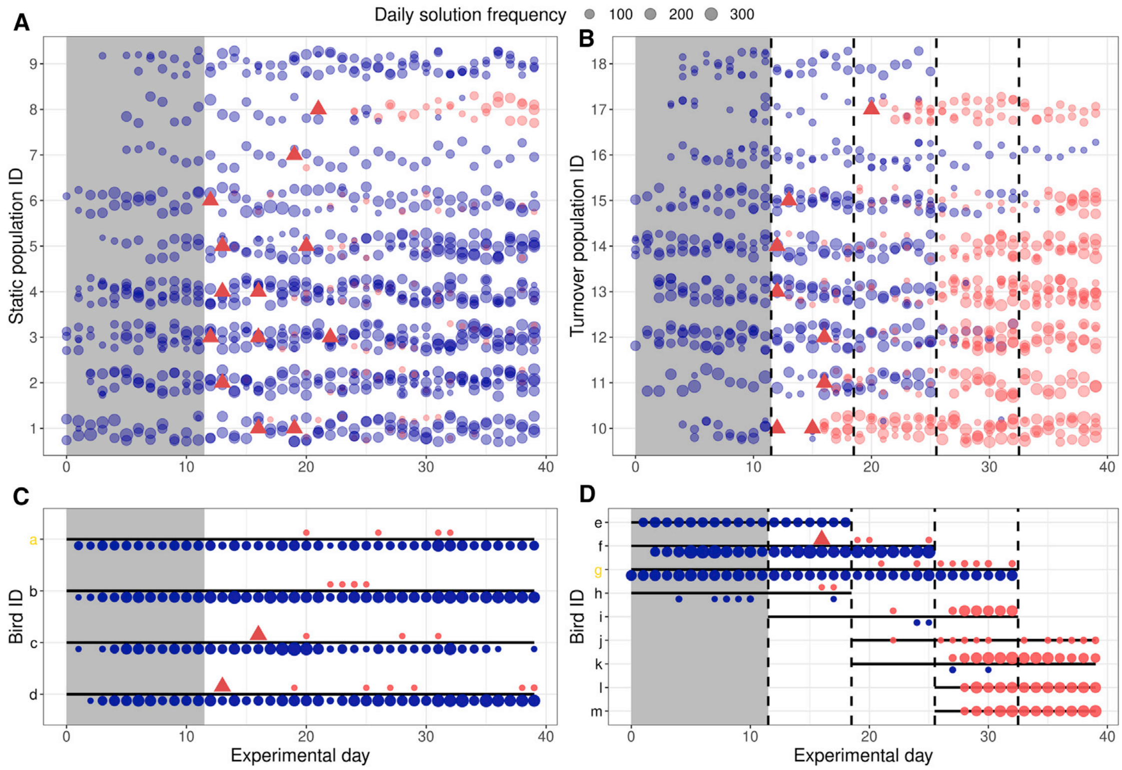

Figure 2. Overview of behavioral frequency data between conditions and within exemplar populations

(A) Each point represents the daily solutions of a unique bird in that population. Type (color), frequency (size), innovation events (triangle shape; see STAR Methods for definition), tutors (gold text), diffusion period (gray 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.

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

Cultural selection generated population-level differences in performance

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

Both conditions exhibited a decreasing trend in TTS (LMM, exp. day [scaled]: $\beta = -0.048 \pm 0.005$, $t = -9.885$, $p < 0.001$; Table S1B). Yet on average, turnover populations had a significantly steeper reduction in their TTS than static populations (LMM, exp. day [scaled]: condition [turnover]: $\beta = -0.077 \pm 0.010$, $t = -7.832$, $p < 0.001$; Figure 3B). Turnover populations were slower than static populations through the first two turnover events, suggesting that the loss of knowledgeable birds may have initially hindered the accumulation of expertise in the inefficient solution. However, by the final week after T4, birds in turnover populations were solving faster than static populations (M_t = 1.66 s, M_s = 1.96 s). The increasing dominance of the efficient solution therefore allowed turnover populations to achieve a lower

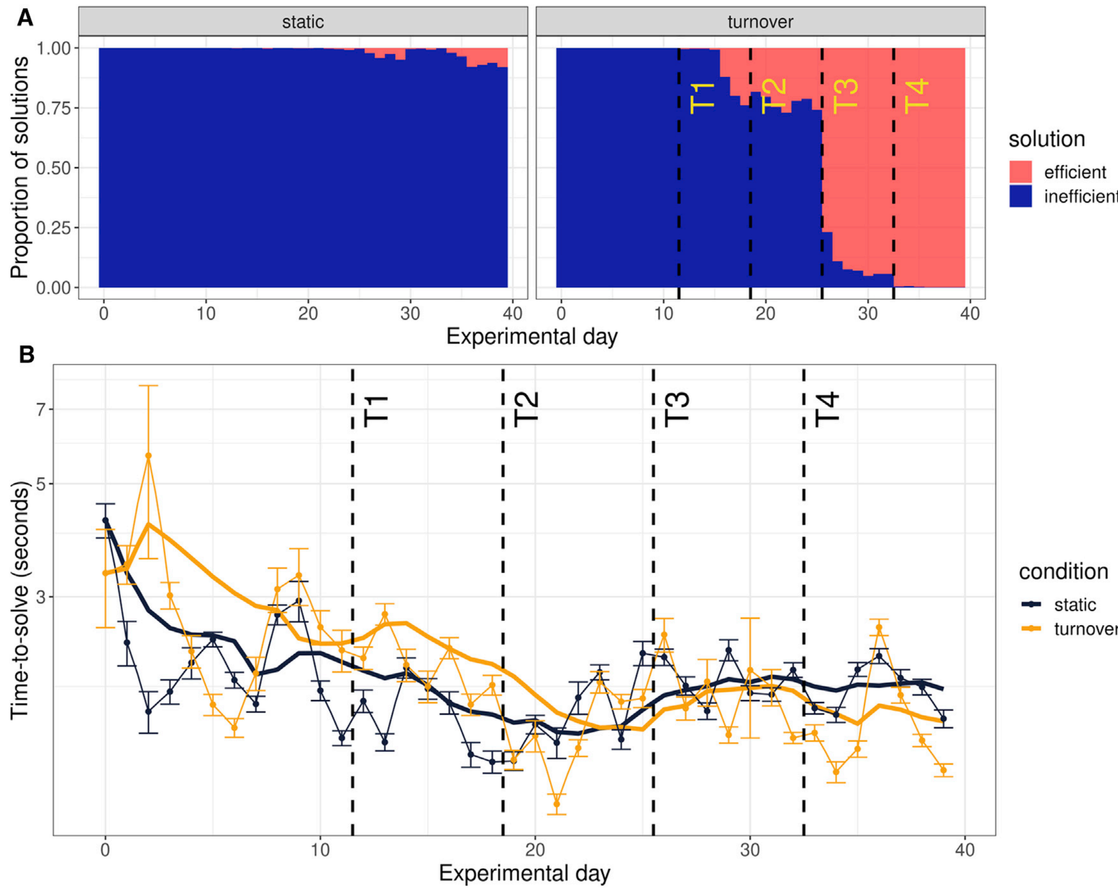

Figure 3. The link between cultural evolution and efficiency

(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 TTS for non-tutors in static and turnover conditions (thin lines, mean ± 95% SE), along with a right-aligned 7 day moving average (thicker lines). y axis log2 coordinates transformed for visualization, and vertical dashed lines show turnover events (T1–T4). In the last 2 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 solutions).

See also Table S1.

TTS despite having less experience solving than individuals in the static condition.

Innovation rates were not the mechanism behind differences in cultural outcomes

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

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

Turnover allowed populations to overcome individual-level behavioral conservatism

Relatively few birds were observed producing large amounts of both solution types—most learners strongly preferred one solution. Out of 53 birds that sampled both solutions, 36 failed to adopt the efficient solution. The effect of experience (habit formation) or conformity could contribute to this behavioral

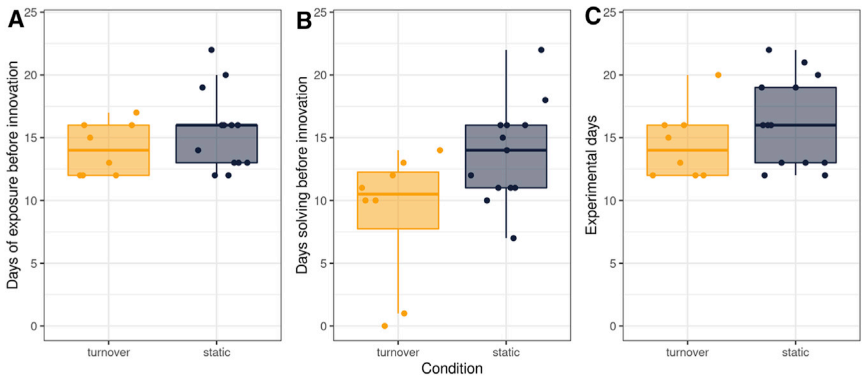

Figure 4. Innovation timing between conditions

(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 these 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.

conservatism. We found that birds were very likely to adopt the efficient solution if they experienced an efficient solution on the first day of solving (GLMM, intercept: $\alpha = -3.421 \pm 1.977$, $Z = -1.730$, p = 0.084; Table S4). However, each day of experience with the inefficient solution significantly increased the probability an individual would not adopt the efficient solution (GLMM, days experience: $\beta = 0.364 \pm 0.132$, $Z = 2.761$, p = 0.006). Conformity, as well as age and sex, were not significant predictors. This suggests that increasing experience reinforced behavioral conservatism, and that the introduction of naive individuals via turnover allowed populations to overcome this inertia.

The positive relationship between turnover and the cultural evolution of efficiency

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

The only other direct experimental test of cultural evolution of efficiency in birds was in homing pigeons,[16] where pairs of birds developed more direct, efficient homing routes over time when one of the pair was repeatedly replaced in a chain design. An alternative mechanism was proposed—that naive individuals might produce behavioral variation on which cultural selection could act. However, flight behavior was a continuously measured variable (straightness), and the authors could not directly quantify innovation events. Our study extends this work in several important ways. First, we conduct turnover in groups, mimicking realistic fission-fusion dynamics and natural flock sizes. Second, we test this process in a foraging context; most work related to this topic in non-human primates has focused on foraging,[42–44] and our work gives new insights into this key behavioral domain. Finally, our experimental design allowed for a discrete step change in efficiency (alternative solution variants), as well as continuous (TTS). We could identify discrete innovation events and their effect on continuous population-level behavior, revealing the mechanism mediating the relationship between turnover and efficiency.

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

Behavioral conservatism is identified as a primary reason for the lack of observed CCE in animal species,[45] yet may be a key reason why population turnover is vital to the evolution of efficiency. Memory loss through the replacement of individuals creates opportunities for unbiased re-sampling of behavioral payoffs. A suggestion of this effect of turnover on cultural inertia comes from translocation studies of blue-headed wrasse, a fish that culturally inherits spawning sites. When all members of a wrasse population were replaced, naive fish resampled the set of potential spawning sites and selected different mating sites from the original population.[31] A second replacement population selected the same sites, suggesting that turnover resulted in more optimal sampling.[46] The successful resampling by naive fish appears analogous to that observed in immigrant tits. Population turnover might therefore provide a broad mechanism for resampling socially transmitted information and potentially moving populations toward more adaptive local optima.

The cultural evolution of refined, efficient behaviors has been considered a precursor to more complex, human-like forms of cumulative culture.[6] While we do not argue that our results demonstrate CCE, they add to the growing evidence that cultural evolution of efficiency is possible in animals and extend this to foraging behavior. This small passerine species is capable of moving the cultural ratchet one tick forward, fulfilling a key description of CCE: a behavior innovated by an individual spreads within a group and persists until future individuals make efficient modifications, which then spread and supplant the previous behavior.[9] Yet it remains an open question as to why repeated instances of selection for efficiency are so rarely observed in the field. Our results suggest this is not due to an inability to select for more efficient variants; rather, population turnover can mitigate behavioral conservatism. The conservatism identified in our study may be surprising given a prior finding that 49% of great tits could switch solutions when the payoff structure of a puzzle box was altered.[40] However, those were free-mixing, wild flocks, further supporting a facilitating role of demographic churn on behavioral flexibility. However, the benefits of turnover carry a risk: the potential loss of knowledgeable individuals and extinction of cultural traits. One turnover population exhibited a complete extinction of the solving behavior. Future work should further explore how varying turnover rate and scale influence cultural dynamics.

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

STAR★METHODS

Detailed methods are provided in the online version of this paper and include the following:

- KEY RESOURCES TABLE
- RESOURCE AVAILABILITY
  - Lead Contact
  - Materials Availability
  - Data and Code Availability
- EXPERIMENTAL MODEL AND SUBJECT DETAILS
- METHOD DETAILS
  - Experimental apparatus
  - Experimental design
- QUANTIFICATION AND STATISTICAL ANALYSIS
  - Individual-level learning and improvement in performance
  - Condition-level differences in solving
  - Innovation
  - Behavioral conservatism

SUPPLEMENTAL INFORMATION

Supplemental information can be found online at https://doi.org/10.1016/j.cub.2021.03.057.

ACKNOWLEDGMENTS

Thank you to Anne Kandler, Brendan Barrett, Dora Biro, Elham Nourani, colleagues in the Cognitive and Cultural Evolution Lab, and the MPIAB animal caretaker team for their input and support. M.C. was funded by the International Max Planck Research School for Organismal Biology. L.M.A. was funded by a Max Planck Research Group Leader Fellowship. Additional funding was provided by the DFG Centre of Excellence 2117 "Centre for the Advanced Study of Collective Behaviour" under Germany's Excellence Strategy—EXC2117—422037984.

AUTHOR CONTRIBUTIONS

Conceptualization, M.C. and L.M.A.; Methodology, M.C., G.A.-N., and L.M.A.; Software, M.C.; Formal Analysis, M.C.; Investigation, M.C., G.A.-N., and L.M.A.; Resources, M.C., G.A.-N., and L.M.A.; Writing – Original Draft, M.C., Writing – Review & Editing, M.C., G.A.-N., and L.M.A.; Visualization, M.C.; Supervision, L.M.A.

DECLARATION OF INTERESTS

The authors declare no competing interests.

Received: February 5, 2021
Revised: March 8, 2021
Accepted: March 16, 2021
Published: April 6, 2021

REFERENCES

1. Schuppli, C., and van Schaik, C.P. (2019). Animal cultures: how we've only seen the tip of the iceberg. Evolutionary Human Sciences *1*, e2.
2. Creanza, N., Kolodny, O., and Feldman, M.W. (2017). Cultural evolutionary theory: how culture evolves and why it matters. Proc. Natl. Acad. Sci. USA *114*, 7782–7789.
3. Mesoudi, A., Whiten, A., and Laland, K.N. (2004). Perspective: is human cultural evolution Darwinian? Evidence reviewed from the perspective of the Origin of Species. Evolution *58*, 1–11.
4. Mesoudi, A. (2017). Pursuing Darwin's curious parallel: prospects for a science of cultural evolution. Proc. Natl. Acad. Sci. USA *114*, 7853–7860.
5. Boyd, R., and Richerson, P.J. (1988). Culture and the Evolutionary Process (University of Chicago press).
6. Mesoudi, A., and Thornton, A. (2018). What is cumulative cultural evolution? Proc. Biol. Sci. *285*, 20180712.
7. Whiten, A., Ayala, F.J., Feldman, M.W., and Laland, K.N. (2017). The extension of biology through culture. Proc. Natl. Acad. Sci. USA *114*, 7775–7781.
8. Jablonka, E., and Lamb, M.J. (2014). Evolution in Four Dimensions: Genetic, Epigenetic, Behavioral, and Symbolic Variation in the History of Life (MIT Press).
9. Tomasello, M. (1999). The human adaptation for culture. Annu. Rev. Anthropol. *28*, 509–529.
10. Aplin, L.M. (2019). Culture and cultural evolution in birds: a review of the evidence. Anim. Behav. *147*, 179–187.
11. Whiten, A. (2017). A second inheritance system: the extension of biology through culture. Interface Focus *7*, 20160142.
12. Tennie, C., Call, J., and Tomasello, M. (2009). Ratcheting up the ratchet: on the evolution of cumulative culture. Philos. Trans. R. Soc. Lond. B Biol. Sci. *364*, 2405–2415.
13. Boyd, R., Richerson, P.J., and Henrich, J. (2011). The cultural niche: why social learning is essential for human adaptation. Proc. Natl. Acad. Sci. USA *108* (*Suppl 2*), 10918–10925.
14. Jesmer, B.R., Merkle, J.A., Goheen, J.R., Aikens, E.O., Beck, J.L., Courtemanch, A.B., Hurley, M.A., McWhirter, D.E., Miyasaki, H.M., Monteith, K.L., and Kauffman, M.J. (2018). Is ungulate migration culturally

transmitted? Evidence of social learning from translocated animals. Science *361*, 1023–1025.

15. Mueller, T., O'Hara, R.B., Converse, S.J., Urbanek, R.P., and Fagan, W.F. (2013). Social learning of migratory performance. Science *341*, 999–1002.
16. Sasaki, T., and Biro, D. (2017). Cumulative culture can emerge from collective intelligence in animal groups. Nat. Commun. *8*, 15049.
17. Whitehead, H., and Lusseau, D. (2012). Animal social networks as substrate for cultural behavioural diversity. J. Theor. Biol. *294*, 19–28.
18. Henrich, J. (2004). Demography and cultural evolution: how adaptive cultural processes can produce maladaptive losses—the tasmanian case. Am. Antiq. *69*, 197–214.
19. Nettle, D. (2012). Social scale and structural complexity in human languages. Philos. Trans. R. Soc. Lond. B Biol. Sci. *367*, 1829–1836.
20. Migliano, A.B., Battiston, F., Viguier, S., Page, A.E., Dyble, M., Schlaepfer, R., Smith, D., Astete, L., Ngales, M., Gomez-Gardenes, J., et al. (2020). Hunter-gatherer multilevel sociality accelerates cumulative cultural evolution. Sci. Adv. *6*, x5913.
21. Derex, M., and Boyd, R. (2016). Partial connectivity increases cultural accumulation within groups. Proc. Natl. Acad. Sci. USA *113*, 2982–2987.
22. Fay, N., De Kleine, N., Walker, B., and Caldwell, C.A. (2019). Increasing population size can inhibit cumulative cultural evolution. Proc. Natl. Acad. Sci. USA *116*, 6726–6731.
23. Bromham, L., Hua, X., Fitzpatrick, T.G., and Greenhill, S.J. (2015). Rate of language evolution is affected by population size. Proc. Natl. Acad. Sci. USA *112*, 2097–2102.
24. Derex, M., Beugin, M.P., Godelle, B., and Raymond, M. (2013). Experimental evidence for the influence of group size on cultural complexity. Nature *503*, 389–391.
25. Kempe, M., and Mesoudi, A. (2014). An experimental demonstration of the effect of group size on cultural accumulation. Evol. Hum. Behav. *35*, 285–290.
26. Foss-Grant, A., Bewick, S., and Fagan, W.F. (2018). Social transmission of migratory knowledge: quantifying the risk of losing migratory behavior. Theor. Ecol. *11*, 257–270.
27. Paxton, K.L., Sebastián-González, E., Hite, J.M., Crampton, L.H., Kuhn, D., and Hart, P.J. (2019). Loss of cultural song diversity and the convergence of songs in a declining Hawaiian forest bird community. R. Soc. Open Sci. *6*, 190719.
28. Parker, K.A., Anderson, M.J., Jenkins, P.F., and Brunton, D.H. (2012). The effects of translocation-induced isolation and fragmentation on the cultural evolution of bird song. Ecol. Lett. *15*, 778–785.
29. Laiolo, P., and Tella, J.L. (2007). Erosion of animal cultures in fragmented landscapes. Front. Ecol. Environ. *5*, 68–72.
30. Shizuka, D., and Johnson, A.E. (2020). How demographic processes shape animal social networks. Behav. Ecol. *31*, 1–11.
31. Warner, R.R. (1988). Traditionality of mating-site preferences in a coral reef fish. Nature *335*, 719–721.
32. Bouwhuis, S., Sheldon, B.C., Verhulst, S., and Charmantier, A. (2009). Great tits growing old: selective disappearance and the partitioning of senescence to stages within the breeding cycle. Proc. Biol. Sci. *276*, 2769–2777.
33. McCleery, R.H., Pettifor, R.A., Armbruster, P., Meyer, K., Sheldon, B.C., and Perrins, C.M. (2004). Components of variance underlying fitness in a natural population of the great tit Parus major. Am. Nat. *164*, E62–E72.
34. Farine, D.R., Aplin, L.M., Garroway, C.J., Mann, R.P., and Sheldon, B.C. (2014). Collective decision making and social interaction rules in mixed-species flocks of songbirds. Anim. Behav. *95*, 173–182.
35. Farine, D.R., Firth, J.A., Aplin, L.M., Crates, R.A., Culina, A., Garroway, C.J., Hinde, C.A., Kidd, L.R., Milligan, N.D., Psorakis, I., et al. (2015). The role of social and ecological processes in structuring animal populations: a case study from automated tracking of wild birds. R. Soc. Open Sci. *2*, 150057.
36. Fisher, J., and Hinde, R.A. (1949). The opening of milk bottles by birds. Br. Birds *42*, 347–357.
37. Lefebvre, L., and Aplin, L.M. (2017). Avian cognition. In Social Learning and Innovation, C. ten Cate, and S.D. Healy, eds. (Cambridge University Press), pp. 93–118.
38. Aplin, L.M., Sheldon, B.C., and Morand-Ferron, J. (2013). Milk bottles revisited: social learning and individual variation in the blue tit, cyanistes caeruleus. Anim. Behav. *85*, 1225–1232.
39. Aplin, L.M., Farine, D.R., Morand-Ferron, J., Cockburn, A., Thornton, A., and Sheldon, B.C. (2015). Experimentally induced innovations lead to persistent culture via conformity in wild birds. Nature *518*, 538–541.
40. Aplin, L.M., Sheldon, B.C., and McElreath, R. (2017). Conformity does not perpetuate suboptimal traditions in a wild population of songbirds. Proc. Natl. Acad. Sci. USA *114*, 7830–7837.
41. Cole, E.F., Cram, D.L., and Quinn, J.L. (2011). Individual variation in spontaneous problem-solving performance among wild great tits. Anim. Behav. *81*, 491–498.
42. Lamon, N., Neumann, C., Gier, J., Zuberbühler, K., and Gruber, T. (2018). Wild chimpanzees select tool material based on efficiency and knowledge. Proc. Biol. Sci. *285*, 1–10.
43. Gruber, T., Muller, M.N., Strimling, P., Wrangham, R., and Zuberbühler, K. (2009). Wild chimpanzees rely on cultural knowledge to solve an experimental honey acquisition task. Curr. Biol. *19*, 1806–1810.
44. Davis, S.J., Vale, G.L., Schapiro, S.J., Lambeth, S.P., and Whiten, A. (2016). Foundations of cumulative culture in apes: improved foraging efficiency through relinquishing and combining witnessed behaviours in chimpanzees (Pan troglodytes). Sci. Rep. *6*, 35953.
45. Mesoudi, A. (2011). Cultural Evolution: How Darwinian Theory Can Explain Human Culture and Synthesize the Social Sciences (University of Chicago Press).
46. Warner, R.R. (1990). Resource assessment versus tradition in mating-site determination. Am. Nat. *135*, 205–217.
47. Van Rossum, G., and Drake, F.L. (2009). Python 3 Reference Manual (CreateSpace).
48. Alarcón-Nieto, G., Graving, J.M., Klarevas-Irby, J.A., Maldonado-Chaparro, A.A., Mueller, I., and Farine, D.R. (2018). An automated barcode tracking system for behavioural studies in birds. Methods Ecol. Evol. *9*, 1536–1547.
49. Therneau, T.M. (2020). A Package for Survival Analysis in R. https://CRAN.R-project.org/package=survival.
50. Bates, D., Mächler, M., Bolker, B., and Walker, S. (2015). Fitting linear mixed-effects models using lme4. J. Stat. Softw. *67*, 1–48.
51. R Core Team (2018). R: A Language and Environment for Statistical Computing (R Foundation for Statistical Computing).

STAR★METHODS

KEY RESOURCES TABLE

REAGENT or RESOURCE	SOURCE	IDENTIFIER
Deposited Data		
Statistical analysis and figures	This paper	https://doi.org/10.5281/zenodo.4644347
Experimental Models: Organisms/Strains		
Great tit, *Parus major*	Wild	N/A
Software and Algorithms		
R	[47]	https://cran.r-project.org/
Python 3.6	[44]	https://www.python.org/
Pinpoint	[45]	https://github.com/jgraving/pinpoint
Custom puzzle box code	This paper	https://github.com/michaelchimento/raspi_tit_scripts
Other		
Raspberry Pi 4 micro-computer	Raspberry Pi Foundation	N/A
RFID reader writer module	Priority1	N/A

RESOURCE AVAILABILITY

Lead Contact

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

Materials Availability

This study did not generate new unique materials.

Data and Code Availability

Original data and code have been deposited to Github: https://doi.org/10.5281/zenodo.4644347.

EXPERIMENTAL MODEL AND SUBJECT DETAILS

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

METHOD DETAILS

Experimental apparatus

The foraging puzzle box consisted of an acrylic box with a bidirectional sliding door. The door (4cm × 6cm × 0.3cm) could be slid to the left or right to reveal a 1-cm hole through which the bird could access a reservoir of meal worms. The hole was off-center by 0.5-cm, such that pushing the red side of the door would be more efficient (1-cm from door-edge to hole) than pushing the blue side (2-cm to hole). This difference provided a significant challenge, given the tit's size. Average time-to-solve (TTS) confirmed that it was faster to use the red side of the door.

The puzzle-boxes were fully automated to minimize disturbance to the birds during the experiment. Puzzle boxes included a Raspberry Pi micro-computer, infrared sensors, a stepper motor to automate the door return mechanism, and an external printed circuit board for RFID data logging (Priority1). They operated using custom software written in Python.[47] An RFID antenna mounted under the perch recorded identities of birds from their PIT tag, as well as their arrival and departure times. Movement of the door was measured using infrared sensors, which were triggered once the door moved past a position that would allow the bird to access the hole. Once an sensor was triggered and the solving bird left, the door would automatically close either after 3 scrounge attempts, or after 3 s, whichever came first. In the second field season (accounting for 12 of 18 total populations), the puzzle also recorded video of the visiting birds, from which identities could be resolved using a bar-code attached to the bird using leg loops and a customized implementation of Pinpoint software.[48] Bar-code data was used 1) to resolve identities of solves without a positive identity from RFID data, 2) to measure TTS. Solvers were defined as birds who had ≥ 20 recorded solutions in all of the following analyses. Since data was collected using an automated system, this minimum was a conservative way to ensure that the birds were indeed solvers, and also allowed for mixed effects models to converge with ID as a random effect.

Experimental design

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

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

QUANTIFICATION AND STATISTICAL ANALYSIS

Individual-level learning and improvement in performance

To compare differences in learning rates between age and sex classes, we used a non-parametric Kaplan-Meier survival analysis[49] (Figure S1), in which an individual's latency to produce their first solution of either type was predicted by an interaction between age (juvenile, adult) and sex. Survival analysis is appropriate for time-to-event data, usually death. In this case, the event was learning to solve the puzzle box.

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

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

Condition-level differences in solving

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

To quantify the difference in selection for efficiency between conditions, we first subset the data to solvers during the experimental period only. We then used a logistic GLMM with the probability of producing an efficient solve regressed on age, sex, and an interaction between experimental day and condition (Table S1). Population and year were included as nested random intercepts.

Individual birds were not included as random intercepts, since the intercept value represented the first experimental day. Since many of the birds in the turnover condition were not present on this day, a random intercept would be creating estimates for large proportions of data which didn't exist.

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

Innovation

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

Behavioral conservatism

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