Demographic turnover facilitates cultural selection for efficiency

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Data and analysis

The repository for this manuscript is located at www.github.com/michaelchimento/DemographicTurnoverEfficiency. The repository contains 3 folders. In the analysis folder, there is all of the R code necessary to re-run the statistical analyses presented in the text. The data folder contains contains the data set of solution behaviors for the experiment, the data set of latency to learn for each bird, and the data set of output from the agent based model. The ABM folder contains the code for the agent based model, written for Python 3.x.

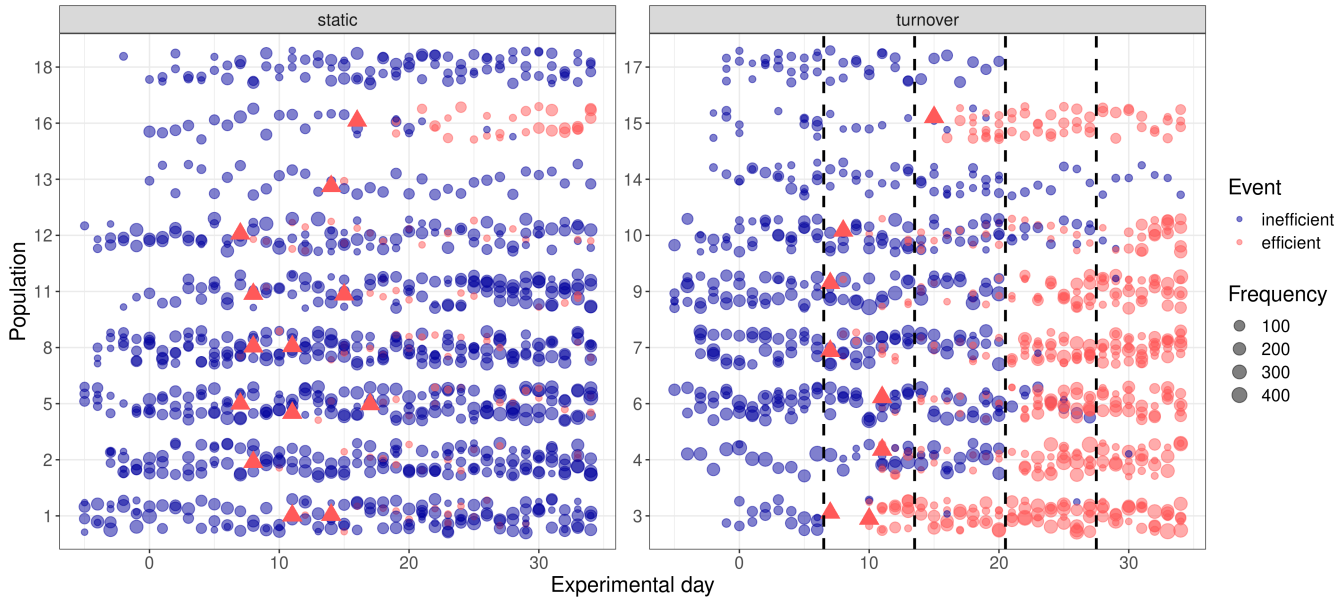

Figure 1: Overview of solution frequency data from all populations over experimental days, faceted by condition. Each colored circle represents the productions produced by one bird in a given day (red: efficient, blue: inefficient), and innovation events are marked with a large triangle. Of interest is 1) in the static condition, the many innovations without selection for the efficient solution and 2) in the turnover condition, the latency between innovation and selection for the efficient behavior. Innovations were widely made by experienced solvers, who then produced the efficient in low frequency, but did not adopt them. Rather, incoming naive birds adopted the efficient solution in the turnover condition, driving cultural selection.

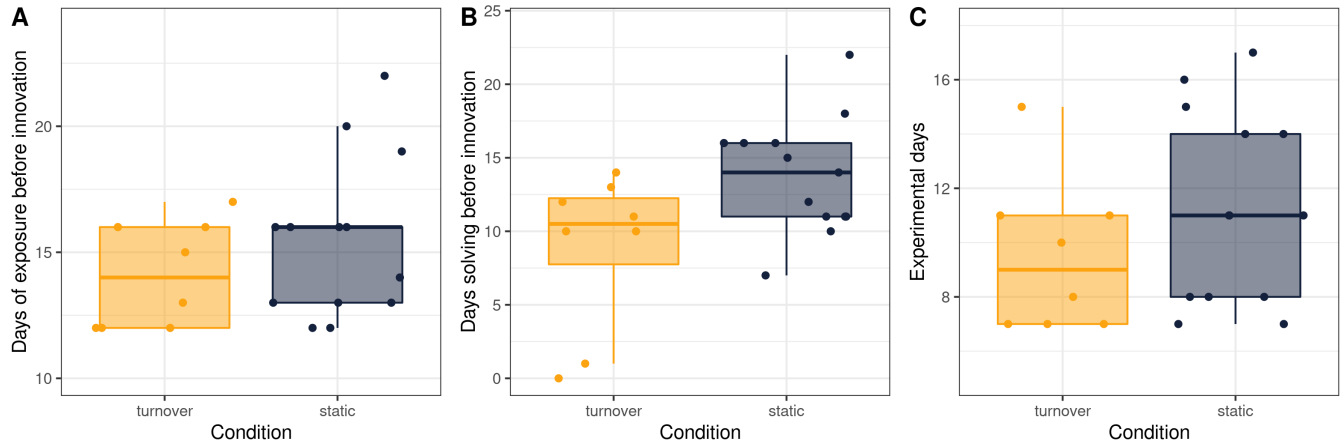

Figure 2: Comparison of innovation timing between conditions (static: dark blue, turnover: yellow). Both days exposure to the task before innovation and experimental day were not found to be significantly lower in the static condition. Days solving before innovation was significantly lower, however note the two data points that drove this difference. From this data, it seems like difference in innovation between conditions was not primarily responsible for the strong selection for efficiency in the turnover condition.

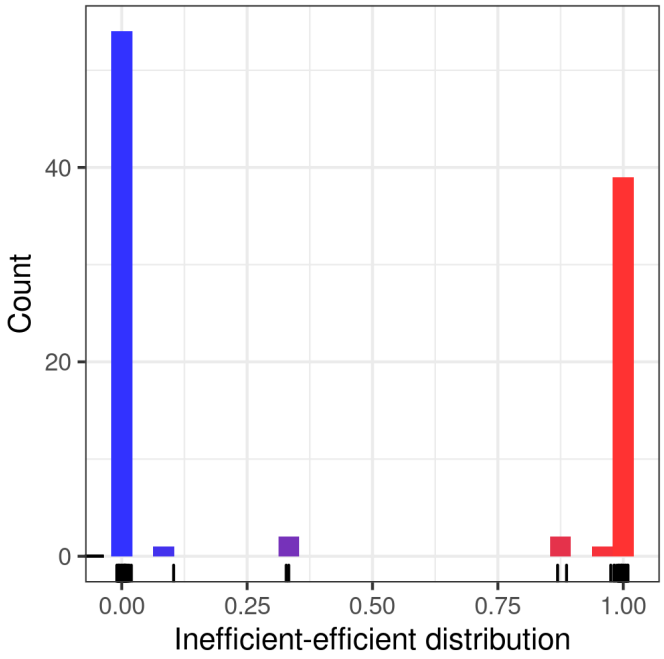

Figure 3: Proportions of solution types produced by each solver bird (count on y axis). A value of 0 indicates an individual that only produces inefficient solutions, 1 indicates an individual that only produces efficient solutions.

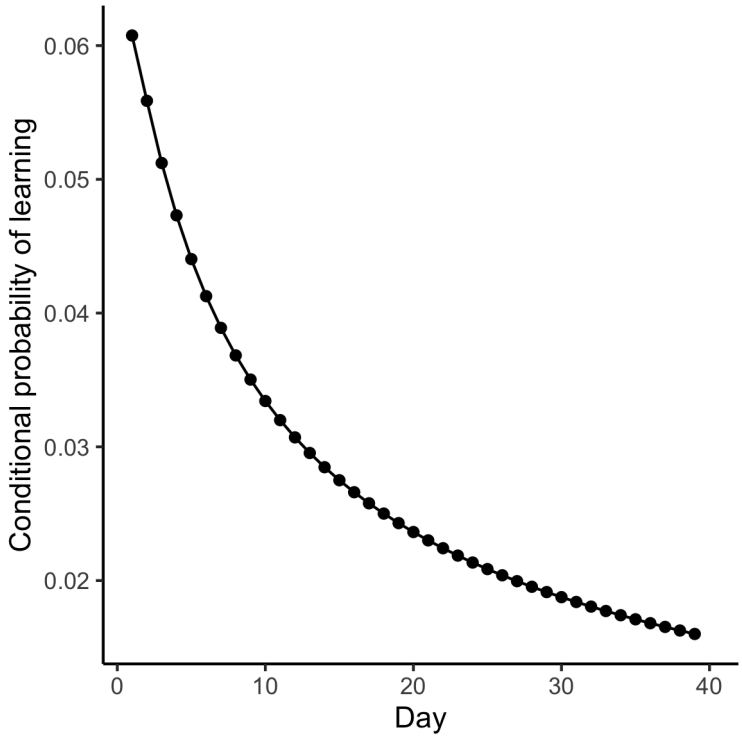

Figure 4: The conditional probability of learning was estimated from a log-normal parametric survival analysis of latency-to-first-solve data. Within an individual bird, they were more likely to socially learn soon after exposure to the puzzle, and this probability decreased over time. This function was used to inform the transition from naive to knowledgeable states in the agent based model.

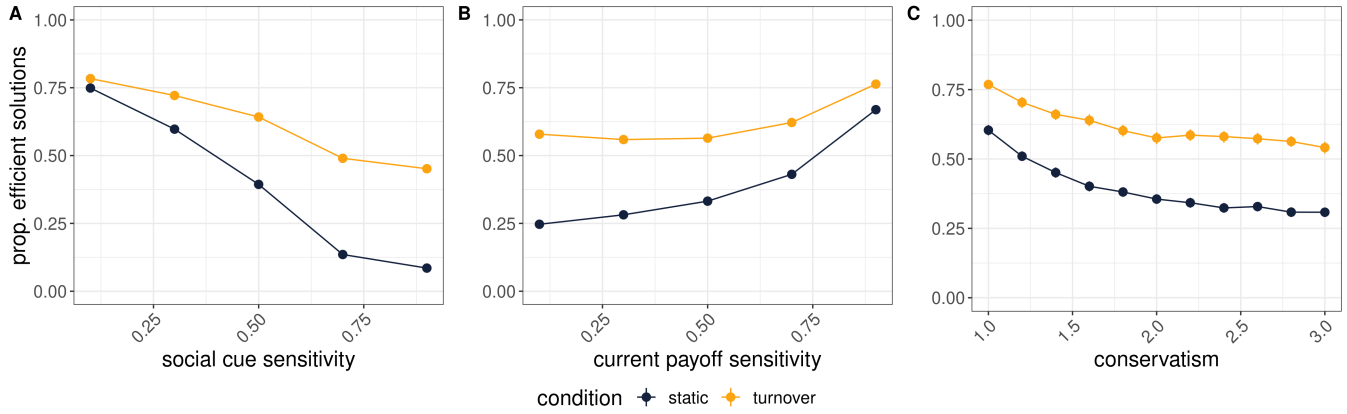

Figure 5: Proportion of efficient solutions at final time step with a reversed conditional probability of learning. Results only differ slightly compared to the model run with experimental data, showing that the effect of turnover should be robust to various real-world contexts in which this learning function may vary.)

Table 1: LMM: Individual improvements with experience

	Dependent variable:
	log(TTS + 1)
age (adult)	-0.169^{*}
	(0.091)
sex (male)	0.014
	(0.082)
scaled(trial)	-0.051^{***}
	(0.002)
intercept	0.810^{***}
	(0.246)
Observations	113,134
Log Likelihood	−93,146.270
Akaike Inf. Crit.	186,310.500
Bayesian Inf. Crit.	186,397.300
Note:	*p<0.1; **p<0.05; ***p<0.01

Table 1: LMM used to determine whether birds were improving their performance with experience, quantified as the log(TTS + 1) to account for non-normality (0 seconds was the shortest recorded TTS). Predictors include age (juvenile as reference), sex (female as reference), a z-scaled trial number (0 as the mean trial for a given bird, values as standard deviations), and random effects of solution type, and nested random effects of ID within population within year. Results indicate that birds reduced their TTS by about 5% by the time they produced 1 standard deviation's worth of solutions of either type. Older birds improved slightly more, and sex did not significantly affect this improvement.

Table 2: GLMM: Selection for efficient solution between conditions

	Dependent variable:
	efficient solution
age (adult)	-1.920^{***}
	(0.079)
sex (male)	-1.582^{***}
	(0.069)
experimental day	0.291^{***}
	(0.010)
condition (turnover)	-2.169
	(1.700)
experimental day:condition (turnover)	0.603^{***}
	(0.016)
intercept	-10.853^{***}
	(1.088)
Observations	141,059
Log Likelihood	$-5,741.569$
Akaike Inf. Crit.	11,499.140
Bayesian Inf. Crit.	11,577.990
Note:	*p<0.1; **p<0.05; ***p<0.01

Table 2: Logistic GLMM used to determine whether populations were selecting for the efficient solution. The response variable was the solution type (efficient: 1, inefficient: 0) Predictors include age (juvenile as reference), sex (female as reference), and an interaction between experimental day and condition (static as reference). Data was subset to after T1, when both solutions were available. Random effects included population nested within year. Solution type was not included as a random effect, since this variable was highly co-linear with condition, and would result in a failed convergence. Additionally, ID was not included as a random effect, since in turnover populations most birds were not in the experiment on the day represented by the intercept. The significant interaction between experimental day and turnover indicates that birds in the turnover condition were significantly more likely to produce the efficient solution as the experiment progressed.

Table 3: LMM: improvement over course of experiment by condition

	Dependent variable:
	log(TTS + 1)
sex (male)	0.002
	(0.004)
age (adult)	-0.158^{***}
	(0.004)
experimental day	-0.0004^{*}
	(0.0002)
condition (turnover)	0.098
	(0.098)
experimental day:condition (turnover)	-0.004^{***}
	(0.0003)
intercept	0.750^{***}
	(0.159)
Observations	113,145
Log Likelihood	−100,226.500
Akaike Inf. Crit.	200,471.000
Bayesian Inf. Crit.	200,557.700
Note:	*p<0.1; **p<0.05; ***p<0.01

Table 3: LMM used to determine whether populations were improving over experimental time, with performance quantified as the log(TTS + 1) to account for non-normality (0 seconds was the shortest recorded TTS). Predictors include age (juvenile as reference), sex (female as reference), and an interaction between experimental day and condition (static as reference). Random effects included population nested within year. Solution type was not included as a random effect, since this variable was highly co-linear with condition, and would result in a failed convergence. Additionally, ID was not included as a random effect, since in turnover populations most birds were not in the experiment on the day represented by the intercept. Results indicate that both conditions improved over experimental time, however the turnover condition improved more than static condition.

Table 4: GLMM: Predictors of failure to adopt efficient solution

	Dependent variable:
	failure to adopt
days experience	0.364^{***}
	(0.132)
socially observed inefficient	0.485
	(2.062)
intercept	-3.421^{*}
	(1.977)
Observations	53
Log Likelihood	-18.481
Akaike Inf. Crit.	46.962
Bayesian Inf. Crit.	56.813
Note:	*p<0.1; **p<0.05; ***p<0.01

Table 4: Logistic GLMM used to determine what predicted the failure to adopt the efficient solution after sampling it. The response variable was failure to adopt, which was calculated by measuring the majority solution of the last 10% of solves produced by an individual bird. Predictors include experience (days spent producing the inefficient solution prior to sampling the efficient solution), as well as conformity (the proportion of socially observed inefficient solutions on the day the bird first produced the efficient solution). Age and sex did not significantly predict the failure to switch, and thus were excluded from the final model. Only days experience significantly predicted whether or not the birds failed to switch, indicating that experience and not conformity was responsible for behavioral conservatism in these birds.

Table 5: Innovators table

	condition	population	ID	age	sex	time of innovation	hours_since_last_efficient_soln
1	static	1	E0DEE	6	F	2020-02-10 09:10:23	NA
2	static	1	DE3CE	5	F	2020-02-13 13:36:11	61
3	static	2	E04AD	5	F	2020-02-07 14:56:37	NA
4	static	5	E289E	6	F	2020-02-06 12:56:07	NA
5	static	5	DBD48	6	M	2020-02-10 15:55:04	99
6	static	5	DEF48	6	M	2020-02-16 14:16:25	73
7	static	8	D9831	5	M	2020-02-07 15:09:18	NA
8	static	8	DACDC	5	F	2020-02-10 15:57:46	73
9	static	11	DDFAA	6	F	2020-02-07 16:34:25	NA
10	static	11	DB4AC	6	F	2020-02-14 14:10:58	147
11	static	12	E2BAC	5	M	2020-02-06 17:20:29	NA
12	static	13	77F08	6	M	2019-02-20 15:24:17	NA
13	static	16	76C9C	6	M	2019-02-22 16:14:56	NA
14	turnover	3	DE875	6	F	2020-02-06 10:15:19	NA
15	turnover	3	DBB1F	5	F	2020-02-09 17:20:09	79
16	turnover	4	DEF9B	5	F	2020-02-10 08:29:51	NA
17	turnover	6	E11CB	5	M	2020-02-10 08:54:54	NA
18	turnover	7	DBC10	6	M	2020-02-06 10:22:42	NA
19	turnover	9	D8CB2	5	M	2020-02-06 10:25:29	NA
20	turnover	10	E1168	6	M	2020-02-07 15:05:19	NA
21	turnover	15	76928	5	M	2019-02-14 16:44:41	NA

Table 5: Table of innovation events, here defined as either the first time the efficient solution was produced by a bird in a population, or the first production within the outliers of the distribution of time-differences between prior production of efficient solution ($\geq$61 hours). NA values are when the innovator was the first to produce the efficient solution in its population.

Table 6: Solution type table

condition	solution type	mean(TTS)	sd(TTS)	included	total solves	excluded(NA TTS)	TTS>60 sec.
static	efficient	1.2	2.14	1489	1592	103	0
static	inefficient	1.73	2.85	81888	88829	6941	12
turnover	efficient	1.52	2.68	33838	39813	5975	4
turnover	inefficient	2.57	11.81	39256	44685	5429	39

Table 6: Summary of TTS by condition and type, along with observations included, and excluded for either an unrecorded TTS or an exceptionally long TTS.