

1 **Strong conformity requires a greater proportion of asocial learning and achieves lower fitness than**
2 **a payoff-based equivalent**

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7

8 **Abstract**

9 There is a growing interest in the relative benefits of the different social learning strategies used to
10 transmit information between conspecifics, and in the extent to which they require input from
11 asocial learning. Two strategies in particular, conformist and payoff-based social learning, have been
12 subject to considerable theoretical analysis, yet previous models have tended to examine their
13 efficacy in relation to specific parameters or circumstances. This study employs individual-based
14 simulations to derive the optimal proportion of individual learning that co-exists with conformist and
15 payoff-based strategies in populations experiencing wide-ranging variation in levels of
16 environmental change, reproductive turnover, learning error, and individual learning costs. Results
17 demonstrate that conformity co-exists with a greater proportion of asocial learning under all
18 parameter combinations, and that payoff-based social learning is more adaptive in 97.43% of such
19 combinations. These results are discussed in relation to the conjecture that the most successful
20 social learning strategy will be the one that can persist with the lowest frequency of asocial learning,
21 and the possibility that punishment of non-conformists may be required for conformity to confer
22 adaptive benefits over payoff-based strategies in temporally heterogeneous environments.

23 **Keywords**

24 Social learning; asocial learning; reproductive rate; environmental change.

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36 **1. Introduction**

37 There is currently considerable interest across a broad range of disciplines in the social learning
38 strategies that facilitate the transmission of information between conspecifics (e.g. Nakahashi et al.
39 2012; Aplin et al. 2015; Muthukrishna et al. 2016). Such research encompasses the development of
40 theoretical models as well as experimental analyses on numerous species. Of primary current
41 interest are two sets of learning strategies: ‘conformist’ strategies, which involve positive frequency-
42 dependent copying (e.g. Boyd and Richerson 1985; Muthukrishna et al. 2016), and ‘pay-off based’
43 strategies, which involve copying in proportion to some measure of success (e.g. Schlag 1998, 1999).

44 On a theoretical basis it has been argued (Boyd and Richerson 1985; Henrich and Boyd 1998) that
45 because those variants favoured by natural selection will often exist at the highest frequencies in a
46 pool of potential targets for copying, conformity provides a simple, adaptive social learning rule
47 under a very broad range of conditions. Conversely, conformity may prevent the spread of beneficial
48 innovations (Eriksson et al. 2007; Kandler and Laland 2009), and may even lead to population
49 collapse in fluctuating environments (Whitehead and Richerson 2009). Conformity becomes less
50 adaptive as rates of environmental change increase (Kendal et al. 2009), and in such situations the
51 conformist bias must either be weakened or coupled with higher rates of individual learning (Kandler
52 and Laland 2013; see also Efferson et al. 2008). The empirical evidence for conformity is weak (e.g.
53 Eriksson et al. 2007; Eriksson and Coultas 2009; Claidière et al. 2012), with studies hampered by the
54 need to demonstrate *positive* frequency dependence; where evidence appears robust, a ‘copy the
55 majority’ rule provides greatest explanatory power (e.g. Pike and Laland 2010; Morgan et al. 2012;
56 Aplin et al. 2015).

57 Empirical evidence for payoff-based strategies is far more prevalent, with numerous findings
58 supporting a ‘copy the best’ rule (e.g. Mesoudi 2008; Mesoudi and O’Brien 2008; Henrich and
59 Broesch 2011) as well as subsidiary rules employing relative payoffs (e.g. ‘copy if better’); the latter
60 appear particularly adaptive when the likelihood of copying a given individual is proportional to how
61 much better that individual is (Schlag 1998; Pike et al. 2010; Morgan et al. 2012). Payoff-based
62 strategies would appear to have an intuitive benefit; they are the only family of social learning
63 strategies that can be considered Darwinian (Godfrey-Smith 2009), and make an indirect reference
64 to the environment by assessing the success of conspecifics. Unlike conformist strategies, they are
65 likely to increase the frequency of rare, beneficial innovations, suggesting that even in rapidly
66 changing environments payoff-based social learning coupled with very low levels of individual
67 learning could form a highly adaptive mixed strategy.

68 The theoretical models surveyed above are largely derived from the evolutionary biology literature,
69 and share a number of common assumptions, often relying on incremental changes to pre-existing
70 modelling frameworks. A parallel literature within the fields of evolutionary computation and
71 artificial life has also arisen to interrogate the conditions under which various learning strategies are
72 beneficial. Although the goals of this latter body of research sometimes differ from those of the
73 evolutionary biology literature, artificial life models have contributed a number of innovative

74 conclusions that have direct bearing on the modelling reported below. Both Jones and Blackwell
75 (2011) and Borg and Channon (2012) show that variable environments promote the evolution of
76 learning capabilities more readily than do static environments. The former paper effectively
77 replicates the initial result of Boyd and Richerson (1985) that static or slowly varying environments
78 can be accommodated through genetic transmission alone, and that rapidly changing environments
79 will promote individual learning; between these two regions exists a third region of moderate
80 environmental change in which social learning is favoured. Jones and Blackwell (2011) also suggest
81 that social learning may play a key role in the aftermath of major environmental changes, allowing
82 solutions to novel adaptive challenges to percolate rapidly through populations. Borg and Channon
83 (2012) also provide an intriguing result suggesting that, against a backdrop on increasingly variable
84 environments, adoption of individual learning is a necessary precursor to the adoption of social
85 learning.

86 Gonzalez and colleagues (2017) look more broadly at conditions favouring the appearance of ‘non-
87 genetic evolutionary systems’ including learning and cultural transmission, and demonstrate that
88 such systems do not require the prior existence of cognitive decision making abilities regarding who
89 to copy. In their model, copying of random others can emerge when both the possible solution space
90 is large and the selection pressure on survival is strong relative to that on reproduction. These
91 authors also formalise the useful concept of ‘genotype-phenotype disengagement’, which provides a
92 minimal definition of what would more broadly be termed plasticity in the evolutionary biology
93 literature. Finally, Bullinaria (2017) has developed a promising series of simulations that examine
94 learning strategies in relation to life-history parameters, in particular a ‘protected period’ during
95 ontogeny that allows for the learning of skills necessary for independence. Importantly, Bullinaria
96 (2017) also considers the interface between life-history, encephalisation and learning, a focus that is
97 simultaneously emerging in evolutionary anthropology (Grove 2017).

98 The model introduced below employs individual-based simulations to derive the optimal proportion
99 of individual learning that co-exists with copy the best and copy the majority (henceforth CtB and
100 CtM) strategies in populations experiencing differing levels of environmental change, reproductive
101 turnover, learning error, and individual learning costs. Basic theoretical predictions, garnered from
102 previous research, are that levels of individual learning will be higher for both strategies when the
103 rate of environmental change is higher, and when reproductive turnover, learning error, and
104 individual learning costs are lower (Boyd and Richerson 1985; Efferson et al. 2008; Lewis and Laland
105 2012; Nakahashi et al. 2012).

106 Individual learning directly references the environment in the current iteration. CtB references the
107 fitness of individuals in the previous iteration, and leads to copying the fittest individual in that
108 generation. CtM references the behaviour of individuals in the previous iteration, and leads to
109 copying the most common behaviour in that iteration, regardless of the fitness associated with that
110 behaviour. Thus the link between environment and behaviour is weakest in CtM, suggesting that it
111 will be less able to track environmental change than CtB, and therefore that populations employing
112 CtM will have to complement this social learning strategy with a greater proportion of individual
113 learning than those employing CtB. This leads to the expectation that (1) CtM will evolve a greater
114 proportion of individual learning than CtB under all parameter combinations in which environmental
115 change occurs. As individual learning is widely and logically considered to engender higher costs
116 than social learning, the fittest social learning strategy should be that which can persist with the

117 lowest frequency of asocial learning (Kendal et al. 2009). A second prediction, therefore, is that (2)
118 because CtM is predicted to evolve a greater proportion of individual learning than CtB, CtB will
119 achieve higher fitness under all parameter combinations in which environmental change occurs.

120 **2. Methods**

121 The above predictions were tested by developing an evolutionary individual-based model in which a
122 population evolves the optimal proportion of individual learning under a comprehensive set of
123 parameter combinations; the following model description follows the ODD protocol (Grimm et al.
124 2010).

125 – *Purpose.* The main purpose of the model is to examine differences in the proportions of
126 individual learning that evolve in populations whose social learning strategy is either ‘copy
127 the majority’ (CtM) or ‘copy the best’ (CtB). Populations using these two social learning
128 strategies are simulated separately. The rationale for simulating the two strategies
129 separately (rather than allowing them to compete directly) is that it provides more accurate
130 results regarding the proportions of individual learning required by each strategy in tracking
131 a changing environment. The optimal proportions of individual learning and the associated
132 fitnesses can then be examined using the model output. Furthermore, in competition
133 scenarios, the fitter social learning strategy often completely displaced the other, and thus
134 the results reverted to those obtained when using a single social learning strategy in each
135 simulation. Simulating the two social learning strategies separately therefore produces a
136 more comprehensive set of results in regard to the research questions outlined in the
137 previous section. Rate of environmental change (δ), learning error (s), reproductive rate (r),
138 and the cost of individual learning (c) are varied systematically to examine their effects on
139 the proportion of individual learning that evolves under the two social learning strategies.

140 – *Entities, state variables, and scales.* The environment is simulated as a symmetrical sawtooth
141 wave that varies in amplitude between simulations. The entities of the model are asexually
142 reproducing individuals that socially learn via either CtM or CtB. Each individual is described
143 by three variables: a behavioural phenotype, a proportion of individual learning, and a
144 fitness score. The proportion of individual learning is the only inherited trait of an individual;
145 the behavioural phenotype is learned anew each iteration and the fitness score is
146 determined by how close the phenotype is to the environmental value in a given iteration.
147 The behavioural phenotype and the environment are measured on the same continuous
148 scale. The behavioural phenotype is updated at the start of each iteration through learning.
149 The proportion of individual learning, α , determines the extent to which the individual
150 depends on individual learning as opposed to social learning in conjunction with either CtM
151 or CtB.

152 The reproductive rate, $r \in \{0.1, 0.5, 0.9\}$, determines what proportion of the population is
153 replaced each iteration; generations are therefore overlapping in the simulations considered
154 here, with the average lifetime of an individual being $1/r$ iterations. The cost of individual
155 learning, $c \in \{0.1, 0.5, 0.9\}$, reflects the time taken to independently establish a behaviour
156 and the risk of injury potentially associated with doing so, and is implemented during
157 evaluation of the fitness function (see Reproduction, below). The rate of environmental
158 change, $\delta \in \{0: 0.05: 1\}$, reflects the wide range of environmental conditions encountered

159 by many animals on often relatively short timescales. Note that here $\{x:y:z\}$ indicates the
160 set of numbers from x to z inclusive, in increments of y . Finally, learning error, $s \in$
161 $\{0:0.05:1\}$, reflects the fact that learning targets, via either individual or social learning, are
162 unlikely to be perfectly met. Simulations, each of 6,000 iterations, were run separately for
163 the two social learning strategies (CtB and CtM), and for each combination of δ , s , r , and c ,
164 yielding 7,938 simulated combinations.

165 – *Process overview and scheduling.* At birth, individuals inherit from their parent a value that
166 determines the proportion of individual learning they will engage in. This value is slightly
167 mutated relative to that of the parent (see ‘Mutation’ below). A learning error (s) applies to
168 both individual and social learning (see ‘Learning’ below). After learning, the fitness of each
169 individual, F , is evaluated according to a Gaussian function that takes into account the cost
170 of individual learning. Reproduction then takes place via fitness-proportionate selection (see
171 ‘Reproduction’ below), with new individuals inheriting only the (mutated) α values of their
172 parents. Prior to the start of the next iteration, the values of the best and most common
173 phenotypes among the survivors are recorded so they can act as targets for social learning in
174 the next iteration. Median values of α and F are recorded at the end of each iteration. The
175 above schedule then begins again.

176 – *Design concepts.* The outputs of the model are the difference in the proportion of individual
177 learning, α , and the difference in fitness, F , between populations employing the two social
178 learning strategies (CtB and CtM) under various combinations of values of the four input
179 variables δ , s , r , and c . Changes in α through time emerge from the combined effects of
180 heredity, mutation, differential survival, and differential reproduction, given the values of
181 the four input variables. Mutation, survival probability, probability of reproduction, and both
182 individual and social learning are affected by stochastic variation. The environment has a
183 constant absolute first derivative (i.e. it changes at a constant rate) during each of the 6,000
184 iterations of any given simulation, thus the principal results are given as the median values
185 of α and F in the population over the last 5,000 iterations of the simulation. The first 1,000
186 iterations of each run were discarded as a burn-in period to ensure that results were not
187 affected in any way by the initialization values; although runs with lower r values took
188 longer to stabilize, runs for all combinations of parameter values had stabilized after 1,000
189 iterations. The retained 5,000 iterations provided a suitably robust sample size over which to
190 calculate medians of the outputs α and F .

191 – *Initialization.* Simulations were initialized with an environmental value of zero. Initial
192 phenotype values were drawn from a normal distribution with a mean of zero and a
193 standard deviation of 0.05. Initial proportions of individual learning were drawn from a
194 uniform distribution on the interval (0,0.1); differences in these starting values did not affect
195 the outcomes of the simulations. All simulations ran with a fixed population size of $n = 500$
196 individuals.

197 – *Input.* The model does not have any external inputs.

198 Submodels

199 – *Environment*. The environment is a symmetrical sawtooth wave. Although this waveform
200 differs from what is traditionally used in the social learning literature, it was chosen because
201 it has constant absolute first derivative (i.e. the rate of environmental change is a constant)
202 and because, though simple, it captures the periodicities found in empirical (palaeo)climatic
203 data. Such periodic signals are of various durations, ranging from sub-annual seasonal
204 fluctuations, through short cycles such as the El Niño Southern Oscillation (2-7 years), to
205 orbital insolation patterns lasting tens to hundreds of thousands of years (e.g. Grove 2012a,
206 2012b; Markonis and Koutsoyiannis 2013; Yun and Timmermann 2018). Results are given in
207 relation to the absolute rate of change, but it is important to note that other aspects of
208 environmental variation may be of similar importance. In particular, since spectral analyses
209 of climatic data often indicate ‘reddened’ signals (i.e. signals with a marked autocorrelation
210 component) it would be profitable in future to study responses to different ‘colours’ of noise
211 in the pink to red spectrum. The value of the current setup is that it provides a simple, easily
212 understandable baseline against which to compare future studies of more complex and
213 more realistic environments. The rate of environmental change per iteration (δ) is varied
214 between simulations in increments of 0.05 from 0 to 1 by increasing the amplitude of the
215 wave in increments of 2.5 from 0 to 25. The wave has a frequency of 1/200 iterations
216 throughout. Experiments demonstrated that altering δ via the frequency rather than the
217 amplitude of the wave did not affect the results.

218 – *Learning*. At the start of each iteration, all individuals update their behavioural phenotype
219 via a combination of social and individual learning, as determined by their inherited value of
220 α . Each individual i learns a behavioural phenotype, P_i , in iteration t as

$$221 \quad P_i(t) = \alpha_i \cdot \beta_i(t) + (1 - \alpha_i) \cdot \gamma_j(t - 1) \quad [1]$$

222 Where α is the proportion of individual learning, β is a value obtained via individual learning
223 and γ is a value obtained via social learning, with the subscript $j \in \{b, m\}$ indicating the
224 social learning strategy followed (either CtB or CtM). An individual aiming for a given target,
225 through either social or individual learning, will achieve a result drawn from a normal
226 distribution with that target as its mean and its learning error value, s , as its standard
227 deviation. The target for individual learning is the environment in the current iteration,
228 $w(t)$, whereas the target for social learning is the best or majority phenotypic value from
229 the previous iteration. Equation [1] embodies a trade-off between individual and social
230 learning, and it should be stressed that the model is therefore not intended to comment on
231 the evolution of the underlying cognitive abilities that support these two forms of learning.
232 Rather, the model assumes that individuals are capable of both, and the output indicates the
233 optimal balance of individual and social learning that obtains under a given set of parameter
234 values.

235 – *Reproduction*. The fitness of each individual, F_i , is evaluated according to a Gaussian
236 function with a mean equal to the current environmental value, $w(t)$, and unit variance,

$$237 \quad (F_i | w(t), P_i) = (1 - c\alpha_i) \cdot \exp(-0.5(w(t) - P_i)^2) \quad [2]$$

238 where c is the cost of individual learning. Simulations are run with $c \in \{0.1, 0.5, 0.9\}$. The
239 least fit $n \cdot r$ individuals are then removed from the population and replaced by $n \cdot r$ new

240 offspring chosen by fitness-proportionate selection from among the $n - n \cdot r$ surviving
241 parents, where $n = 500$ is population size and $r \in \{0.1, 0.5, 0.9\}$ is the proportion of the
242 population replaced each iteration. This reproduction scheme effectively couples both a
243 truncation procedure and fitness-proportionate selection; the scheme is implemented in this
244 way to accelerate the progress of the population towards asymptotic proportions of
245 individual learning, which are the results of interest. Eliminating the truncation element of
246 this scheme does not affect results, but does ensure that asymptotic proportions are
247 achieved after fewer iterations, thus reducing the burn-in time in the simulations. New
248 individuals inherit only the (mutated) α values of their parents.

249 – *Mutation.* Offspring inherit a value determining the proportion of individual learning they
250 engage in; however, this value undergoes mutation as it is transmitted from parent to
251 offspring. Mutation is carried out via an additive Gaussian operator of the form $\alpha' = \alpha + \lambda$,
252 where α' is the value of α after mutation and λ is a value called from a normal distribution
253 with mean zero and a standard deviation of 0.05. As the proportion of individual learning
254 can never be <0 or >1 , mutated values that are <0 are reset to 0 and those that are >1 are
255 reset to 1.

256 – *Targets for social learning.* At the end of each iteration the values of the fittest and most
257 common phenotypes from the parent population are recorded; these values are used as the
258 targets of social learning in the next iteration. The best phenotype is simply that achieving
259 the highest fitness, whilst the most common phenotype is calculated via a binning
260 procedure. As phenotypic values are recorded at high precision a simple calculation of the
261 modal value is insufficient, as it is unlikely (even in large populations) that any two
262 individuals' phenotypic values will be exactly the same. Surviving phenotypes are therefore
263 assigned to $\lceil (n - n \cdot r)^{0.5} \rceil$ bins of equal width covering the range of values in a given
264 iteration; the most common phenotypic value is considered to occur at the mid-point of the
265 modal interval (i.e. the mid-point of the bin containing the greatest number of phenotypes).
266 This technique for mode estimation was shown to have desirable properties such as
267 insensitivity to outliers and to the shape of the distribution by Chernoff (1964); a proof of
268 strong consistency was subsequently provided by Nadaraya (1965).

269 3. Results

270 Figures 1 and 2 show indicative single runs of the model in full, tracking changes in phenotype,
271 proportion of individual learning, and fitness for both CtB and CtM. Figure 1 shows the case in which
272 there is no environmental change ($\delta = 0$), with other parameters set to intermediate values
273 ($s = c = r = 0.5$). Figure 2 shows the case in which environmental change, learning error, cost of
274 individual learning, and reproductive rate are all set to intermediate values ($\delta = s = c = r = 0.5$).
275 Subsequent figures present the medians from iterations 1001-6000 of each model run, across all
276 parameter values simulated.

277 The basic predictions garnered from previous research are supported, with the exception that high
278 learning error does *not* always lead to low proportions of individual learning. At low reproductive
279 rates, high learning error can lead to higher levels of individual learning than those recorded at
280 intermediate levels of learning error for both strategies (see Figure 3A i, iv, vii, and viii and 3B i, iv, vii

281 and viii). Prediction (1), that CtM will evolve a greater proportion of individual learning than CtB
 282 under all parameter combinations in which environmental change occurs, is supported; Figure 4A
 283 demonstrates that the proportion of individual learning evolved under CtB minus the proportion
 284 evolved under CtM is always negative. There are, however, areas in which the difference in the
 285 evolved proportion of individual learning between the two strategies is negligible. In some cases this
 286 follows from more basic predictions, in that it occurs under low rates of environmental change or
 287 learning error, when both strategies evolve low or high proportions of individual learning,
 288 respectively. They also occur, however, at high reproductive rates when learning error is high
 289 relative to the rate of environmental change; this latter case is discussed below.

290 Prediction (2) is supported in the vast majority of cases. Figure 4B demonstrates that the fitness of
 291 CtB minus the fitness of CtM is almost always positive, and therefore that the fitness of CtB is almost
 292 always higher. Of the 3,969 paired simulations represented in Figure 4B, CtM achieves higher fitness
 293 in only 102 of them (2.57%). These exceptions occur in a small region of Figure 4B in which $r = 0.9$
 294 and $c = 0.1$, where a minimal amount of individual learning provides an advantage to CtM in a
 295 region in which CtB continues in the absence of individual learning. Although differences in fitness
 296 (Figure 4B) correspond well to differences in the proportion of social learning (Figure 4A), the
 297 greatest differences in fitness occur not when differences in the proportion of individual learning
 298 area greatest, but when *both* the proportion of individual learning under CtB is zero *and* the
 299 proportion under CtM is greater than zero. Thus the greatest *relative* losses in fitness under CtM
 300 occur when it begins to incorporate small amounts of individual learning under conditions in which
 301 CtB does not.

302 4. Discussion

303 Figure 3 (3A i, iv, vii, & viii, and 3B i, iv, vii, & viii) demonstrates that for both CtB and CtM at [$r =$
 304 $0.5, c = 0.1$] and in all cases where $r = 0.1$, higher learning errors can lead to *increases* in individual
 305 learning under low to moderate rates of environmental change (δ). This partially contradicts the
 306 basic expectation, outlined in the introduction, that higher proportions of individual learning will be
 307 more likely to evolve as learning error approaches zero. The reason for this pattern is as follows. The
 308 target for individual learning is the environment in the current iteration, $w(t)$, which is also the
 309 optimal phenotypic value. As such, increasing learning error (s) will always be detrimental to
 310 individual learning, because it will inevitably lead to phenotypes that are further from the optimum
 311 than they would have been had learning been error-free. However, increasing s can also be
 312 detrimental to social learning, where the target is the behaviour of a conspecific. Given a univariate
 313 environment and a Gaussian learning error distribution, and assuming that in the previous iteration
 314 social learning attained the optimal phenotype, at $s < \delta$ on average half the copies produced by
 315 social learning in the current iteration will be worse than the target. This is because these copies will
 316 have moved in the ‘wrong’ direction along the environmental axis. At $s > \delta$, however, *more than*
 317 half of the copies produced by social learning in the current iteration will be worse than the target,
 318 because in addition some will have ventured too far in the ‘correct’ direction. Formally, the
 319 probability of a given individual attaining *exactly* the optimal phenotype in iteration t given that she
 320 is copying an individual who had done so in iteration $t - 1$ is

$$321 \quad \varphi = \frac{1}{\sqrt{2\pi s^2}} e^{-\frac{\delta^2}{2s^2}} \quad [3]$$

322 Note that the numerator of the exponentiated part of this equation is δ^2 because the environment
323 has shifted exactly δ since the previous iteration; the environment (and therefore the optimal
324 phenotypic value) in the previous iteration is regarded as being located at zero.

325 φ thus declines with increasing s when $s > \delta$ and declines rapidly to zero with decreasing s when
326 $s < \delta$. Figure 5 provides a rendering of equation [3] over the range of s and δ employed in the
327 simulations. This graph demonstrates that the greatest advantage to social learning occurs towards
328 the bottom left of the graph, at values of relatively low δ and s . It is in this region that very high
329 levels of social learning evolve under both CtM and CtB, even under low costs of individual learning
330 and low reproductive rates (see Figure 3). Note that as learning error (s) increases from this region,
331 the advantage of social learning *decreases*. This demonstrates that at very low rates of
332 environmental change, greater learning error can decrease the value of social learning and thus
333 increase reliance on individual learning. The regions in which individual learning is advantageous in
334 this way are of course decreased by higher costs of individual learning, and are also decreased by
335 higher reproductive rates. The reason for this latter pattern is that as reproductive rate increases, it
336 increases the strength of selection (because fewer members of each generation survive to
337 reproduce); this increases the advantages of social learning, because the only the very fittest
338 individuals survive long enough to be copied.

339 For 97.43% of parameter combinations, the results reported above support the contention (Kendal
340 et al. 2009) that the fittest social learning strategy will be the one that can persist with the lowest
341 frequency of asocial learning; furthermore, they suggest that this strategy will not be CtM. Although
342 the model employed here does not involve direct competition between the two strategies, it does
343 raise the question of how conformity could possibly evolve in situations in which an alternative
344 strategy is demonstrably more adaptive. One interpretation is simply that these results accord very
345 well with the sparse empirical evidence for conformity (e.g. Eriksson et al. 2007; Eriksson and
346 Coultas 2009; Claidière et al. 2012; van Leeuwen and Haun 2013, 2014; Acerbi et al. 2016). Although
347 the empirical studies of, for example, van de Waal and colleagues (2013) and Aplin and colleagues
348 (2015) appear robust, questions remain as to the validity of inferring individual-level processes from
349 population-level analyses and the extent to which apparent signatures of conformist social learning
350 could have been produced by alternative processes (Acerbi and van Leeuwen 2017; Barrett in press).
351 The simulations of Acerbi and colleagues (Acerbi et al. 2016; Acerbi and van Leeuwen 2017)
352 demonstrate that preference for one cultural trait over another or social learning from small subsets
353 of the population can lead to results indistinguishable from those expected under conformist social
354 learning. Although these alternative generating processes may be realistic only under a limited set of
355 conditions (Smaldino et al. 2017), they raise a substantive equifinality problem that deserves greater
356 attention (Barrett in press).

357 A second interpretation relates to the form of the environment used as the basis for the current
358 model. Although periodic oscillations of various frequencies dominate climatic signals, they are
359 augmented by high-frequency variability which can reasonably be characterised as white (i.e.
360 Gaussian) noise (e.g. DeLong et al. 2009; Trauth 2015). Adding such variability to the model
361 environment employed in the current simulations would reduce the fitness advantage of CtB over
362 CtM when the strength of the variability is low relative to the periodic component, and drive
363 populations towards pure individual learning when the strength of the variability is high relative to

364 the periodic component. Further research is required to fully elucidate the differing effects of these
365 two components, and to quantify their relative importance in empirical climatic signals.

366 There are a number of additional interpretations that relate these results more closely to previous
367 theoretical research. Firstly, a number of previous theoretical studies have drawn the conclusion
368 that conformist social learning is more likely to evolve in a spatially variable environment than it is in
369 a temporally variable environment (e.g. Boyd and Richerson 1985; Henrich and Boyd 1998;
370 Nakahashi et al. 2012). Such results often rely on the evolution of what might be termed *local*
371 *conformity*. Payoff-based social learning becomes maladaptive if the payoffs being monitored are
372 achieved under environmental conditions that are different from those currently experienced by the
373 social learner; in such cases, conformist copying of local individuals (those experiencing the same
374 environmental conditions) can be more adaptive than payoff-based learning from the whole
375 population. Efferson and colleagues (2016) generalise this result to the inevitable conclusion that
376 conformist copying is beneficial when the same behaviour is optimal for both the copier and the
377 copied. Unfortunately, such conclusions fail to compare like with like; local conformity may be
378 preferable to global payoff-based copying, but it will only be preferable to local payoff-based
379 copying when temporal environmental variability is negligible. It is hard to imagine an empirical
380 scenario in which there is no temporal variability in environmental conditions, unless the study
381 encompasses an exceptionally short temporal interval. Further to this, the evolution of conformity
382 under such models is also sometimes reliant on the assumptions that payoff-based copying is more
383 costly than conformist copying, or that payoffs are more difficult to discern than the behaviours that
384 generated them (e.g. Nakahashi et al. 2012). While one or both of these assumptions may be
385 justified under certain conditions, additional research is will be required to reveal exactly what those
386 conditions are, and how widespread they may be.

387 Secondly, the model outlined above employs the strongest possible form of conformity. A previous
388 model (Kandler and Laland 2013) found a positive relationship between the strength of conformity
389 and the degree of individual learning required. Individual learning serves essentially two purposes:
390 (1) it enables individuals to sample and therefore to track a changing environment, and (2) in doing
391 so it introduces variation in the form of ‘innovations’ into the population. However, variation can
392 also be *introduced* by social learners with high rates of learning error, or *maintained* in proportion to
393 the ‘weakness’ of the social learning strategy. When beneficial variation is introduced by individual
394 learners or social learners with high learning error, it is likely to be eradicated by strong conformity
395 but spread by payoff-based learning at a rate proportional to the payoff bias. The weaker the
396 conformist bias, the more likely it is that (rare) beneficial variation will survive social learning and be
397 spread by natural selection; conversely, the weaker the payoff bias, the less likely this is to occur.

398 It is argued therefore that the result reported above, that at high r and high s the proportions of IL
399 under CtB and CtM are very similar, is analogous to the result of Kandler and Laland (2013) that
400 weak conformity requires a lower proportion of individual learning; the difference being that in the
401 model above beneficial variation is introduced by high social learning error rather than being
402 maintained by weak conformity. The high reproductive rates ensure that this variation is capitalised
403 upon by natural selection. This line of reasoning suggests that conformity might co-exist with
404 relatively low rates of individual learning when either conformity is weak (as per Kandler and Laland
405 2013) or when learning error and reproductive rates are high. The latter scenario is effectively a
406 cultural bet-hedging strategy, and may be optimal for species that produce multiple offspring

407 simultaneously (i.e. in litters) and whose generation times are short relative to the rate of
408 environmental change. The former scenario is more likely to apply to long-lived / slowly reproducing
409 species such as *Homo sapiens*, particularly given the emerging consensus that *cumulative* culture
410 requires high fidelity transmission (i.e. low learning error: Tomasello 1999; Lewis and Laland 2012).

411 A third argument relates to the potential social costs of non-conformity, an element rarely
412 considered in models of social learning, presumably because empirical evidence for it comes almost
413 exclusively from humans (e.g. Fehr and Fischbacher 2004). The normative nature of human social
414 learning can lead to third-party punishment of non-conformists, a pattern not found in other
415 primates (Fehr and Fischbacher 2004), and almost certainly linked to in-group / out-group
416 distinctions in the context of cultural group selection (e.g. Tennie et al. 2009). If the costs of non-
417 conformity equate to actual declines in fitness via, for example, ostracism or reproductive
418 suppression, this would imply an additional cost to both individual learning (innovation) and social
419 learning strategies other than conformity. Whilst it is routine for theoretical models to assume a
420 greater cost to individual than to social learning, there remains the additional possibility that social
421 learning strategies themselves attract differing costs due simply to the ways in which their outcomes
422 are viewed by other group members. Figure 4B demonstrates that there are regions, even at low
423 reproductive rates, in which the fitness difference between CtM and CtB is low; in such regions, even
424 minor social costs to non-conformity could promote CtM as the most adaptive strategy.

425 In summary, the results detailed above demonstrate that the optimal proportion of individual
426 learning co-existing with strong conformity is greater under all parameter combinations than for an
427 equivalent payoff-based strategy. Populations practicing the optimal combination of individual and
428 payoff-based social learning are fitter than their conformist counterparts in 97.43% of simulations,
429 supporting the conjecture that the most adaptive social learning strategy will be that which co-exists
430 with the lowest proportion of individual learning, and suggesting that conformity is unlikely to
431 evolve under a temporally varying environment unless reinforced by the social punishment of non-
432 conformists.

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446 2017. The comments of James Borg and Isa Romanowska were particularly insightful. The comments
447 of three anonymous reviewers also considerably clarified aspects of the manuscript, and suggested
448 productive avenues for future research.

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451 **Note on Model Code**

452 The full code for the model is supplied as Grove_ESM2.txt, with the code for producing the figures
453 supplied in Grove_ESM1.txt. All code is written in Matlab R2017a (The MathWorks Inc., Natick, MA,
454 USA).

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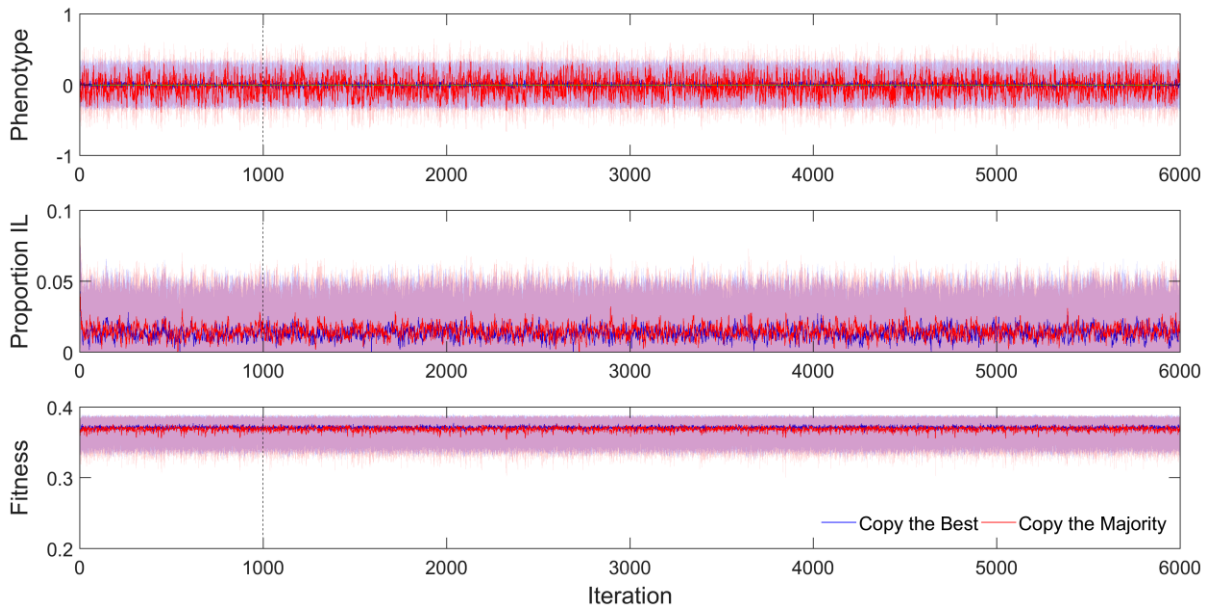
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605 **Figures**

606 **Figure 1.** Output of a single model run when the environmental does not change ($\delta = 0$), with other
607 parameters set to intermediate values ($s = c = r = 0.5$). Translucent shaded regions show inter-
608 quartile ranges, with solid lines showing medians in each case. The environment is shown in green in
609 the 'Phenotype' plot. The dashed line at 1,000 iterations shows the end of the burn-in period. IL =
610 individual learning.



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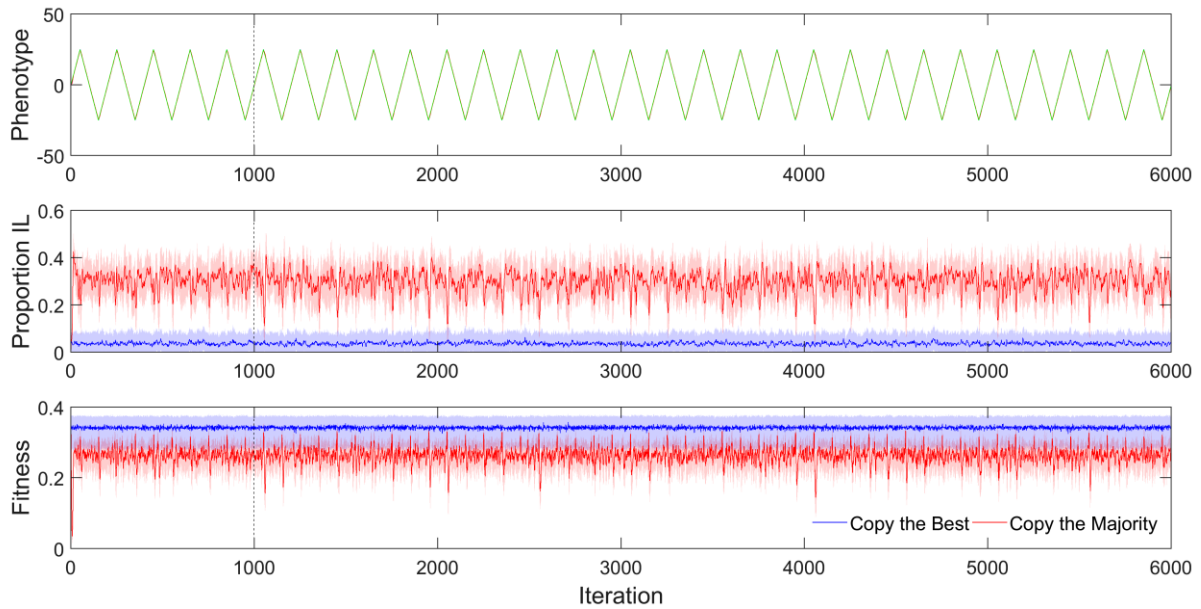
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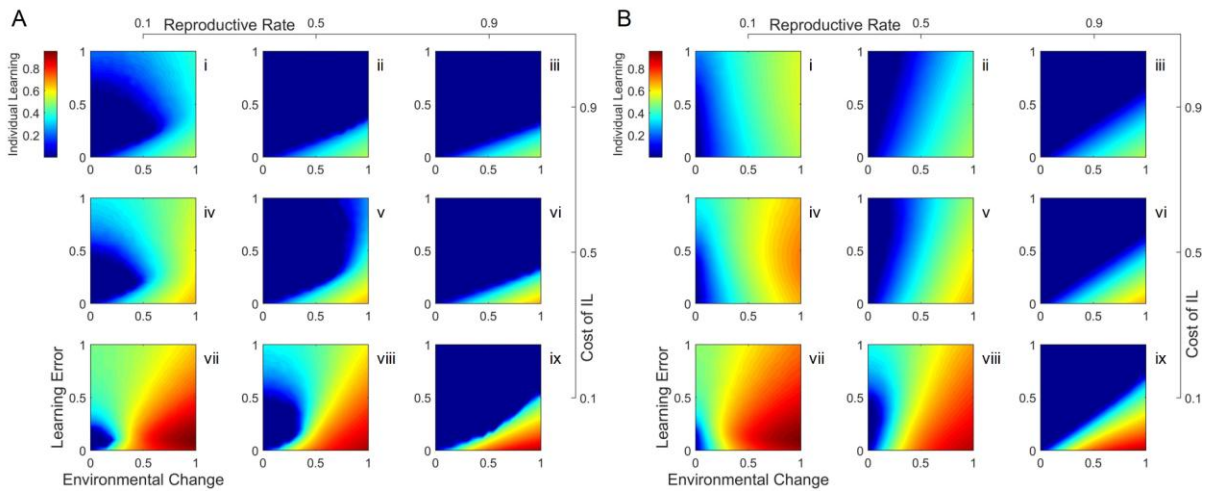
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625 **Figure 2.** Output of a single model run with environmental change, learning error, cost of individual
 626 learning, and reproductive rate are all set to intermediate values ($\delta = s = c = r = 0.5$). Translucent
 627 shaded regions show inter-quartile ranges, with solid lines showing medians in each case. The
 628 dashed line at 1,000 iterations shows the end of the burn-in period. Note that the phenotypes of
 629 neither the 'copy the best' or the 'copy the majority' strategies are visible in the upper plot, as both
 630 perfectly follow the environment (shown in green). IL = individual learning.



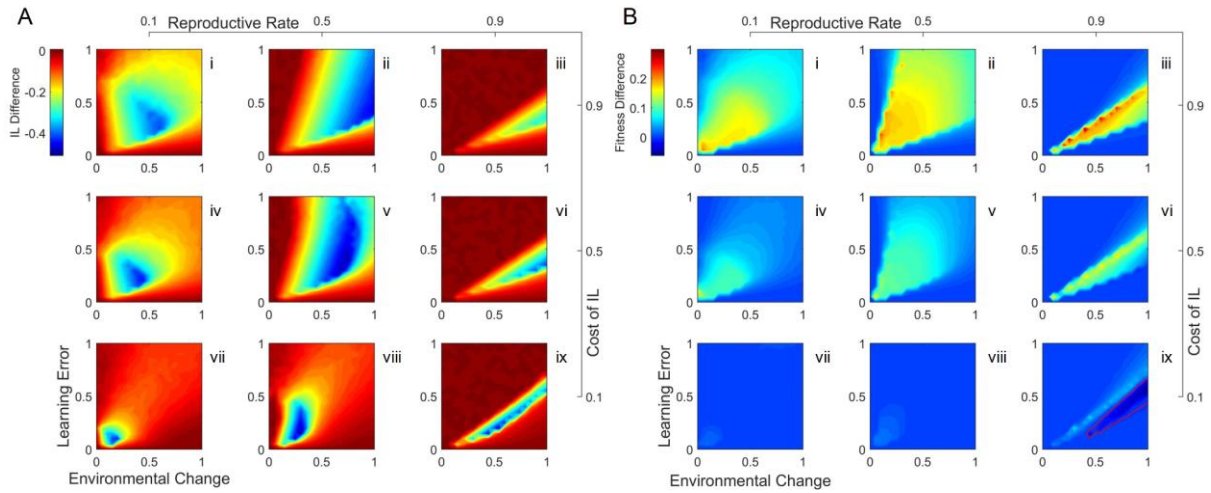
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645 **Figure 3.** Optimal proportions of individual learning when coexisting with (A) payoff-based and (B)
 646 conformist social learning. The indexes i – ix are used to identify specific combinations of
 647 reproductive rate and cost of individual learning in the text. IL = individual learning.



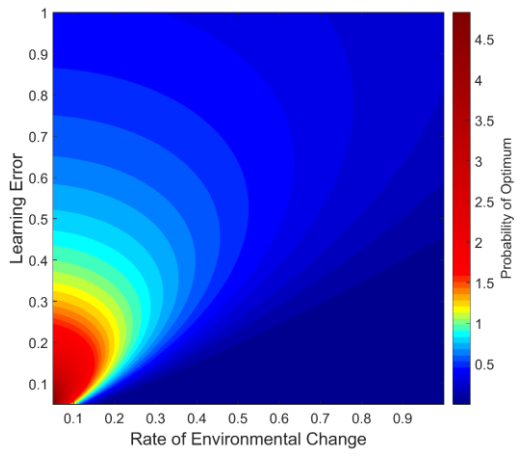
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666 **Figure 4.** Differences between (A) the evolved proportion of individual learning and (B) fitness under
 667 CtM and CtB, measured as the result for CtB minus that for CtM in both cases. The indexes i – ix are
 668 used to identify specific combinations of reproductive rate and cost of individual learning in the text.
 669 The red contour line in B(ix) encloses the only area in which fitness is higher under conformist
 670 learning than it is under payoff-based learning. IL = individual learning.



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688 **Figure 5.** Rendering of equation [3] over the range of s and δ employed in the simulations.



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