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Animal Learning as a Source of Developmental Bias

In: Developmental Bias in Evolution,
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31 **ABSTRACT.** As a form of adaptive plasticity that allows organisms to shift their phenotype
32 toward the optimum, learning is inherently a source of developmental bias. Learning may be
33 of particular significance to the evolutionary biology community because it allows animals to
34 generate adaptively biased novel behavior tuned to the environment and, through social
35 learning, to propagate behavioral traits to other individuals, also in an adaptively biased
36 manner. We describe several types of developmental bias manifest in learning, including an
37 *adaptive bias, historical bias, origination bias* and *transmission bias*, stressing that these can
38 influence evolutionary dynamics through generating nonrandom phenotypic variation and/or
39 nonrandom environmental states. Theoretical models and empirical data have established
40 that learning can impose direction on adaptive evolution, affect evolutionary rates (both
41 speeding up and slowing down responses to selection under different conditions), and
42 outcomes, influence the probability of populations reaching global optimum, and affect
43 evolvability. Learning is characterized by highly specific, path-dependent interactions with the
44 (social and physical) environment, often resulting in new phenotypic outcomes.
45 Consequently, learning regularly introduces novelty into phenotype space. These
46 considerations imply that learning may commonly generate plasticity first evolution.

47

48 **KEYWORDS:** Learning, developmental bias, plasticity, plasticity first, evolvability

49

50 **RESEARCH HIGHLIGHTS:** Learning is a major source of developmental bias in animals. Here we
51 review the different types of developmental bias manifest in learning, and show how these
52 influence evolutionary dynamics.

53

54 A central, largely unresolved, issue in the field of evolutionary biology is whether and how
55 developmental processes contribute to evolutionary change (Love 2015), and one much-
56 discussed means by which development might do so is through generating a biased
57 distribution of phenotypic variation (i.e. ‘developmental bias’; Maynard-Smith et al 1995;
58 Brakefield, 2006; Uller et al 2018). Perhaps some developmental biologists will not think of
59 learning as a ‘developmental’ process, as it is typically studied without consideration of
60 gastrulation, cell division or hox genes. However, if development is viewed broadly to
61 comprise all of the changes in size, shape, and function that take place during the life of an
62 organism, learning is unquestionably a developmental process. Viewed in this manner, any
63 biases in behavioral phenotypes that are generated through learning are a form of
64 developmental bias.

65

66 This point takes on new significance once some well-documented properties of learning are
67 recognized. What is immediately apparent to most students of animal learning, but perhaps
68 less obvious to many other biologists, is that learning typically is a highly flexible form of
69 adaptive plasticity that shifts many aspects of the phenotype towards the optimum. Also self-
70 apparent is the fact that animals commonly learn knowledge and skills through observing and
71 interacting with other animals, including other species, again with a strong tendency to
72 acquire adaptive knowledge.

73

74 In this article we describe how phenotypes generated through animal learning are generally
75 not just biased, but adaptively biased. Moreover, such phenotypes are not just manifest in a
76 single individual but commonly rapidly propagated to multiple individuals and, through social
77 transmission, passed on to descendants. We also review the evidence that novel phenotypes
78 propagated through learning can impact genetic evolution. Here we set out to present the
79 evidence, both experimental and theoretical, that leads us to the view that learning should
80 be regarded as an important source of developmental bias in animals, and a profound
81 influence on adaptive evolution.

82

83 **DEFINITIONS**

84 *What is developmental bias?*

85 The term ‘developmental bias’, as commonly deployed, is somewhat ambiguous because it is

86 manifestly subject to two distinct readings: Is it the products of development that are biased
87 (i.e. are a biased set of phenotypic variants generated)? Or are developmental processes
88 biasing something else – most obviously, the course of evolution? While the most evident
89 way in which developmental processes can bias the course of evolution is through biasing
90 phenotypic variation, in principle, these two readings can be disassociated. Biased phenotypic
91 variation need not affect the course of evolution (e.g. if dynamics are dominated by
92 selection), whilst developmental processes could affect the course of evolution even if
93 phenotypic variation were isotropic (e.g. through nonrandom modification of selective
94 environments). We suspect that usage of the term slips between these two meanings, with
95 users perhaps sometimes unaware of the inherent ambiguity, and frequently committed to
96 both interpretations. This slippage may partly account for the diversity of usage of this term.

97 One way of resolving the ambiguity is to distinguish between the two usages explicitly:
98 that is, distinguishing between a biased product of development (henceforth
99 ‘developmentally biased phenotypic variation’), and a biasing process of development
100 (‘developmentally biased evolutionary process’). This approach has proven useful in helping
101 to clarify a similar ambiguity in the use of the term ‘innovation’ (Reader & Laland, 2003).

102 To characterize the process or the product of development as ‘biased’ we must have
103 some notion of what an unbiased product/process would look like. Hence, ideally a definition
104 of developmental bias would state relative to what baseline the bias arises. Here, following
105 Uller et al (2018, p949), we define developmentally biased phenotypic variation as *‘the bias*
106 *imposed on the distribution of phenotypic variation, arising from the structure, character,*
107 *composition, or dynamics of the developmental system, relative to the assumption of isotropic*
108 *variation’*. We also define a developmentally biased evolutionary process as *‘any bias in the*
109 *rate, dynamics and pattern of evolution arising from the production of nonrandom phenotypic*
110 *variation (broadly construed), relative to the expected rate, dynamics and pattern of evolution*
111 *arising from random genetic variation.’*

112 We introduce the qualification ‘broadly construed’ as our use of this term will
113 encompass cases in which organisms express their nonrandom (extended) phenotypic
114 variation in the external environment, for instance through building nests, burrows, mounds,
115 webs, and pupal cases, or modifying local soils, hydrology, chemistry, nutrients, or flows (i.e.
116 niche construction), and which thereby bias the sources of selection that they, and other
117 ecologically interacting populations, experience (Odling-Smee et al, 2003; Laland et al., in

118 press).

119 In this article, we are interested in both the specific form of developmentally biased
120 phenotypic variation that arises from animal learning, and in its evolutionary consequences.
121 We suggest that the forms of bias that result from learning are of relevance to the
122 evolutionary biology community because, (1) through learning, animals tune their behavior
123 to environments, including novel environments, by selectively generating, retaining and
124 refining adaptive behaviors more readily than non-adaptive ones. Moreover, (2) these
125 adaptive novel phenotypic variants are commonly propagated to other individuals, including
126 nonrelatives, and across generations, through social learning. This social transmission of
127 behavior is a second source of bias towards the propagation of adaptive variants – evidence
128 from diverse species of animals demonstrates that the likelihood of social transmission of
129 novel learned knowledge and skills is significantly higher for adaptive than for non-adaptive
130 behavioral variants. In addition, (3) learned and socially transmitted behavior can bring about
131 consistent changes in the social and ecological environments, thereby biasing the selective
132 environment of both the learner and of other species that experience modified conditions
133 (i.e. niche construction). We submit that by generating and propagating novel phenotypes
134 that are *adaptive* (i.e. nonrandom with respect to fitness), and modifying selective
135 environments in reliable ways, animal learning biases the course of evolution. We go on to
136 make further distinctions between different types of developmental bias manifest in, and
137 resulting from, learning (Table 1).

138

139 *What is animal learning?*

140 Learning is generally defined as a relatively permanent change in behavior (or potential
141 behavior) that results from experience (Dickinson 1981; Rescorla, 1988; Kirkpatrick & Hall,
142 2004). Central to definitions of learning is the requirement that there must be a memory trace
143 of what has been learned, allowing the animal on subsequent occasions to recall or do what
144 they have learned previously. Transient changes, such as reflexes, do not qualify. Learning is
145 usually inferred from changes in observable behavior, but is not always immediately manifest,
146 and can be stored to influence future performance.

147 There are many forms of learning (Kirkpatrick & Hall, 2004; Staddon 2016). Animals
148 may learn about a single event through habituation or sensitization, or form associations
149 between events, which includes ‘classical’ (a.k.a. ‘Pavlovian’) and ‘operant’ (a.k.a.

150 ‘instrumental’) conditioning. The latter is of most interest here, as it is thought to be the
151 primary means by which animals acquire behaviour (Staddon, 2016). This kind of learning
152 occurs through reinforcement, in which positive or negative experiences provide animals with
153 a mechanism for the selection of appropriate behavior. Actions that bring about positive
154 consequences (e.g. finding food, avoiding danger) are more likely to be performed in the
155 future, whilst those with negative consequences (causing pain, missing out on reward)
156 become less likely. Such actions occur in a particular context, or in response to a particular
157 cue, and the learning that takes place is described as ‘associative’ because the animal learns
158 to produce the action in response to the cue (i.e. stimulus-response learning) or else learns
159 that the action has a particular consequence (i.e. response-reinforcement learning).

160 That animals learn through operant conditioning has been known for a long time
161 (Thorndike, 1898) and has been demonstrated in so many species, including countless
162 invertebrates, that it is commonly regarded as virtually universal across animals. Skinner
163 (1938) stressed three general features of animal learning: (i) animals are frequently active,
164 and hence are continuously emitting behavior; (ii) these emitted behavior patterns frequently
165 have consequences that influence the frequency with which the behavior is repeated in the
166 future; and (iii) the effects of the consequences are influenced by the animal’s motivational
167 state, as well as by the physical and social environment. The first of these is rarely
168 emphasized, but important. Learned behavior is often the result of an exploratory search
169 conducted over multiple trials, through which individuals hone their behavior to exploit their
170 environment. This exploratory component to learning is significant, because it generates
171 behavioral flexibility and variability. There is seemingly no end to the associations that many
172 animals could form.

173 In their natural environment, animals frequently learn from other individuals. In this
174 manner, animals rapidly acquire skills and functional information concerning what to eat,
175 where to find it, how to process it, pathways to take through their environment, what a
176 predator looks like, how to escape the predator, calls, songs, and more (Hoppitt & Laland,
177 2013). Social learning is defined as *learning that is facilitated by observation of, or interaction*
178 *with, another individual or its products* (Heyes 1994; Hoppitt & Laland 2013). It is also
179 widespread amongst animals, including invertebrates, and even in species described as
180 ‘solitary’ (Wilkinson et al, 2010). Theoretical analyses and experimental studies both strongly
181 suggest that social learning is more efficient than individuals learning alone, for instance,

182 through trial-and-error (Rendell et al, 2010; Hoppitt & Laland, 2013). That is because when
183 animals learn socially, the aforementioned ‘exploratory search’ is effectively expanded to
184 encompass the trials and associated experiences of multiple individuals. Social learning is
185 particularly valuable in helping animals to solve difficult problems where the optimal action
186 is one of many possible actions, or when a long sequence of actions is required to be
187 performed in the correct order to elicit the reward (Whalen et al, 2015). If finding the optimal
188 behavior is like searching for a needle in a haystack, then learning is as if someone tells you
189 when you are getting close (Hinton & Nowlan, 1987; Maynard Smith 1987); social learning is
190 when someone actually shows you where to look.

191 Social learning occurs throughout the lifespan, and from many different individuals,
192 and thereby allows for the propagation of phenotypic variants amongst unrelated individuals,
193 often within timespans significantly shorter than a generation (*e.g.* social transmission of
194 predator recognition in minnows, *Pimphales promelas*; Chivers & Smith 1995; socially learned
195 mating preferences in grouse, *Centrocercus urophasianus*; Gibson et al, 1991). Socially
196 transmitted activities (*e.g.* foraging) can modify ecological circumstances, sometimes in ways
197 that feed back to impact natural selection (niche construction). Social learning generates an
198 additional mechanism of inheritance operating parallel to genes ‘cultural inheritance’
199 (Hoppitt & Laland 2013; Whiten *et al.* 2017).

200

201 **BIASES IN PHENOTYPIC VARIATION ARISING FROM ANIMAL LEARNING**

202 This section focuses on developmentally biased phenotypic variation resulting from animal
203 learning.

204

205 *Biases arising from individual learning*

206 Experimental research in a very large number of species of animals provides compelling
207 evidence that learning typically increases the rate of reinforcement, and reduces the rate of
208 punishment, experienced by animals (Dickinson 1980; Kamil, 1983; Kirkpatrick & Hall, 2004;
209 Staddon, 2007, 2016). Faced with multiple potential food sites, an animal will typically sample
210 the alternatives and choose the option yielding the highest return. The decision made, the
211 amount of sampling, the number of times the animal performs the action (*e.g.* if on a ‘fixed-
212 reinforcement schedule’), the timing of the performance (*e.g.* when on an ‘interval
213 schedule’), and other parameters, have all been reliably shown to improve over trials with

214 relevant experience (Krebs et al, 1978; Dickinson 1980; Kamil, 1983; Kirkpatrick & Hall, 2004;
215 Staddon, 2016). Similar findings apply to learning to avoid threats.

216 This kind of associative learning is widespread and has general properties that allow
217 animals to learn about the causal relationships among a wide variety of events (Dickinson,
218 1980; Mackintosh, 1974). Learning can occur through quite simple rules. One example is the
219 theory known as the *Rescorla–Wagner rule*, which describes updates in knowledge as a linear
220 combination of current knowledge and new information. It has proved useful in explaining
221 the results of experiments on foraging in honeybees, avoidance conditioning in goldfish, and
222 inferential reasoning in humans (Rescorla & Wagner, 1972).

223 Thirty years ago, inspired by *optimal foraging theory* (Stephens & Krebs, 1986), there
224 was extensive theoretical interest in the idea that learned behavior might maximize the rate
225 of reinforcement, and thereby generate optimal behavior (Kamil, 1983; Staddon, 2007). That
226 particular research agenda met only partial success (Staddon, 2007): animals were found to
227 learn optimally only under restricted conditions, with their behavior often following
228 mechanical rules that seemingly evolved to produce close-to-optimal behavior only under
229 natural conditions encountered by the species during its evolutionary history. Yet this does
230 not undermine the general conclusion that the learned behavior of animals is typically
231 adaptive, and that reinforcement learning generally shifts behavior towards the optimum.
232 Learning is adaptive precisely because animals have been fashioned by evolution actively to
233 seek out high-fitness behavioral outcomes, and to forestall activities that might negatively
234 impact their survival and reproduction (Pulliam & Dunford 1980; Staddon 2016).

235 Skinner’s (1953) bold claim that “reinforcement shapes behavior as a sculptor shapes
236 a lump of clay” somewhat exaggerates the power of reward and punishment to influence
237 behavior. In practice, evolved predispositions bias what learning takes place (a.k.a.
238 ‘constraints on learning’; Hinde & Stephenson-Hinde, 1973). Garcia and Koelling (1966)
239 famously gave rats food and then radiation that made them sick. The rats tended
240 subsequently to avoid food with that taste or smell, but struggled to learn an association
241 between other characteristics of the food and sickness, and were extremely slow to learn that
242 a sound or light predicts illness. From an evolutionary perspective, this makes sense, as
243 sickness generally results from eating rather than from noises or lights and taste is a reliable
244 indicator of a food’s nature. Likewise, Mineka and Cook (1988) demonstrated that laboratory-
245 reared, juvenile rhesus monkeys exhibit fear responses to snakes only after watching adults

246 respond fearfully to snakes. The monkeys failed to acquire fear responses to either a toy
247 rabbit or flowers after watching video sequences of conspecifics appearing to behave fearfully
248 toward them, but such video presentations were sufficient to induce fear of snake-like stimuli.
249 Interestingly, an earlier study had found that these monkeys could be socially conditioned to
250 fear other arbitrary stimuli (kitchen utensils) (Stephenson 1967). A similar study of blackbirds,
251 which learn to recognize predators through attending to the mobbing behavior of
252 conspecifics, also found that they could be conditioned to acquire a fear of arbitrary objects,
253 in this case, plastic bottles, in this manner (Vieth et al., 1980; Curio, 1988). Seemingly, the
254 monkeys have evolved a perceptual bias that enhances the salience of snake-shaped stimuli,
255 making it easier for them to learn about snakes than flowerpots, but not precluding their
256 acquiring fears of novel stimuli through observational conditioning. In comparison, the
257 blackbirds do not yet seem to have evolved this kind of perceptual bias. The adaptive value
258 of an observational-conditioning mechanism, whereby animals learn to be fearful of objects
259 or events that conspecifics fear, is easy to envisage. Sensitivity to persistent threats (e.g.
260 snakes, in the case of monkeys) can be heightened through natural selection up-regulating
261 the salience of such stimuli, yet the general observational-conditioning mechanism allows the
262 animal to learn about novel threats with rapidity and flexibility.

263 These data suggest that learned behavior is neither always optimal, nor infinitely
264 malleable through reinforcement. Animal learning typically begins with an exploratory search
265 or sampling procedure, and the initial trials may not be biased towards adaptive decisions
266 (e.g. in which direction to search of food, or which food patch to try first). However, after a
267 small number of trials the animal's behavior will adjust to the patterns of reinforcement
268 encountered. The final form of the behavior, after repeated trials, is generally highly adaptive
269 (foraging efficiency is enhanced, the best food patch is selected, dangers are avoided, and so
270 forth) (Staddon, 2016). This generic shift towards adaptive or optimal behavior as a
271 consequence of reinforcement learning we label here an *adaptive bias* (see Table 1).

272 Learning may generally be adaptive but it is not universally optimal. Evolved
273 predispositions themselves bias the learning process, a phenomenon that we refer to as an
274 *historical bias* (see Table 1). Seemingly, animals have been tuned by their evolutionary history
275 to form some associations more readily than others, or to perform particular actions in
276 particular contexts. Apparently, ancestral natural selection has fashioned dedicated learning
277 predispositions or motivational priorities tailored to the particular ecological circumstances

278 of each species. However, the generality of the observed mechanisms of learning imply that
279 the observed species-specificity is better regarded as selection tinkering with a general
280 system than as selection constructing an independent set of species-specific learning
281 processes (Bolhuis & MacPhail, 2001). *What* an animal learns may vary adaptively between
282 species, but *how* animals learn appears to be broadly similar across diverse taxa
283 (Shettleworth, 2000).

284 Nonetheless, the aforementioned literature also makes it clear that historical biases
285 exert a *probabilistic* influence on learning and are rarely hard or prohibitive constraints. This
286 is because learning by definition results from historically contingent experiences, which often
287 depend on complex interactions between many environmental factors. For example, why an
288 animal learns to forage on one specific food type instead of another may be because of the
289 idiosyncratic sequence of food items it encountered during earlier decision-making episodes.
290 Such contingencies could not have been predicted at the outset of its development because
291 of chance events experienced, the recursive interactions between learning on many
292 environmental factors, and decision-making based upon the knowledge of other individuals
293 in the local environment. This contrasts with many other sources of phenotypic plasticity that
294 can more satisfactorily be characterized as reaction norms to an environmental factor (but
295 see Sultan, forthcoming). On the one hand, this means that the existence of evolutionary
296 biases on learning cannot always prevent the coincidental development of non-adaptive
297 behavior, even under normal environmental conditions. On the other hand, it means that
298 evolutionary biases do not preclude the acquisition of entirely novel and yet adaptively biased
299 behavior, one consequence of which is that learning is a major source of behavioral
300 innovation.

301 Through learning, for instance, how to discover and exploit new foods, or devising
302 novel means to escape or avoid a threat, animals can introduce new behavior into the
303 population's repertoire. Such instances are labeled *behavioral innovations*, defined by Reader
304 & Laland, (2003, p 14) as *new or modified learned behavior not previously found in the*
305 *population*. Innovations are novel functional solutions tailored to new challenges or hitherto
306 unexploited opportunities. Not all cases of learning result in innovation, since animals
307 frequently learn associations that other members of their population have learned previously.
308 However, behavioral innovation, as currently generally understood, requires learning, since
309 otherwise innovation could not be distinguished from exploration, or from any idiosyncratic

310 or accidental behavior (Reader & Laland, 2003). Learned behavioral innovation is now
311 extensively documented in animals (Reader & Laland, 2003; Reader et al, 2016). Examples
312 include killdeer feeding on live frogs (a novel food item; Scharsien & Jackson, 1982),
313 Northwestern crows fishing for sand eels by digging in the sand at low tide (i.e. inventing
314 novel foraging technique; Robinette & Ha, 1997), and New Caledonian crows crafting hooked
315 tools for foraging (e.g. devising novel tools; St Clair et al. 2018). Learned behavioral
316 innovations are thus novel phenotypes – traits not previously observed in the lineage.
317 However, while analogous to genetic mutation in the respect that they introduce novel
318 variation, as the above examples highlight, behavioral innovations are usually not random but
319 exhibit an adaptive bias (Snell-Rood et al, 2018).

320 Innovations may also exhibit historical biases. Perhaps the most famous example of
321 an animal innovation is the invention of the habit of washing sweet potatoes in water by
322 Japanese macaques (Kawai, 1965). Subsequent research established that food washing is
323 common in several species of macaques, which means that this particular innovation involved
324 the application of an established behavior to a novel food (Reader & Laland, 2003). In fact,
325 many animal innovations fall into this category of established behavior applied in a novel
326 context, or to a novel stimulus (Reader & Laland, 2003; Reader et al, 2016). Behavioural
327 innovation through learning commonly allows the generalization or new application of a
328 behavioral phenotype to novel environments or contexts, as well as the *de novo* invention of
329 novel solutions. There is a lot of interest currently in whether organisms adapt to the rapidly
330 changing world, and the role that plasticity plays in this (Snell-Rood et al, 2018; Fox et al,
331 2019), but few articles in a recent special edition on this topic (Fox et al, 2019) even mention
332 learning. Nonetheless, this community have stressed how the processes of plasticity and
333 adaptation, traditionally considered independently of each other, need to be viewed
334 synergistically (Fox et al, 2019). Greater attention to how animals adjust to novel
335 environments through learning is surely merited.

336 Additionally, unlike genetic mutations, which generally occur equally likely across all
337 members of the population, behavioral innovations may be significantly more likely to arise
338 amongst particular classes of individuals in the population. For instance, inexperienced
339 individuals may be more likely to try novel behaviors, as in several large migratory bird species

340 where juveniles exhibit more variation in migratory routes than older individuals (Mueller et
341 al., 2013; Oppel et al., 2015; Vansteelant et al., 2017), particularly when there are few
342 experienced adults in the population (Mueller et al., 2013; Oppel et al., 2015). Although
343 juveniles suffer from higher mortality, they are thought to be more likely to discover novel
344 adaptive routes. Conversely, amongst nonhuman primates, the inventors of novel behavior
345 are usually more likely to be older, experienced individuals than youngsters (Reader & Laland,
346 2001; Kendal et al., 2005), and more commonly low-ranking than dominants (Reader & Laland,
347 2001). We characterize these patterns as manifestations of another type of developmental
348 bias, which we call an *origination bias*, since they exhibit a bias in where the innovation will
349 originate (see Table 1).

350

351 *Biases arising from social learning*

352 Animals frequently acquire knowledge and skills from conspecifics and heterospecifics,
353 including adopting innovations devised by others. Here, the mechanism of transmission can
354 influence the frequency of phenotypic variants in the next generation. This contrasts with the
355 genetic inheritance system that follows the Hardy-Weinberg principle, implying that the
356 mechanism of genetic transmission does not by itself cause changes in allele frequencies and,
357 by implication, the frequency distribution of phenotypes. There are many mechanisms that
358 cause exceptions to this principle, such as inter-species hybridization and the presence of
359 standing genetic variation. This is important for evolution, because these processes can bias
360 novel phenotypic variation towards adaptive variants (e.g. Rieseberg et al., 2003; Seehausen,
361 2014; Lai et al., 2019). Social learning is rarely considered in this context, perhaps because it
362 is not expected to cause differences between alleles in the probability that they are being
363 passed on to the offspring; it nonetheless clearly *does* affect the frequency distribution of
364 phenotypes, and typically will do so in adaptive ways. Moreover, it also provides a mechanism
365 for the inheritance of these phenotypes across generations.

366 Typically, animals do not copy at random, nor at all conceivable opportunities, nor
367 simply copy the first individual that they see (Coussi-Korbel & Fragaszy, 1995; Laland, 2004).
368 Rather, animals copy highly selectively, deploying *social learning strategies*, which are
369 *transmission biases* in copying (Boyd & Richerson, 1985; Henrich & McElreath, 2003, see Table
370 1). There are well-documented tendencies of animals to copy successful individuals and high-
371 payoff behaviour preferentially, to conform to the majority behavior (known to be adaptive

372 in spatially variable environments; Boyd & Richerson, 1985), and also to copy more when
373 uncertain or when learning asocially would be costly or difficult (Laland, 2004; Rendell et al
374 2011; Kendal et al., 2018). Strategic copying is a general feature of animal social learning,
375 whilst random copying is a comparatively rare special case (Hoppitt & Laland, 2013). Almost
376 all animal (including human) social learning is subject to a transmission bias.

377 Extensive experimental evidence has accumulated showing that animals exhibit a
378 range of non-random copying strategies, often causing a transmission bias towards the more
379 adaptive trait variants (Rendell *et al.* 2011; Kendal et al., 2018). A prime example is success-
380 biased copying. For instance, red knots are more likely to join groups of foraging conspecifics
381 that are successful at obtaining food (Bijleveld *et al.* 2015), whilst red-winged blackbirds copy
382 feeding conspecifics except when they exhibit an aversive reaction to the food (Mason &
383 Reidinger 1982). Animals may also have a copying bias towards demonstrators that are more
384 likely to be successful. For example, young female guppies have a preference for older over
385 younger female models during mate-choice copying (Amlacher & Dugatkin 2005). Similarly,
386 nine-spined sticklebacks can monitor the foraging success of other fish through observation
387 and subsequently select the richer of the alternative food patches, a mechanism that allows
388 them to converge on the optimum (Coolen et al, 2003; Kendal et al., 2009). Whether animals
389 copy, and whom they copy, can depend on their relative state of knowledge. For example,
390 less-experienced pigeons are more likely to follow more-experienced pigeons than vice versa
391 (Flack *et al.* 2012). Bats that are unsuccessful at locating food alone follow previously
392 successful bats to feeding sites, using cues indicative of recent feeding, such as defecation
393 (Wilkinson, 1992). Insects and birds too are known to copy the nest-site decisions of
394 successful conspecifics and heterospecifics (Sarin & Dukas, 2009; Pasqualone & Davis, 2011;
395 Seppanen et al 2011; Forsman & Seppanen, 2011). One consequence of the existence of these
396 transmission biases is that learned information does not spread randomly, but along specified
397 (i.e. biased) pathways.

398 A second source of transmission bias in social learning stems from the fact that the
399 learned traits an individual exhibits (unlike the individual's genes) are modified during the
400 course of its development through experience. The net consequence is that the set of
401 behavior patterns performed, and hence available to other individuals to copy, is not a
402 random set but rather a biased set of high-performance, high-payoff behaviors. This
403 mechanism leads to 'adaptive filtering' (Enquist & Ghirlanda 2007), and a transmission bias

404 to propagate adaptive knowledge. This adaptive bias associated with socially learned
405 information was demonstrated by Rendell et al (2010), who found that social learning was
406 highly adaptive under normal circumstances, where demonstrators chose to perform the
407 highest-payoff option in their repertoire. But when the adaptive filtering of demonstrators
408 was artificially switched off, such that demonstrators drew from their repertoire at random,
409 social learning was no longer advantageous.

410 Teaching (i.e. behavior that functions to facilitate learning in another individual;
411 Hoppitt et al 2008; Thornton & Raihani, 2010) is a third source of transmission bias. While
412 social learning is widespread amongst animals, teaching is rarer. Nonetheless, there is
413 evidence for teaching in a small number of species, including some ants, bees, birds and
414 meerkats, with other plausible but not yet experimentally demonstrated cases (Hoppitt et al
415 2008). Theory shows that it is only worth investing in teaching (by definition, a costly means
416 of information donation) if the adaptive advantage of the trait is large (Fogarty et al, 2011).
417 This conclusion is supported by experimental data. For example, honeybees actively
418 communicate potential nesting sites to the colony in autumn, but only after they have
419 decided that the nesting site is of appropriate quality (Seeley 1977; Seeley & Buhrman 2001).
420 As a consequence, the more adaptive behavioral choice is more readily transmitted through
421 the colony.

422 Transmission biases on the part of the receiver, adaptive filtering by the information
423 transmitter, and teaching combine to reinforce the adaptive bias generated through asocial
424 learning. They ensure that 'good information' (supporting fitness-enhancing behavior) is far
425 more likely to be propagated than 'bad information'. Social learning is applied flexibly,
426 encompassing learning from both conspecifics and heterospecifics, which means that animals
427 are not restricted to learning solely about those environmental features previously
428 encountered by their lineage (*e.g.* established predators or foods). Animals can also learn
429 about entirely novel stimuli or events, and devise appropriate responses to them (*e.g.* birds
430 learn to evade a novel predator; Davies & Welbergen, 2009; Thorogood & Davies, 2012). In
431 addition, learning can also generate opportunities for phenotypic change in the absence of
432 any immediate environmental change or stressor (such as when orangutans, *Pongo*
433 *pygmaeus*, proactively devise new food-processing techniques, social learning allows others
434 to access hitherto-unexploited foods, in this case palm heart; Russon, 2003). Thus, through

435 learning, animals can generate adaptive responses to conditions without the prior evolution
436 of dedicated traits with suitable reaction norms.

437 Various biases in the distribution of phenotypic variation that result from animal
438 learning are summarized in Table 1, together with illustrative examples. These terms are
439 neither mutually exclusive (for instance, historical, origin and transmission biases will also
440 often be adaptive) nor is our classification designed to be exhaustive (plausibly, biases may
441 exist that do not fit any of the categories in Table 1).

442
443 Table 1 about here
444

445 446 **THE EVOLUTIONARY CONSEQUENCES OF BIASED VARIATION ARISING THROUGH LEARNING**

447 Thus far, our focus has been on the learning processes responsible for the *generation of*
448 *biased phenotypic variation*. In this section, we move on to consider *the evolutionary*
449 *consequences of biased variation* arising through learning. We show that the production of
450 nonrandom phenotypic through animal learning causes biases in the rate, dynamics and
451 pattern of evolution (i.e. triggers developmentally biased evolutionary processes). In fact,
452 learning can influence evolutionary processes in at least two separate ways: either through
453 generating some phenotypic forms more readily than others (a variational bias) or through
454 generating some environmental states more readily than others (a selective bias, a.k.a. ‘niche
455 construction’).

456 457 *Learning affects evolutionary rates*

458 Theoretical work has established that learning can both speed up and slow down genetic
459 evolution (Cavalli-Sforza & Feldman 1981; Boyd & Richerson 1985; Ancel 2000; Borenstein et
460 al. 2006), consistent with the role of phenotypic plasticity in both driving and inhibiting
461 genetic evolution (e.g. Chevin et al., 2010; Edelaar et al., 2017; Ghalambor et al., 2007; Price
462 et al., 2003). Learning has an advantageous effect on adaptation in relatively quickly changing
463 environments, allowing individuals to acclimate to changes that cannot be tracked by
464 selection of genes (Cavalli-Sforza & Feldman 1981; Boyd & Richerson 1985; Todd 1991; Aoki
465 & Feldman, 2014). The benefits of learning in stationary or slowly changing environments are
466 more complex. Hinton and Nowlan (1987) suggested that learning could accelerate evolution

467 in a static environment by helping genotypes to locate otherwise difficult-to-find fitness
468 peaks. However, learning can also weaken selection by reducing phenotypic differences
469 between genotypes (Anderson 1995; Ancel 2000; Frank 2011). These seemingly conflicting
470 results follow from different theoretical assumptions (Borenstein et al. 2006; Paenke et al.
471 2007; Frank 2011). The emerging consensus is that individual learning typically slows
472 evolution in static unimodal fitness landscapes, but typically accelerates evolution in dynamic
473 or static multimodal fitness landscapes. In the latter case, the existence of multiple optima
474 usually slows down evolution as populations get trapped on suboptimal fitness peaks. By
475 generating adaptive variation and thereby smoothing the fitness landscape, learning
476 increases the likelihood of a directly increasing path of fitness to the global optimum
477 (Borenstein et al. 2006; Mills and Watson 2006; Frank 2011).

478 *Learning can generate ‘plasticity first’ evolution*

479 The ‘plasticity first hypothesis’ is “a mechanism of adaptive evolution in which environmental
480 perturbation leads, via phenotypic plasticity, to ... a novel developmental variant (i.e., trait)
481 that ... is subsequently refined through ‘genetic accommodation’” (Levis & Pfennig, 2016,
482 p564). Here, ‘genetic accommodation’ means the refinement or stabilization of the trait
483 through selection of underlying genetic variation. Where learning accelerates evolution,
484 phenotypic change (a.k.a. ‘phenotypic accommodation’) precedes, and then facilitates,
485 genetic adaptation by modifying selection on genetic variation (West-Eberhard, 2003; Levis
486 & Pfennig, 2016). Conversely, when sources of learning are reliably present (e.g. the
487 availability of a parent when a chick hatches), social learning can buffer selection on genetic
488 variation that would otherwise lead to genetic adaptation, as selection cannot favor a trait
489 that compensates for the loss of developmental input that is reliably present (Griffiths 2002).
490 However, in many cases this buffering will not be perfect, and hence will not preclude
491 selection of alleles that increase the probability of producing, or the performance of, the
492 learned phenotype, a form of genetic accommodation known as ‘genetic assimilation’ (West-
493 Eberhard, 2003). Indeed, (particularly stochastic) learning can facilitate genetic adaptation
494 through producing adaptively biased phenotypic variation that changes the selection on
495 genotypes (Borenstein et al. 2006).

496 There is empirical evidence that learning can generate plasticity first evolution
497 (Whitehead et al, 2019). For instance, killer whale (*Orcinus orca*) populations exhibit culturally

498 transmitted specializations on particular prey resources (e.g. fish, dolphins, pinnipeds). These
499 dietary traditions have favored population-specific genes influencing morphology and
500 digestion, giving rise to different killer whale “ecotypes” (Foote et al., 2016; Hoelzel & Moura,
501 2016). Population-genomic studies confirm that these lineages have diverged genetically, and
502 that functional genes associated with digestion differ between ecotypes, suggesting that this
503 is an instance of genetic assimilation (Foote et al., 2016; Hoelzel & Moura, 2016). Seemingly,
504 the ecotypes arose through culturally mediated specialization in matrilineal groups, which
505 later developed reproductive barriers (Riesch et al 2012). Here, learning and social
506 transmission appears to have triggered the evolution of multiple lineages considered to be
507 undergoing speciation, influencing the direction of adaptive evolution.

508 Social learning can also trigger genetic adaptation in other traits (Whitehead et al,
509 2019). For instance, in some fruit flies, fishes, birds and mammals, the choice of mating
510 partner is influenced by the mate-choice decisions of other individuals (mate-choice copying).
511 This propagates mating preferences over short periods, such as a season, yet experimental
512 data and population-genetic models demonstrate that it can strongly influence the sexual
513 selection of male traits (Gibson et al., 1991; Kirkpatrick & Dugatkin, 1994; Nöbel et al., 2018).
514 Birdsong provides another illustration of how animal culture can be consequential for genetic
515 evolution, affecting patterns of migration and assortative mating, and facilitating speciation
516 (Beltman et al, 2003; Lachman & Slater 1999). There is evidence for reed warbler learning
517 driving the evolution of plumage patterns in cuckoos (Davies & Welbergen, 2009; Thorogood
518 & Davies, 2012), and for social learning reducing genetic diversity in socially structured whale
519 populations (Whitehead, 1998). Finally, extensive empirical evidence now implicates learning
520 in mate choice, sexual selection, and reproductive isolation, where experimental studies
521 clearly show that learning imposes biases on signal evolution (ten Cate & Rowe, 2007;
522 Verzijden et al., 2012). Hence, the theoretical expectation of genetic accommodation and
523 genetic assimilation in response to animal learning is supported by a small and growing
524 number of studies.

525 In these examples, learning is not just changing the rate of evolution but co-directing
526 the outcome. It was the culturally transmitted dietary tradition of each killer whale population
527 that caused the natural selection of genes for a morphology and digestive physiology that
528 matches their learned dietary habits. Similar points can be made with respect to the mate
529 choice, bird song, and plumage evolution examples.

530 Learning can also modify natural selection and trigger plasticity first evolution through
531 bringing about physical changes in environments, or through learned habitat choice. Over the
532 past 50,000 years, humans have spread from Africa around the globe, begun to exploit
533 agriculture, witnessed rapid increases in densities as a direct consequence, domesticated
534 hundreds of species of plants and animals and, by keeping animals, experienced a new
535 proximity to animal pathogens. Each of these events represents a major transformation in
536 human selection pressures, recognized though substantive genetic change in human
537 populations, and each is a self-induced change in environmental conditions (Laland et al,
538 2010). Humans have modified selection through their learning and culture, for instance by
539 dispersing into new environments with different climatic regimes, by devising agricultural
540 practices or domesticating livestock, and causing extinctions and dramatic shifts in
541 community structure (Boivin et al, 2016). It is now well-established that dairy farming created
542 the selection pressure that led to the spread of alleles for adult lactase persistence (Gerbault
543 et al, 2011). Similarly, agricultural practices, such as cultivating yams, appear to have
544 inadvertently promoted the spread of malaria in some West African populations, leading to
545 the selection of the HbS allele which confers some resistance to malaria in the heterozygote
546 form, but leads to Sickle-cell anaemia in homozygotes (Durham, 1991). The same practices
547 appear also to have favored high copy number of the salivary amylase (AMY1) gene that
548 facilitate the breakdown of the excess starch in agricultural diets (Perry et al, 2007). Again,
549 such examples illustrate how learning can affect evolutionary outcomes, and not just rates.
550 Producing and consuming milk and alcohol has selected for alleles for adult lactose absorption
551 and alcohol dehydrogenase, whilst the agricultural practices that led to greater consumption
552 of starch, protein, lipids and phosphate have selected for alleles that metabolize these foods
553 (Laland et al 2010). Given that both niche construction and learning are ubiquitous in animals,
554 it would seem highly likely that the learned environmental modification of other animals has
555 similar consequences, although well-researched examples are rare.

556 Learned human activities are also driving evolutionary responses in other animals.
557 Recent studies have demonstrated strong phenotypic changes in organisms in response to
558 urban and other anthropogenic environments, ranging from supplemental feeding affecting
559 beak shape in garden birds, to earthworms and insects evolving tolerance of pollutants
560 (Palkovacs et al, 2012; Alberti, 2015; Alberti et al, 2017; Sullivan et al, 2017). Anthropogenic
561 change studies suggest plasticity is important to evolutionary responses (Snell-Rood et al,

562 2018; Fox et al, 2019), and the field could benefit from greater consideration of the role
563 played by animal learning in these adaptive responses.

564

565 *Learning can generate ‘adaptation’ without natural selection*

566 It is often claimed that natural selection is the only process that can systematically lead to
567 increments in fitness across generations, but adaptive evolution can also result from
568 phenotypic plasticity, habitat choice and niche construction (Edelaar & Bolnick, 2019). This is
569 an important point, since it is widely, and mistakenly, believed that incremental
570 improvements in a trait over generations, with corresponding enhancements in fitness, can
571 only arise through the natural selection of genetic variation.

572 Experimental evidence reveals that social learning (a form of adaptive phenotypic
573 plasticity) can cause offspring fitness to be higher than that of their parents, even in novel
574 habitats. This is, at least to some extent, recognized for humans where, for example,
575 agricultural advances (irrigation methods, fertilizers, breeding programs, insecticides, etc)
576 have repeatedly underpinned population growth (i.e. increased absolute fitness). However,
577 evidence is starting to emerge for similar processes operating in other animals. For instance,
578 Jesmer et al (2018) showed that bighorn sheep and moose adjust to novel environments in
579 the course of several generations, through a process of learning and cultural transmission.
580 These animals generally migrate through exploiting the high-quality forage manifest in
581 “green-wave surfing” (van der Graaf et al. 2006), which requires possessing the requisite
582 knowledge of where and when to find high-quality food; a typical needle-in-a-haystack
583 problem. The study shows that after translocation to a novel environment, the animals do
584 not show their typical migratory behavior. Apparently, past natural selection did not enable
585 individuals to find the optimal foraging strategy in a single lifetime. Rather, the study shows
586 an iterative increase over generations in the fraction of translocated populations that
587 migrate, and that – due to these movements – their whereabouts increasingly overlaps with
588 the phenology of suitable habitat. The bighorn sheep acquire and accumulate this
589 ‘adaptation’ to a novel habitat not through natural selection of genes, but through learning.
590 Seemingly, individual learning allows each generation to exploit high-quality forage more
591 effectively than their parental generation, and social learning allows these iterative
592 improvements to be transmitted to the rest of the group, including the next generation. Here

593 improvements in the adaptive fit between individuals and their environment accumulate over
594 generations.

595 The semi-natural experiment of translocated sheep is unique in its temporal and
596 spatial scale, but similar processes likely operate widely. Sasaki & Biro (2017) demonstrate
597 the process of incremental increase in movement efficiency (which in the wild should
598 correlate with fitness) amongst gps-tagged homing pigeons, which arises through ‘cumulative
599 culture’. Similarly, sticklebacks have been found to exhibit a hill-climbing learning strategy of
600 selectively adopting the food-patch choices of fish more successful than them (Coolen et al,
601 2003; Kendal et al., 2009). While these studies do not demonstrate increases in fitness across
602 generations, they do show that adaptive phenotypic plasticity mechanisms exist that mimic
603 ‘adaptation’ without the natural selection of genetic variation.

604 The evolutionary relevance of such mechanisms will not go unnoticed to those familiar
605 with the Price equation. In addition to the selective term, the Price equation contains a term
606 that captures whether the next offspring systematically differ from their parents, which can
607 be rendered positive by adaptive phenotypic plasticity (Edelaar & Bolnick, 2019). Many open
608 questions remain as to the extent of such phenomena among different taxa and in the wild,
609 but there can be little doubt that they have far-reaching consequences for evolution (Berdahl
610 et al. 2018; Edelaar & Bolnick, 2019; Brakes et al., 2019).

611

612 *Learning can help explain the existence of maladaptation*

613 Without gainsaying the general conclusion that learning typically generates adaptive
614 phenotypic variation, there are restricted and reasonably well-understood circumstances in
615 which learning can generate, propagate and maintain maladaptive behavior. It is commonly
616 assumed that natural selection will shape organisms to reflect environmental conditions, but
617 cultural transmission can allow animal behavior to become partially disconnected from their
618 environments. For instance, Bluehead wrasse *Thalassoma bifasciatum* mating sites cannot be
619 predicted from knowledge of environmental resource distributions (Warner, 1988, 1990).
620 Rather, removal and replacement experiments demonstrate that mating sites are maintained
621 as traditions, with young fish and newcomers adopting the mating sites of residents (similar
622 findings are observed in French grunts; Helfman & Schultz, 1984). Under restricted
623 circumstances arbitrary and even maladaptive information can spread, or initially-but-no-
624 longer-adaptive traits can be preserved (Richerson & Boyd, 2005). Traditions are maintained

625 as Nash equilibria, in which it rarely pays any individual to abandon the tradition unilaterally;
626 each is forced to do what others are doing, leaving populations locked into conventions that
627 track changing environments only slowly. In animals that aggregate for protection, like
628 shoaling fishes, taking the same route as others to a resource, such as a food site, offers
629 fitness benefits even when the route is sub-optimal, since going it alone is dangerous (Laland
630 & Williams 1998). This behavior, and other conformist tendencies (Day et al, 2001), help
631 explain the traditions observed in natural fish populations. In the case of the wrasse, initially
632 adaptive pathways were rendered suboptimal by environmental change, but the population
633 remained locked into a difficult-to-change convention. Another case is informational
634 cascades, where individuals base behavioral decisions on prior decisions of others (Giraldeau
635 et al. 2002). For instance, among lekking sage grouse *Centrocercus urophasianus*, the
636 decisions of females using social information to decide with whom to mate were less closely
637 correlated with male traits indicating quality than were the decisions of females making their
638 own judgments about males (Gibson et al. 1991). These instances are a form of historical bias,
639 although distinct from genetically evolved biases.

640 Theoretical studies suggest further ways by which learning can generate
641 maladaptation. As described above, reinforcement learning typically comprises an
642 exploratory search (information gathering) followed by decision-making (information
643 exploitation). However, the two stages are not mutually exclusive: rather reinforcement
644 learning often entails both processes operating simultaneously, or in repeated sequence,
645 allowing animals to gain information from a decision-making experience and to refine their
646 decision in the light of updated knowledge, in an iterative manner (Sutton & Barto, 1998). As
647 a consequence, biases in decision-making can bias the acquisition of knowledge, and vice-
648 versa (Hertwig & Erev, 2009; March, 1996). This sequential, path-dependent nature of animal
649 learning can be a crucial determinant of the behavior manifest in the population. For instance,
650 March (1996) demonstrated formally how animal learning could lead to risk-averse behavior
651 when its expected reward was lower than a risky alternative. Animals must strike a balance
652 between exploration and exploitation, which typically leads them to reduce the rate of
653 sampling of apparently inferior options. As a result, risky alternatives, which usually give a
654 poor reward but occasionally give a very good reward, are interpreted as worse than they
655 actually are, leading individuals to over-exploit safe alternatives (March, 1996; Denrell, 2007;
656 empirical examples of learning-induced risk aversion are reviewed in Weber et al. 2004, whilst

657 similar ‘peak shift’ phenomena are described by ten Cate & Rowe, 2007). Outside of humans,
658 cases of the cultural transmission or maintenance of maladaptive behavior appear rare: more
659 commonly, social learning strategies allow individuals to revisit superior options, even despite
660 repeated personal failures, circumventing potentially maladaptive risk aversion (Rendell et al,
661 2010; Arbilly et al. 2011).

662

663 **CONCLUSIONS**

664 Developmental biases remain contentious in evolutionary biology, in part because of the
665 claim that developmental processes may impose direction on adaptive evolution and/or
666 account for adaptation – a claim that ostensibly challenges the widespread belief that natural
667 selection does all of the explanatory work in accounting for adaptive evolution (Maynard
668 Smith et al, 1985; Arthur, 2004; Brakefield 2006; Laland et al 2015; Uller et al, 2018). Given
669 that developmental processes themselves evolve, it is perhaps tempting to respond to such
670 claims by regarding the bias as itself a product of natural selection, a stance that might (at
671 least in some researcher’s eyes) restore natural selection’s privileged status. However, at
672 least in the case of developmental biases that result from learning, such a response appears
673 inadequate.

674 Whilst the general capacity to learn has clearly evolved through natural selection, the
675 above literature leaves no doubt that the content of learning (the precise associations
676 formed, and the behavioral phenotypes that result) is rarely, if ever, specified by ancestral
677 selection. As documented above, animals are able to learn to exploit foods, or evade threats,
678 even when they are novel and have not been encountered by the lineage, often acquiring
679 them from other species. Moreover, such learning is frequently evolutionarily consequential.
680 In such instances, the traditional line that ancestral natural selection favored genes or
681 genotypes with reaction norms that allow animals to adjust their phenotypes to
682 environmental inputs appears overly simplistic. In learning, ancestral selection has conferred
683 on animals an unusually rich form of plasticity that appears to possess some level of
684 autonomy to generate ‘adaptive fit’ within an individual as a result of its experience, through
685 an ontogenetic selective process that in many respects resembles natural selection (Plotkin
686 1994; Snell-Rood et al 2018).

687 Above we present clear evidence that (i) individual learning commonly allows animals
688 to generate novel and adaptively biased behavior tuned to the local environment, (ii) social

689 learning further biases the propagation of these phenotypic improvements to other
690 individuals, (iii) this learning can modify selection and affect evolutionary dynamics, and (iv)
691 culture sometimes allows animals to improve mean fitness iteratively across generations in a
692 process that resembles ‘adaptation’. While these observations are well-recognized within the
693 animal learning literature, they remain poorly appreciated within the evolutionary biology
694 community. For instance, in an otherwise admirable book, Bonduriansky and Day (2018) claim
695 that “only cognitively sophisticated animals” could learn adaptive solutions to novel
696 circumstances, and suggest that maladaptive behavior would spread just as readily as
697 accessing a novel food – claims that are badly out of touch with the literature. There is now
698 extensive data showing that, through learning, a very broad range of species of animals
699 regularly invent and propagate adaptive behavior that introduces novelty into phenotype
700 space.

701 The significance of these findings may be profound. Recently, the suggestion
702 (associated with the extended evolutionary synthesis) that “novel phenotypic variants will
703 frequently be directional and functional” (Laland et al, 2015, p10) excited considerable
704 contention (e.g. Charlesworth et al, 2017). Yet we suspect to readers familiar with the above
705 referenced literature on animal learning, the assertion would not appear unreasonable.
706 Almost all animal innovation, and almost all socially transmitted knowledge and skills, are
707 likely to be adaptive, and those cases that are not can be predicted a priori. Animal learning
708 is an important addition to a range of phenomena that are now broadly accepted to
709 undermine the classic view that adaptation arises solely from natural selection acting on
710 random genetic variation.

711 The reason that learning evolved to become an unusually rich form of adaptive
712 plasticity is precisely because of the benefits to animals of being able to respond
713 appropriately to unanticipated eventualities (Plotkin, 1994; Staddon, 2016). The term
714 ‘evolvability’ attempts to capture the capacity of a system for adaptive evolution. There are
715 diverse definitions of evolvability, many inherently assuming that adaptive evolution requires
716 genetic change. However, we embrace the broader definition provided by Kirschner &
717 Gerhart (1998) – “an organism’s capacity to generate heritable phenotypic variation” – in the
718 context of which it is possible to recognize how learning (a source of novel, frequently
719 heritable, phenotypic variation) contributes to evolvability. Through behavioral innovation
720 and social learning, animals can adjust to environments phenotypically, sometimes buffering

721 genetic responses, but perhaps more commonly triggering genetic accommodation. The
722 impact of learning on evolvability is further suggested by recent studies showing a robust
723 relationship between innovativeness and speciosity in birds (Nicolakkis et al, 2003; Sol et al
724 2005; Lefebvre et al., 2016). These data reinforce the aforementioned evidence that learning
725 can impose direction on adaptive evolution, affecting evolutionary rates, and influencing the
726 probability of populations reaching global optimum.

727 There are many open questions ripe for investigation. For instance, do biases that
728 arise through learning differ from other developmental biases, for instance, in the level of
729 integration or diversity of phenotypes generated? Are there different patterns of bias
730 associated with individual and social learning? Will success-based copying generate more
731 rapid convergence through genetic accommodation on fitness peaks than conformist social
732 learning, which is prone to historical lags? Further investigation is required, but there is
733 already sufficient data to suggest that phenotypic accommodation through learning may be
734 common, rapid and powerful, particularly in vertebrates, and that developmentally biased
735 evolutionary processes resulting from learning may be a truly fundamental feature of animal
736 evolution.

737

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743

744 **REFERENCES**

745 Alberti, M. (2015). Eco-evolutionary dynamics in an urbanizing planet. *Trends in Ecology &*
746 *Evolution*, 30, 114-126.

747 Alberti, M., Correa, C., Marzluff, J.M., Hendry, A.P., Palkovacs, E.P., Gotanda, K.M., ... & Zhou,
748 Y. (2017). Global urban signatures of phenotypic change in animal and plant
749 populations. *Proceedings of the National Academy of Sciences*, 201606034.

- 750 Allen, J., Weinrich, M., Hoppitt, W. & Rendell, L. (2013) Network-based diffusion analysis
751 reveals cultural transmission of lobtail feeding in humpback whales. *Science* 340: 485-
752 488.
- 753 Amlacher, J. & Dugatkin, L.A. (2005) Preference for older over younger models during mate-
754 choice copying in young guppies. *Ethology Ecology & Evolution*, 17: 161-169
- 755 Ancel, L. (2000). Undermining the Baldwin expediting effect: does phenotypic plasticity
756 accelerate evolution? *Theor. Popul. Biol.* 58: 207–319.
- 757 Anderson, R. (1995). Learning and evolution: a quantitative genetics approach. *J. Theor. Biol.*
758 175: 89–101.
- 759 Aoki K & Feldman MW (2014) Evolution of learning strategies in temporally and spatially
760 variable environments: A review of theory. *Theor. Pop. Biol.* 91: 3-19
- 761 Arbilly M, Motro U, Feldman MW, & Lotem A (2011) Evolution of social learning when high
762 expected payoffs are associated with high risk of failure. *J. Roy. Soc. Interface*, 8: 1604-
763 1615.
- 764 Arthur, W. (2004) The effect of development on the direction of evolution: toward a twenty-
765 first century consensus. *Evol. Dev.* 6: 282–288
- 766 Beltman, J., Haccou, P. & Ten Cate, C. (2003) The impact of learning foster species' song on
767 the evolution of specialist avian brood parasitism. *Behav. Ecol.* 14: 917-923.
- 768 Berdahl, A.M., Kao, A.B., Flack, A., Westley, P.A.H., Codling, E.A., Couzin, I.D., Dell, A.I. & Biro,
769 D. (2018) Collective animal navigation and migratory culture: from theoretical models
770 to empirical evidence. *Philosophical Transactions of the Royal Society B: Biological*
771 *Sciences*, 373: 20170009.
- 772 Bijleveld, A.I., van Gils, J.A., Jouta, J. & Piersma, T. (2015) Benefits of foraging in small groups:
773 an experimental study on public information use in red knots *Calidris canutus*.
774 *Behavioural Processes*, 117: 74-81.
- 775 Boivin NL, Zeder MA, Fuller DQ et al (2016) Ecological consequences of human niche
776 construction: examining long-term anthropogenic shaping of global species
777 distributions. *Proc. Natl. Acad. Sci. USA* 113(23): 6388-96
- 778 Bolhuis, J. J. & MacPhail, E. M. (2001). A critique of the neuroecology of learning and memory.
779 *Trends in Cognitive Sciences*, 5, 426–433.
- 780 Bonduriansky R & Day T (2018) *Extended Heredity*. Princeton University Press.

781 Borenstein, E., I. Meilijson, and E. Ruppin. (2006). The effect of phenotypic plasticity on
782 evolution in multipeaked fitness landscapes. *Journal of Evolutionary Biology* 19:1555–
783 1570.

784 Boyd R & Richerson PJ (1985). *Culture and the Evolutionary Process*. Chicago University Press.

785 Brakefield, P. M. (2006) Evo-devo and constraints on selection. *Trends Ecol. Evol.* 21: 362–
786 368.

787 Brakes P et al. (2019) Animal cultures matter for conservation. *Science* 363(6431): 1032-4

788 Breland K & Breland M (1961). The misbehavior of organisms. *Am. Psychol.* 16: 661-4

789 Cavalli-Sforza LL & Feldman MW (1981). *Cultural Transmission and Evolution*. Princeton
790 University Press

791 Charlesworth, D., N. H. Barton & B. Charlesworth (2017) The sources of adaptive variation.
792 *Proceedings of the Royal Society B-Biological Sciences* 284: 20162864.

793 Chevin, L. M., Lande, R., & Mace, G. M. (2010). Adaptation, plasticity, and extinction in a
794 changing environment: towards a predictive theory. *PLoS biology*, 8(4), e1000357.

795 Chivers, D. P. & Smith, R. J. F. (1995) Chemical recognition of risky habitats is culturally
796 transmitted among flathead minnows, *Pimephales promelas* (Osteichthyes,
797 Cyprinidae). *Ethology* 99: 286-296.

798 Coolen, I., Day, R.L. & Laland, K.N. (2003). Species difference in adaptive use of public
799 information in sticklebacks. *Proceedings of the Royal Society London B* 270: 2413–
800 2419.

801 Coussi-Korbel, S. and Fragaszy, D. M. (1995) On the relation between social dynamics and
802 social learning. *Anim. Behav.* 50(6): 1441-53.

803 Curio, E. (1988). Cultural transmission of enemy recognition by birds. In: *Social Learning:
804 Psychological and Biological Perspectives*, B. G. Galef and T. R. Zentall, Eds. Hillsdale,
805 NJ: Erlbaum. Pp. 75–97.

806 Davies, N. B. & Welbergen, J. A. (2009) Social transmission of a host defense against cuckoo
807 parasitism. *Science* 324: 1318-1320.

808 Day, R., MacDonald, T., Brown, C., Laland, K.N. & Reader, S.M. (2001). Interactions between
809 shoal size and conformity in guppy social foraging. *Animal Behaviour* 62: 917–925.

810 Denrell J. (2007). Adaptive Learning and Risk Taking. *Psychological Review.* 114: 177-187.

811 Dickinson A (1980) *Contemporary animal learning theory*. Cambridge University Press

812 Dukas R & Ratcliffe JM (eds.) (2009) *Cognitive Ecology II*. University of Chicago Press.

813 Durham WH (1991) *Coevolution. Genes, Culture and Human Diversity*. Stanford University
814 Press.

815 Edelaar P & Bolnick DI (2019) Appreciating the multiple processes increasing individual or
816 population fitness. *Trends Ecol. Evol.* <https://doi.org/10.1016/j.tree.2019.02.001>

817 Edelaar, P., Jovani, R., & Gomez-Mestre, I. (2017). Should I change or should I go? Phenotypic
818 plasticity and matching habitat choice in the adaptation to environmental
819 heterogeneity. *The American Naturalist*, 190(4), 506-520.

820 Enquist, M. & Ghirlanda, S. (2007) Evolution of social learning does not explain the origin of
821 human cumulative culture. *Journal of Theoretical Biology*, 246: 129-135.

822 Flack, A., Pettit, B., Freeman, R., Guilford, T. & Biro, D. (2012) What are leaders made of? The
823 role of individual experience in determining leader–follower relations in homing
824 pigeons. *Animal Behaviour*, 83: 703-709.

825 Fogarty, L, Strimling P. & Laland K.N. (2011). The evolution of teaching. *Evolution*. 65: 2760-
826 2770.

827 Foote, A. D. *et al.* (2016) Genome-culture coevolution promotes rapid divergence of killer
828 whale ecotypes. *Nat. Commun.* 7: 11693

829 Forsman, J. and Seppanen, J. (2011). Learning what (not) to do: testing rejection and copying
830 of simulated heterospecific behavioural traits. *Anim. Behav.* 81: 879–883.

831 Fox RJ, Donelson JM, Schunter C, Ravasi T, Gaitán-Espitia JD. 2019 Beyond buying time: the
832 role of plasticity in phenotypic adaptation to rapid environmental change. *Phil. Trans.*
833 *R. Soc. B* 374: 20180174. <http://dx.doi.org/10.1098/rstb.2018.0174>

834 Frank SA (2011). Natural selection II. Developmental variability and evolutionary rate. *J. Ev.*
835 *Biol.* 24: 2310-2320.

836 Garcia, J. & Koelling, R. A. (1966). Prolonged relation of cue to consequence in avoidance
837 learning. *Psychonomic Science*, 4: 123–124.

838 Gerbault, P., A. Liebert, Y. Itan, A. Powell, M. Currat, J. Burger, D. M. Swallow, and M. G.
839 Thomas. (2011). Evolution of lactase persistence: an example of human niche
840 construction. *Philosophical Transactions of the Royal Society B* 366:863–877.

841 Ghalambor, C. K., McKay, J. K., Carroll, S. P., & Reznick, D. N. (2007). Adaptive versus non -
842 adaptive phenotypic plasticity and the potential for contemporary adaptation in new
843 environments. *Functional ecology*, 21(3), 394-407.

844 Gibson, R. M., Bradbury, J. W. & Vehrencamp, S. L. (1991) Mate choice in lekking sage grouse
845 revisited: the roles of vocal display, female site fidelity, and copying. *Behav. Ecol.* 2:
846 165-180.

847 Giraldeau, L. A., Valone, T. J. and Templeton, J. J. (2002). Potential disadvantages of using
848 socially acquired information. *Phil. Trans. R. Soc. Lond. B* 357: 1559–1566.

849 Goodall, J. (1986) *The chimpanzees of Gombe: patterns of behavior*. Harvard University Press,
850 Cambridge, MA.

851 Griffiths, P.E. (2002) What Is Innateness? *The Monist*, 85, 70-85.

852 Helfman G. S., Schultz, E. T. (1984). Social transmission of behavioural traditions in a coral reef
853 fish. *Anim. Behav.* 32: 379–384.

854 Henrich, J. and McElreath, R. (2003). The evolution of cultural evolution. *Evol. Anthropol.* 12:
855 123–135.

856 Hertwig R & Erev I. (2009). The description-experience gap in risky choice. *Trends Cog. Sci.*
857 13:517-523.

858 Heyes, C.M. (1994) Social learning in animals: categories and mechanisms. *Biological Reviews*,
859 69: 207-231.

860 Hinde RA (1982) *Ethology*. Glasgow. Fontana.

861 Hinde RA & Stephenson-Hinde (1973) Constraints on learning. Limitations and
862 Predispositions. Academic Press

863 Hinton GE & Nowlan SJ (1987) How learning can guide evolution. *Complex Systems* 1: 495-
864 502.

865 Hoelzel, A. & Moura, A. (2016) Killer whales differentiating in geographic sympatry facilitated
866 by divergent behavioural traditions. *Heredity* 117: 481-482.

867 Hoppitt, W. & Laland, K.N. (2013) *Social learning: an introduction to mechanisms, methods*
868 *and models*. Princeton University Press, Princeton, NJ.

869 Hoppitt, W.J.E., Brown, G.R., Kendal, R., Rendell, L., Thornton, A., Webster, M.M. & Laland,
870 K.N. (2008) Lessons from animal teaching. *Trends in Ecology & Evolution*, 23: 486-493.

871 Huey, R. B., Hertz, P. E., & Sinervo, B. (2003). Behavioral drive versus behavioral inertia in
872 evolution: a null model approach. *The American Naturalist*, 161(3), 357-366.

873 Jesmer BR et al (2018) Is ungulate migration culturally transmitted? Evidence of social
874 learning from translocated animals. *Science* 361: 1023-5

875 Kamil AC (1983). Optimal foraging theory and the psychology of learning. *American Zoologist*
876 23: 291-302

877 Kawai, M. (1965). Newly-acquired pre-cultural behavior of the natural troop of Japanese
878 monkeys on Koshima islet. *Primates* 6: 1–30.

879 Kendal, R.L., Coe, R.L. & Laland, K.N. (2005). Age differences in neophilia, exploration and
880 innovation in family groups of Callitrichid monkeys. *American Journal of Primatology*
881 66: 167–188.

882 Kendal, J.R., Rendell, L., Pike, T.W. & Laland, K.N. (2009). Nine-spined sticklebacks deploy a
883 hill-climbing social learning strategy. *Behavioural Ecology* 20: 238–244.

884 Kendal RL, Boogert NJ, Rendell L, Laland KN, Webster M & Jones PL. (2018) Social learning
885 strategies: bridge-building between fields. *Trends in Cognitive Sciences* 22(7):651-665

886 Kirschner M & Gerhardt J 1998. Evolvability. *Proc. Natl. Acad. Sci. USA* 95(15): 8420-7

887 Kirkpatrick, M. and L. A. Dugatkin. (1994). Sexual selection and the evolutionary effects of
888 copying mate choice. *Behav. Ecol. Sociobiol.* 34: 443–449.

889 Kirkpatrick K & Hall G (2004) Learning and Memory. In Bolhuis JJ & Giraldeau LA (eds) *The*
890 *Behavior of Animals: Mechanisms, Function, and Evolution*. Blackwell.

891 Krebs, J. R., A. Kacelnik, and P. Taylor. (1978). Test of optimal sampling by foraging great tits.
892 *Nature* 275:27-31.

893 Lachlan, R. F. and Slater, P. J. B. (1999). The maintenance of vocal learning by gene-culture
894 interaction: the cultural trap hypothesis. *Proc. R. Soc. Lond, B* 266: 701–706.

895 Lai, Y.-T., Yeung, C.K.L., Omland, K.E., Pang, E.-L., Hao, Y., Liao, B.-Y., Cao, H.-F., Zhang, B.-W.,
896 Yeh, C.-F., Hung, C.-M., Hung, H.-Y., Yang, M.-Y., Liang, W., Hsu, Y.-C., Yao, C.-T., Dong,
897 L., Lin, K., and Li, S.-H. (2019) Standing genetic variation as the predominant source for
898 adaptation of a songbird. *Proceedings of the National Academy of Sciences* 116: 2152-
899 2157.

900 Laland, K.N. (2004). Social learning strategies. *Special edition of Learning and Behavior on*
901 *Studies of Social Learning and Imitation*. Galef, B.G. Jr. & Heyes, C.M. (eds). 32: 4–14.

902 Laland, K.N. & Williams, K. (1998). Social transmission of maladaptive information in the
903 guppy. *Behavioural Ecology* 9: 493–499.

904 Laland, K.N., Odling-Smee, F.J. & Myles, S. (2010). How culture has shaped the human
905 genome: Bringing genetics and the human sciences together. *Nature Reviews Genetics*
906 11: 137–148.

907 Laland KN, Uller T, Feldman MW, Sterelny K, Müller GB, Moczek A, Jablonka E & Odling-Smee
908 FJ (2015) The extended evolutionary synthesis: its structure, assumptions and
909 predictions. *Proc R Soc B* 282: 20151019.

910 Laland KN, Odling-Smee J & Feldman MW. (In Press) Understanding niche construction as an
911 evolutionary process. In: Uller T & Laland KN (eds.) *Evolutionary Causation. Biological
912 and Philosophical Reflections*. MIT Press: Cambridge, Mass.

913 Lefebvre, L., P. Whittle, E. Lascaris, and A. Finkelstein. (1997). Feeding innovations and
914 forebrain size in birds. *Animal Behaviour* 53:549–560.

915 Lefebvre, L., S. Ducatez, and J. N. Audet. (2016). Feeding innovations in a nested phylogeny of
916 Neotropical passerines. *Philosophical Transactions of the Royal Society of London B*,
917 371: 20150188.

918 Levis, N. A. & Pfennig, D. W. (2016) Evaluating ‘plasticity-first’ evolution in nature: key criteria
919 and empirical approaches. *Tr. Ecol. Evol.* 31: 563-574.

920 Love AC (ed) (2015) *Conceptual Change in Biology*. Springer.

921 Mackintosh N (1974) *The psychology of animal learning*. Academic Press

922 March, J. G. (1996). Learning to be risk averse. *Psychological Review*, 103, 309–319.

923 Mason, J.R. & Reidinger, R.F. (1982) Observational learning of food aversions in red-winged
924 blackbirds (*Agelaius phoeniceus*). *Auk*, 99: 548-554.

925 Maynard-Smith, J., R. Burian, S. Kauffman, P. Alberch, J. Campbell et al., (1985)
926 Developmental constraints and evolution. *Q. Rev. Biol.* 60: 265–287.

927 Maynard-Smith J. (1987) When learning guides evolution. *Nature* 329: 761-2

928 Mills, R., and R. A. Watson (2006) On crossing fitness valleys with the Baldwin effect, pp. 493–
929 499 in *Proceedings of the Tenth International Conference on the Simulation and
930 Synthesis of Living Systems*. MIT Press, Cambridge, MA.

931 Mineka, S. and Cook, M. (1988). Social learning and the acquisition of snake fear in monkeys.
932 In: *Social Learning: Psychological and Biological Perspectives*, B. G. Galef and T. R.
933 Zentall, Eds. Hillsdale, NJ: Lawrence Erlbaum. Pp. 51–73.

934 Moczek AP (2008). On the origins of novelty in development and evolution. *BioEssays* 30(5):
935 432-47

936 Moczek AP, Sears KE, Stollewerk et al. (2015) The significance and scope of evolutionary
937 developmental biology: a vision for the 21st century. *Evolution & Development*. 17(3):
938 198-219

939 Mueller T, O’Hara RB, Converse SJ, Urbanek RP, Fagan WF (2013) Social learning of migratory
940 performance. *Science* 341:999-1002.

941 Muñoz, M. M., & Losos, J. B. (2018). Thermoregulatory behavior simultaneously promotes
942 and forestalls evolution in a tropical lizard. *The American Naturalist*, 191(1), E15-E26.

943 Nicolakakis, N., D. Sol, and L. Lefebvre. (2003). Behavioral exhibity predicts species richness in
944 birds, but not extinction risk. *Animal Behaviour* 65:445–452.

945 Nöbel S, Allain M, Isabel G, Danchin E. (2018) Mate copying in *Drosophila melanogaster* males.
946 *Anim Behav* . 141:9–15.

947 Odling-Smee, F.J., Laland, K.N. & Feldman, M.W. (2003). *Niche Construction. The Neglected*
948 *Process in Evolution*. Monographs in Population Biology 37. Princeton University Press.

949 Opiel, S., Dobrev, V., Arkumarev, V., Saravia, V., Bounas, A., Kret, E., Veleviski, M., Stoychev,
950 S. & Nikolov, S.C. (2015) High juvenile mortality during migration in a declining
951 population of a long-distance migratory raptor. *Ibis*, 157, 545-557.

952 Paenke, I., B. Sendhoff, and T. J. Kawecki, (2007) Influence of plasticity and learning on
953 evolution under directional selection. *Am. Nat.* 170: E47–E58.

954 Palkovacs, E. P., Kinnison, M. T., Correa, C., Dalton, C. M. & Hendry, A. P. (2012). Fates
955 beyond traits: ecological consequences of human-induced trait
956 change. *Evolutionary Applications*, 5, 183–191.

957 Pasqualone, A. A. and Davis, J. M. (2011). The use of conspecific phenotypic states as
958 information during reproductive decisions. *Anim. Behav.* 82: 281-4

959 Perry, G. H., N. J. Dominy, K. G. Claw, A. S. Lee, H. Fiegler, R. Redon, J. Werner, et al. (2007).
960 Diet and the evolution of human amylase gene copy number variation. *Nature*
961 *Genetics* 39:1256–1260.

962 Plotkin HC (1994) Darwin machines and the nature of knowledge. Penguin

963 Price, T. D., Qvarnström, A., & Irwin, D. E. (2003). The role of phenotypic plasticity in driving
964 genetic evolution. *Proceedings of the Royal Society of London. Series B: Biological*
965 *Sciences*, 270(1523), 1433-1440.

966 Pulliam H & Dunford C (1980) Programmed to Learn. Columbia University Press.

967 Reader SM, Laland KN. (2001) Primate innovation: sex, age and social rank differences. *Int. J.*
968 *Primatol.* 22, 787–805.

969 Reader, S.M. & Laland, K.N. (2002). Social intelligence, innovation and enhanced brain size in
970 primates. *Proceedings of the National Academy of Sciences USA* 99: 4436–4441.

- 971 Reader SM, Laland KN. (2003) Animal innovation. Oxford, UK: Oxford University Press.
- 972 Reader SM, Flynn E, Morand-Ferron J & Laland KN (2016) Innovation in animals and humans:
973 understanding the origins and development of novel and creative behaviour. *Phil.*
974 *Trans. R. Soc. B* Vol 371: 1690
- 975 Rendell, L., Boyd, R., Cownden, D., Enquist, M., Eriksson, K., Feldman, M.W., Fogarty, L.,
976 Ghirlanda, S., Lillicrap, T. & Laland, K.N. (2010) Why copy others? Insights from the
977 social learning strategies tournament. *Science*, 328: 208-213.
- 978 Rendell, L., Fogarty, L., Hoppitt, W.J.E., Morgan, T.J.H., Webster, M.M. & Laland, K.N. (2011)
979 Cognitive culture: theoretical and empirical insights into social learning strategies.
980 *Trends in Cognitive Sciences*, **15**, 68-76.
- 981 Rescorla, RA (1988) Pavlovian Conditioning. *Am. Psychol* 43(3): 151-160
- 982 Rescorla, R. A. & Wagner, A. R. (1972). A theory of Pavlovian conditioning: Variations in the
983 effectiveness of reinforcement and nonreinforcement. In A. H. Black & W. F. Prokasy
984 (Eds.), *Classical Conditioning II: Current Research and Theory* (pp. 64–99). New York:
985 Appleton.
- 986 Richerson, P. J. & Boyd, R. (2005). *Not by Genes Alone: How Culture Transformed Human*
987 *Evolution*. Chicago: Chicago University Press.
- 988 Riesch, R., Barrett-Lennard, L. G., Ellis, G. M., Ford, J. K. B. & Deecke, V. B. (2012) Cultural
989 traditions and the evolution of reproductive isolation: ecological speciation in killer
990 whales? *Biol. J. Linn. Soc.* 106: 1-17.
- 991 Rieseberg, L.H., Raymond, O., Rosenthal, D.M., Lai, Z., Livingstone, K., Nakazato, T., Durphy,
992 J.L., Schwarzbach, A.E., Donovan, L.A., and Lexer, C. (2003) Major ecological transitions
993 in wild sunflowers facilitated by hybridization. *Science* 301:1211-1216.
- 994 Robinette, R. L. & Ha, J. C. (1997). The significance of fishing by northwestern crows. *Wilson*
995 *Bulletin*, 109, 748–749
- 996 Russon, A. E. (2003) Innovation and creativity in forest-living rehabilitant orang-utans *In:*
997 *Animal Innovation* (eds Reader, S. M. & Laland, K. N.). 279-306 Oxford University Press,
998 New York, NY.
- 999 Sargeant, B. L. & Mann, J. (2009) Developmental evidence for foraging traditions in wild
1000 bottlenose dolphins. *Anim. Behav.* 78: 715-721.

1001 Sarin, S. and Dukas, R. (2009). Social learning about egg laying substrates in fruit flies. *Proc. R.*
1002 *Soc. Lond. B* 276:4323–4328.

1003 Sasaki, T. & Biro, D. (2017) Cumulative culture can emerge from collective intelligence in
1004 animal groups. *Nature Communications*, 8, 15049.

1005 Schardien, B. J. & Jackson, J. A. (1982). Killdeers feeding on frogs. *Wilson Bulletin*, 94, 85–87.

1006 Seehausen, O. (2004). Hybridization and adaptive radiation. *Trends in Ecology & Evolution* 19:
1007 198-207.

1008 Seeley, T. (1977) Measurement of nest cavity volume by the honey bee (*Apis mellifera*).
1009 *Behavioral Ecology and Sociobiology*, 2, 201-227.

1010 Seeley, T.D. & Buhrman, S.C. (2001) Nest-site selection in honey bees: how well do swarms
1011 implement the "best-of-n" decision rule? *Behavioral Ecology and Sociobiology*, 49,
1012 416-427.

1013 Seppanen, J., Forsman, J., Monkkonen, M., et al. (2011) New behavioural trait adopted or
1014 rejected by observing heterospecific tutor fitness. *Proc. R. Soc. B* 278:1736–1741.

1015 Shettleworth, S. (2000). Modularity and the evolution of cognition. In C. Heyes & L. Huber
1016 (Eds.), *The Evolution of Cognition* (pp. 43–60). Cambridge, MA: MIT Press.

1017 Skinner BF (1938) The behavior of organisms. Appleton Century Crofts.

1018 Skinner BF 1953. Science and Human Behavior. The Free Press: New York, NY.

1019 Snell-Rood EC, Kobiela ME, Sikkink KL, Shepherd AM. (2018) Mechanisms of plastic rescue in
1020 novel environments. *Ann. Rev. Ecol. Evol. Syst.* 49, 331 - 354.

1021 Sol, D., D. G. Stirling, and L. Lefebvre. (2005) Behavioral drive or behavioral inhibition in
1022 evolution: subspecific diversification in Holarctic passerines. *Evolution* 59:2669–2677.

1023 Staddon J.E.R. (2007) Is Animal Learning Optimal?. In: *Constructal Theory of Social*
1024 *Dynamics*. Springer, Boston, MA

1025 Staddon JER (2016) *Adaptive Behavior and Learning*. 2nd Edition. Cambridge University
1026 Press.

1027 St Clair, JJH, Klump, BC, Sugasawa, S, Higgott, CG, Colegrave, N & Rutz, C (2018) 'Hook
1028 innovation boosts foraging efficiency in tool-using crows' *Nature Ecology and*
1029 *Evolution*, vol 2, pp 441–444. DOI: 10.1038/s41559-017-0429-7

1030 Stephens, D. W. & Krebs, J. R. (1986). *Foraging Theory*. Princeton, NJ: Princeton University
1031 Press.

- 1032 Stephenson G (1967) Cultural acquisition of a specific learned response among rhesus
1033 monkeys. In D Starck, R Schneider & H Kuhn (eds.) Progress in Primatology. Stuttgart:
1034 Gustav Fisher Verlag.
- 1035 Sullivan, A. P., Bird, D. W., & Perry, G. H. (2017). Human behaviour as a long-term ecological
1036 driver of non-human evolution. *Nature Ecology & Evolution*, 1, 0065.
- 1037 Sultan, S. (forthcoming) Genotype-environment interaction and the unscripted reaction
1038 norm. In: Evolutionary Causation, edited by KN Laland and T Uller. MIT Press,
1039 Cambridge, MA.
- 1040 Sutton, R. S., & Barto, A. G. (1998). Reinforcement learning: An introduction. Cambridge, MA:
1041 MIT Press.
- 1042 ten Cate C & Rowe C (2007) Biases in signal evolution: learning makes a difference. Trends
1043 Ecol. Evol. 22(7): 380-7
- 1044 Thorndike, E. L. (1898) Animal intelligence: An experimental study of the associative
1045 processes in animals. Psychological Review Monographs, 2 (Whole No. 8).
- 1046 Thornton A & Raihani NJ (2010) Identifying teaching in wild animals. Learning & Behavior
1047 38(3): 297-309
- 1048 Thorogood, R. & Davies, N. B. (2012) Cuckoos combat socially transmitted defenses of reed
1049 warbler hosts with a plumage polymorphism. *Science* 337: 578-580.
- 1050 Todd, P. M. G. (1991) Exploring adaptive agency II: simulating the evolution of associative
1051 learning, pp. 306–315 in From Animals to Animals: Proceedings of the First
1052 International Conference on Simulation of Adaptive Behavior, edited by J. M. S.
1053 Wilson. MIT Press, Cambridge, MA.
- 1054 Uller T, Moczek AP, Watson RA, Brakefield PM, Laland KN. 2018. Developmental bias and
1055 evolution: A regulatory network perspective. *Genetics* 209 (4): 949-966
- 1056 van der Graaf, A.J., Stahl, J., Klimkowska, A., Bakker, J.P. & Drent, R.H. (2006) Surfing on a
1057 green wave: how plant growth drives spring migration in the barnacle goose. *Ardea*,
1058 94, 567-577.
- 1059 Vansteelant, W.M.G., Kekkonen, J. & Byholm, P. (2017) Wind conditions and geography shape
1060 the first outbound migration of juvenile honey buzzards and their distribution across
1061 sub-Saharan Africa. Proceedings. Biological sciences, 284, 20170387.
- 1062 Verzijden MN, ten Cate C, Servedio MR, Kozak GM, Boughman JW & Svensson EI (2012) The
1063 impact of learning on sexual selection and speciation. Trends. Ecol. Evol. 27(9): 511-9

1064 Vieth W, Curio E & Ernst U (1980) The adaptive significance of avian mobbing. III. Cultural
1065 transmission of enemy recognition in blackbirds: Cross-species tutoring and
1066 properties of learning. *Anim. Behav.* 28: 1217-29

1067 Warner, R. R. (1988) Traditionality of mating-site preferences in a coral reef fish. *Nature* 335:
1068 719–721.

1069 Warner, R. R. (1990) Male versus female influences on mating-site determination in a coral-
1070 reef fish. *Anim. Behav.* 39: 540–548.

1071 Weber E, Shafir S, & Blais A (2004) Predicting Risk Sensitivity in Humans and Lower Animals:
1072 Risk as Variance or Coefficient of Variation. *Psych. Rev.*, **111**, 430-445. (doi:
1073 10.1037/0033-295X.111.2.430)

1074 West-Eberhard, M. J. (2003) *Developmental plasticity and evolution*. (Oxford University Press,
1075 Oxford, UK.

1076 Whalen A, Cownden D & Laland KN (2015) The learning of action sequences through social
1077 transmission. *Animal Cognition* DOI 10.1007/s10071-015-0877-x.

1078 Whitehead, H. (1998) Cultural selection and genetic diversity in matrilineal whales. *Science*
1079 282: 1708-1711.

1080 Whitehead H, Laland KN, Rendell L, Thorogood R & Whiten A (2019) The reach of gene-culture
1081 coevolution in animals. *Nature Communications*. 10: 2405

1082 Whiten, A., Ayala, F.J., Feldman, M.W. & Laland, K.N. (2017) The extension of biology through
1083 culture. *Proceedings of the National Academy of Sciences* 114: 7775-7781.

1084 Wilkinson, G. (1992). Information transfer at evening bat colonies. *Anim. Behav.* 44: 501–518.

1085 Wilkinson, A., Kuenstner, K., Mueller, J., & Huber, L. (2010). Social learning in a non-social
1086 reptile (*Geochelone carbonaria*) *Biology Letters*, 6 (5), 614-616

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Category	Examples
<p>Adaptive bias</p> <p><i>Developmental variation biased towards adaptive outcomes</i></p>	<ul style="list-style-type: none"> ● Reinforcement learning (Staddon, 2007) ● Adaptive filtering and biased cultural transmission (Enquist & Ghirlanda, 2007; Rendell et al. 2010) ● Teaching behavior in ants, bees, meerkats and pied babblers (Hoppitt et al 2008; Thornton & Raihani, 2010)
<p>Historical bias</p> <p><i>Developmental variation biased by historical legacy (e.g. ancestral selection, or tradition)</i></p>	<ul style="list-style-type: none"> ● Rats avoid taste or smell of poisoned food, but are slow to learn that a sound or light predicts illness (Garcia & Koelling 1966). ● Lab-reared rhesus monkeys learn a fear of snakes more readily than a fear of arbitrary objects, after watching conspecifics behaving fearfully (Mineka and Cook,1988; but see Stephenson 1967). ● Raccoons could not be conditioned to pick up coins and place them in a money box for a food reward (Breland & Breland, 1961).
<p>Origination bias</p> <p><i>Developmental variation biased in its origination</i></p>	<ul style="list-style-type: none"> ● Juveniles of some migratory birds exhibit more route variation than older individuals (Mueller et al., 2013; Oppel et al., 2015; Vansteelant et al., 2017) ● The inventors of novel behavior are usually more likely to be experienced individuals than youngsters in nonhuman primates (Reader & Laland, 2001; Kendal et al, 2005), and more commonly low-ranking than dominants (Reader & Laland, 2001). ● Innovativeness of monkey species was predicted by their reliance on extractive foraging (Kendal et al, 2005)
<p>Transmission bias</p> <p><i>Biased transmission of developmental variation, with some forms being propagated more readily than others</i></p>	<ul style="list-style-type: none"> ● Red-winged blackbirds copy feeding conspecifics except when they show an aversive reaction to food (Mason & Reidinger 1982). ● Bats unsuccessful at locating food alone follow successful bats to feeding sites, using cues indicative of feeding, e.g. defecation (Wilkinson, 1992). ● Insects and birds copy the nest-site decisions of successful conspecifics and heterospecifics (Sarin & Dukas, 2009; Pasqualone & Davis, 2011; Seppanen et al 2011; Forsman & Seppanen, 2011).
<p>Variational bias</p> <p><i>Developmental processes bias evolutionary processes through generating some phenotypic forms more readily than others</i></p>	<ul style="list-style-type: none"> ● Culturally transmitted dietary traditions in killer whale have favored population-specific genes influencing morphology and digestion, (Foote et al., 2016; Hoelzel & Moura, 2016). ● Mate choice copying influences sexual selection of male traits (Gibson et al., 1991; Kirkpatrick & Dugatkin, 1994; Nöbel et al., 2018). ● Reed warbler learning drives the evolution of plumage patterns in cuckoos (Davies & Welbergen, 2009; Thorogood & Davies, 2012).
<p>Selective bias</p> <p><i>Developmental processes bias evolutionary processes through generating some environmental states more readily than others (niche construction)</i></p>	<ul style="list-style-type: none"> ● Dairy farming created selection alleles for adult lactase persistence (Gerbault et al, 2011) ● Agricultural practices (e.g. cultivating yams) have inadvertently promoted the spread of malaria in some populations, leading to selection of the HbS allele which confers resistance (Durham, 1991). ● The farming and consumption of starchy foods has favored high copy number of AMY1, which facilitates the breakdown of the excess starch in agricultural diets (Perry et al, 2007).

1091 **Table 1.** Categories of developmental bias generated by learning, with examples (see text for
1092 details).