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Effects of learning on evolution: robustness, innovation and speciation

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All animals are highly plastic and rely on the modulation of gene action, physiology and behaviour to continuously modify their phenotypes. Compared to other types of plasticity, learning, defined as the internal representation of novel information, allows animals to better exploit environmental features unique to certain times and places. This distinctive property of learning gives it an enormous potential to promote evolution through increased robustness, innovation and speciation rate. First, learning can enhance robustness because it allows individuals to adopt new resources and avoid novel threats. Empirical examples include the modification of egg-laying timing and nesting site selection in birds and of egg-laying substrate choice in insects. Second, learning can lead to innovation because it often has an exploratory stage that can lead to the discovery and refinement through trial and error of new, fitness-enhancing features. The best examples are cases of social learning that lead to the exploitation of novel food sources followed by genetic changes that optimize use of the new diet. Finally, learning can increase the levels of assortative mating that lead to population divergence either when young imprint on their parents or when individuals restrict their mate choice criteria based on interactions with prospective mates. While the notion that learning can have strong effects on evolution is backed by theory and some data, we currently lack broad experimental evidence to support that claim.

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The notion that plasticity in general, and learning in particular, have been major factors driving evolution has a long history. Baldwin (1896), Morgan (1896) and Osborn (1896) independently articulated the idea in 1896 and it has been discussed extensively over the past 116 years (Baldwin 1902; Simpson 1953; Robinson & Dukas 1999; West-Eberhard 2003; Bateson & Gluckman 2011). In spite of this extensive record, central issues concerning plasticity, learning and evolution are not fully resolved. I will thus begin this review with a brief introduction on the role of variation in organismal life and its relation to the evolution of adaptive plasticity and learning. The rest of my review will focus on three central means by which learning can promote evolution.

All organisms encounter variation in the quantity and quality of resources that affect fitness. The basic genetic architecture of all organisms is based on modulation, meaning that there is continuous adjustment of activity based on a variety of inputs and feedbacks. Modulation is necessary for key life functions including development, growth, reproduction, achieving optimal internal environment, seeking external resources and responding to external abiotic and biotic factors. Through the modulation of gene action, physiology and behaviour, all organisms continuously modify

their phenotypes. Perhaps the best studied example for plasticity is bacterial chemotaxis (Fig. 1a), for which the molecular mechanisms from nutrient sensing through information processing to moving are thoroughly understood at the molecular level (Koshland 1980; Berg 2003; Eisenbach & Lengeler 2004; Wadhams & Armitage 2004; Baker et al. 2006). For further discussion of plasticity, see Snell-Rood (2013).

While plasticity is ubiquitous in all living things, learning, which is a special type of plasticity, is more restricted in its taxonomic distribution. Learning involves internal representations of new information obtained from the current external and internal environments. While other types of plasticity allow individuals to execute behaviour in response to given information based on evolved innate mechanisms, learning is unique because it allows individuals to internally represent both currently perceived information and new motor patterns. In animals with nervous systems, rich internal representations of novel information are produced via neuronal modulation. Compared to other types of plasticity, learning allows animals to better exploit environmental features unique to certain times and places, to respond to a larger variety of features, and to increase their behavioural repertoire. For example, a bee can acquire a neuronal representation of the spatial features unique to her nest location, record the spatial location, odour and colour of her preferred flowers, and learn new motor patterns for optimizing the handling of these flowers (Fig. 1b, c). In many species, individuals gain from learning to identify their parents,

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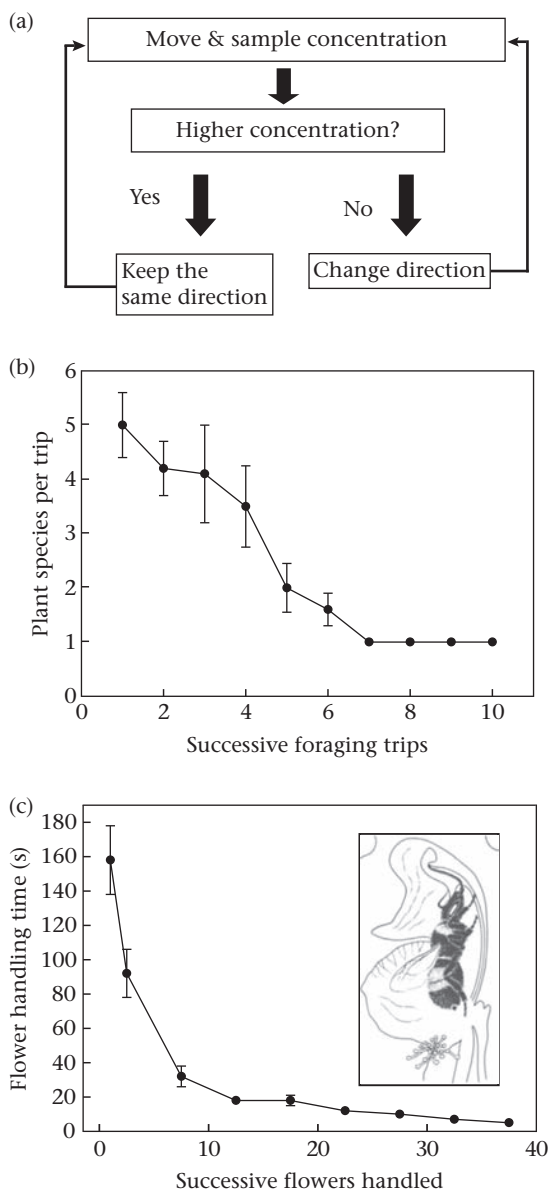


Figure 1. (a) All organisms are plastic. Illustrated here is chemotaxis, a well-studied plastic mechanism for seeking food (shown) and avoiding danger (not shown). Compared to other types of plasticity, learning involves internal representations of new information, which open a variety of new opportunities. For example, (b) a bee (*Bombus vagans*) encountering a variety of novel plants in bloom (and no competition) starts by sampling many of these plants, but quickly restricts her visits to the most rewarding one (data from Heinrich 1979). (c) Bees (*Bombus fervidus*) can also learn new motor skills for handling unusual novel flowers, such as those of monkshood (*Aconitum napellus*) shown in the inset (data and inset from Laverty & Plowright 1988), and the spatial location of their preferred flower patches in relation to their nest (not shown).

neighbours, competitors, potential mates and offspring (Dukas 1998, 2008b, 2009b). Because learning allows individuals to take advantage of novel environmental features, it has enormous potential to influence evolution, which is the main focus of this review.

ROBUSTNESS

Robustness can be defined as the ability to succeed under a wide range of conditions (see Merriam-Webster 2012). Because learning enables individuals to adjust rapidly to novel conditions, it can

enhance their robustness and hence survival and reproduction in new and changing environments (Baldwin 1896; Morgan 1896; Osborn 1896; Robinson & Dukas 1999). The unique quality of learning is that it allows individuals to acquire novel information. This can help individuals to adopt new resources and avoid novel threats. Some features such as landmarks can be learned instantly. Other tasks, like motor learning or choosing among alternative food types differing in quality, require a trial-and-error process during which feedback from previous trials is recorded and used to improve performance in subsequent trials. That is, without learning, individuals facing novel conditions may either die or fail to reproduce. With learning, individuals can explore ways to maximize survival and reproduction in novel settings, and respond to either novel threats or reproductive failure by adjusting their behaviour based on specific information and feedback acquired in their current setting. The three sections below respectively illustrate cases where individuals rely on pertinent information to adjust subsequent decisions, learn in order to either reduce the chance of subsequent failure or increase the probability of further success, and learn to seek cues indicating parental success.

Timing of Egg Laying in Birds

Young females in many bird species face the challenge of timing their egg laying so that the nestling period, which occurs a few weeks later, will coincide with peak food availability. Failing to accurately predict the peak in food availability would result in poor provisioning and reduced nestling survival. Theoretically, the best possible solution is for the birds to rely on the available cues in year 1, such as the recent ambient temperature (Visser et al. 2009), new leaf development and food availability. The birds can then assess the degree of synchronization between peak food and their nestling feeding period and, based on this information, adjust the timing of egg laying in year 2 (Nager & van Noordwijk 1995). For example, suppose that the best predictor for peak food is the appearance of leaf buds, but that the time interval between the appearance of leaf buds and peak food varies between habitats. Furthermore, suppose that the long-term average period between leaf buds and peak food across habitats is 3 weeks. Birds can then time their first egg laying assuming that peak food occurs 3 weeks following the appearance of leaf buds. If birds in habitat 1 experience peak food 2 rather than 3 weeks following leaf buds, they can lay eggs earlier in relation to leaf buds in the following year. On the other hand, if birds in habitat 2 experience peak food 4 rather than 3 weeks following leaf buds, they can lay eggs later in relation to leaf buds in the following year. That is, rather than continue to miss peak food in successive years, individuals can enhance their breeding success over time by learning to adjust to the local settings.

Grieco et al. (2002) suggested that blue tits, *Cyanistes caeruleus*, rely on such learning to improve the timing of their egg laying. They provided food to all birds during the egg-laying stage, to ensure that all females had ample resources for egg laying. Then, they gave food only to the supplemented birds during the nestling period while letting the control birds rely on naturally available food, predominately caterpillars. While the control birds experienced the natural peak in food availability, the supplemented birds experienced an artificial late peak in food availability.

In the following year, the control birds showed no change in the degree of synchronization between the peak nestling period and peak natural caterpillar availability while the food supplemented birds responded to their previous year experience of experimentally induced late peak food by laying eggs later. As a result, the experimental birds were less synchronized with the naturally available food than the control birds (Fig. 2a). This suggested that the experimental birds relied on learning to adjust timing of egg

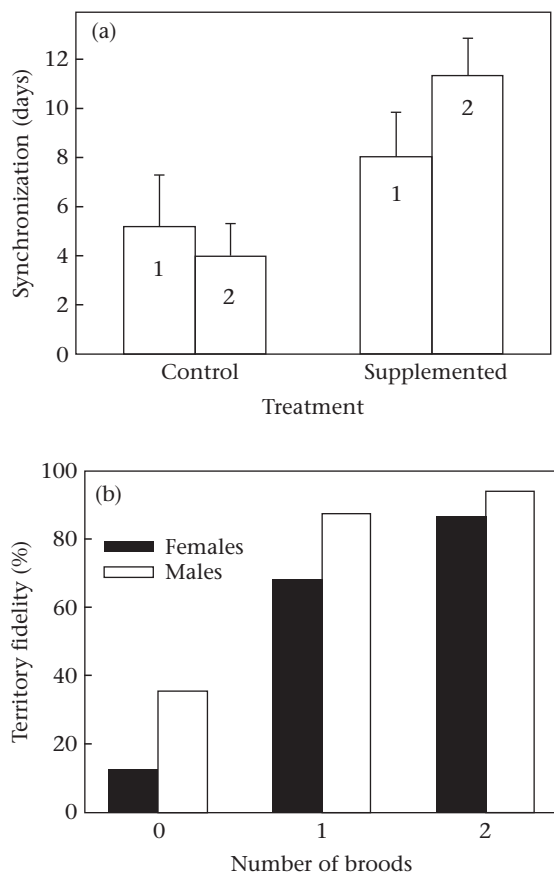


Figure 2. (a) Degree of synchronization (mean \pm SE, where 0 indicates the highest synchronization and 12 indicates the lowest synchronization), calculated as the difference in days between the peak nesting period of blue tits and peak local caterpillar availability in years 1 and 2 (shown as numbers inside the bars). Birds that were food supplemented, and thus experienced an artificial late peak of food availability during the nesting period in year 1, laid eggs significantly later in year 2 than in year 1 (data from Grieco et al. 2002). (b) Territory fidelity of female and male prothonotary warblers that were experimentally manipulated to have 0, 1 or 2 successful broods in the previous year (data from Hoover 2003).

laying. In general, such adjustment to local conditions via learning can increase survival and reproduction of individuals in new and changing environments. That is, learning can make individuals more robust to change. While the timing of egg laying is crucial for nesting success, choosing the proper site is as important, and learning can play a major role in site selection as well.

Nest Site Selection in Birds

Many birds consider food availability and predation risk when choosing their nest location. Individuals can rely on the available information to choose a site perceived to be of high quality. Their own experience in nesting, however, may be the best source of relevant information. Hence individuals that succeed in their nesting attempt should return to the same site in successive years while individuals that fail should change locations. In some species, a simple plastic rule that does not involve learning is sufficient for nest site selection: stay if successful, move if not. However, in migratory species that spend the nesting season in one geographical region and spend the rest of the year elsewhere, spatial learning and superb long-term memory are crucial for relocating the nest site from the previous year.

Many studies indicate that birds that successfully rear a brood are more likely to renest in the same territory than are birds that

fail (Greenwood & Harvey 1982). Experimental manipulations of nesting success provided direct evidence that birds indeed modify their nest site selection based on their own nesting success. Hoover (2003) randomly assigned prothonotary warblers, *Protonotaria citrea*, nesting in nestboxes to one of three treatments: zero, one or two broods. Nestboxes were mounted on greased conduit (to protect them from raccoons) for zero, one or two broods per pair, respectively, within a season. The zero brood treatment failed in all their nesting attempts owing to the naturally high predation rates by raccoons, *Procyon lotor*, at the area. The treatments of one and two broods succeeded in rearing one and two broods, respectively, as their nestboxes were protected from raccoons. The experimentally manipulated nesting success strongly affected the warblers' frequency of returning to the same territory in the subsequent year (Fig. 2b).

Haas (1998) provided similar experimental data for American robins, *Turdus migratorius*, and brown thrashers, *Toxostoma rufum*. Intriguingly, in the prothonotary warbler study, males whose nesting attempts failed were more likely to return to the same site in the following year if they had successful neighbours rather than failed neighbours, perhaps because the males monitored neighbouring territories, where they may have fathered offspring through extrapair copulations (Hoover 2003). In short, learning in the context of nest site selection can increase animal reproduction in new and changing environments.

Substrate and Nest Site Selection in Insects

The trial-and-error learning in the bird examples above, requires that individuals receive feedback about their nesting success. Many animals, however, do not have the opportunity to acquire such feedback either because they do not provide parental care (e.g. many lizards and amphibians) or because their life span is too short (e.g. most insects). Optimal nesting decisions may involve factors that an individual cannot evaluate owing to perceptual limitations, the lack of pertinent information, or because some factors influence offspring survival after the parents have either left the nest area or died. For example, although mould and parasites are the major causes of mortality in pre-adult stages of ground-nesting solitary hymenoptera (Batra 1984), it is unknown to what extent females perceive and attempt to avoid these dangers. Animals that do not have a chance to learn from their own nesting success, however, can still rely on a type of learning that may be called implicit social learning (Dukas 2010). In many animals, egg-to-adult survival is very low. Hence a newly eclosed adult can assume that its mother has made some successful decisions resulting in it being alive. Such decisions should be adopted by the young adult where possible and relevant (Stamps et al. 2009a).

A key decision in many insects involves the choice of egg-laying substrate. Many insects eclose at or near the substrate chosen by their mothers, or their pupal cases retain the odour from that substrate (Barron & Corbet 1999). Because a young female knows that the substrate from which she has eclosed is successful, she may learn the substrate's characteristics and seek similar substrates for her own egg laying. Such substrate learning is well known in insects (Jaenike 1983; Stamps & Blozis 2006). Newly eclosed adults may learn a variety of other features that reflect their mother's successful decisions. As far as I know, however, this possibility has not been studied. By learning to follow apparently successful choices made by their mothers rather than some innate preferences, individuals may enhance reproduction in new and changing environments. Overall though, the most obvious decision a newly eclosed adult can make, which may not require learning, is to simply stay in the same site because it has been successful, perhaps owing to factors that the newly eclosed adult cannot assess. Indeed

philopatry is well known in ground-nesting bees and wasps (Batra 1984; Potts & Willmer 1997) and probably occurs in many other insects as well.

The above examples illustrate how learning can enhance animal robustness: without learning, individuals may simply fail and the population goes extinct under novel conditions. With learning, individuals can either learn from cues indicating past success and failure, or through exploration of new ways for maximizing survival and reproduction in changed and novel environments. Lower rates of extinction and higher rates of reproduction enhance the probability that populations evolve in new environments (e.g. Baldwin 1902; Simpson 1953; Robinson & Dukas 1999; Price et al. 2003; Bateson & Gluckman 2011).

INNOVATION

Innovation means making changes in something established (Stevenson 2010). Compared to other types of plasticity, learning opens up a variety of opportunities to innovate because tasks that animals learn must be acquired by each individual in each generation. First, the mere fact that numerous individuals in a given population go through an exploratory stage suggests that such a massive search, recurring with every generation, would lead to the discovery and adoption of new, fitness-enhancing features. Second, by definition, trial-and-error learning means that naïve individuals make changes in their behaviour based on their own experience in their present settings. Hence, if a given task (e.g. finding the best food source) has a new optimum in a new environment (e.g. settings with novel food sources), individuals may find that optimum via trial-and-error learning. That is, learning is a mechanism that naturally leads to innovation.

Some modifications to behaviour that enhance performance in a changed environment can be readily acquired via individual learning. More drastic changes, however, may be attained rarely or perhaps by only a single individual. Such unique innovations may only have a negligible impact on evolution if they disappear when their innovators die. Fortunately, in species with social learning, individuals may learn new behaviours from innovators, allowing innovations to spread within populations and over successive generations (Boyd & Richerson 1985; Zentall & Galef 1988; Reader & Laland 2003). Hence the combination of individual learning leading to innovation and social learning, which facilitates the spread of innovations, may have been a major factor in evolution. A possible example involves black rats, *Rattus rattus*, adopting a novel habitat in Israel.

After the establishment of Israel in 1948, Israelis initiated massive reforestation efforts involving primarily Jerusalem pine trees (*Pinus halepensis*). Some time later, black rats invaded these forests and started to nest in the trees and feed on pine seeds, a highly nutritious yet mostly unexploited food in this region, which contains neither squirrels nor other arboreal mammals that feed on pine seeds (Aisner & Terkel 1992). Accessing the pine seeds, which are well protected inside pinecones, is a challenging task. Indeed, experiments with naïve rats indicated that none mastered the task of feeding on pinecones. On the other hand, pups reared with foster mothers familiar with the stripping techniques for opening pinecones readily acquired this efficient handling method (Aisner & Terkel 1992). It is likely that one or a few out of many black rats exploring the newly created pine habitat discovered, through trial and error, the efficient stripping technique for opening pinecones, transmitted this information to their offspring via social learning, and thus opened up a novel habitat for exploitation by their descendants.

The black rats' move to the new pine habitat where they continue to live and feed has probably led to some genetic changes.

Unfortunately, possible evolution following innovation has not been studied in the black rats. However, evolution following dietary change attributed to innovation and social learning is known in humans, in which some groups, including agricultural societies and hunter gatherers in arid environments, have adopted a diet high in starch. The amylase enzyme in the human mouth hydrolyses starch. More copies of the human salivary amylase gene, *AMY1*, lead to higher concentrations of amylase in the saliva and, presumably, more efficient starch digestion. Perry et al. (2007) found that human populations with a higher reliance on starch in their diet have more copies of *AMY1* than human groups with low-starch diets (Fig. 3). The analyses by Perry et al. (2007) indicate that the switch to a high-starch diet, presumably due to innovation and social learning, was followed by the evolution of additional copies of *AMY1*. Another well-studied case of evolution following dietary change attributed to innovation and social learning in humans involves the convergent evolution of the ability to digest milk as adults following the innovative cultivation of cows and the addition of cow's milk to the diet in human populations in Africa and Europe (Tishkoff et al. 2007).

SPECIATION

Speciation is the separation of populations originally able to interbreed into independent evolutionary units that can no longer interbreed owing to accumulated genetic differences (Allaby 2009). Speciation is important because it produces new gene complexes capable of ecological shifts and of advancing evolution (Mayr 1963). Learning can increase speciation rate through several processes. First, both increased robustness and enhanced ability to innovate, as discussed in the two sections above can, respectively, contribute to lower probabilities of extinction in new or changed environments, and to the exploitation of new resources. I know of no studies directly linking enhanced robustness owing to learning to higher speciation rates. Indirect evidence, however, links larger brain size to lower mortality rates in birds (Sol et al. 2007), and higher success rates in novel environments in birds and mammals (Sol et al. 2002, 2008). As for innovation, comparative data in birds indicate a positive correlation between the frequency of reported novel feeding behaviours and the number of species per taxon (Nicolakakis et al. 2003). In this section, however, I will focus on the

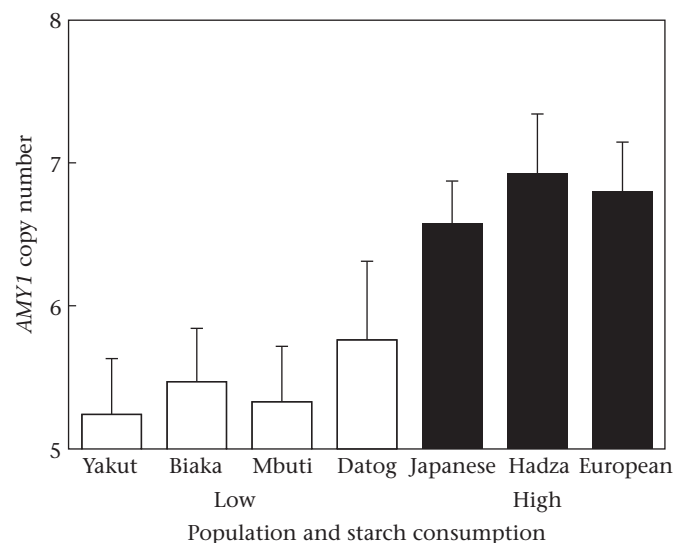


Figure 3. Human populations that rely more heavily on starch have more copies (mean \pm SE) of the salivary amylase gene, *AMY1* (data from Perry et al. 2007).

direct effects learning may have on population divergence. I will first discuss cross-generational interactions involving juveniles learning from their biological or step parents and then review data on learning within generations pertaining to either males or females interacting with prospective mates.

In many vertebrates, young learn parental characteristics during an early, sensitive period and later seek such features in sexual partners, a process termed imprinting (Lorenz 1937; Bateson 1966; Immelmann 1972). Theoretically, imprinting could accelerate population divergence (Immelmann 1975; Irwin & Price 1999; Lachlan & Servedio 2004; Verzijden et al. 2012). The most convincing data linking imprinting to speciation are for indigobirds (*Vidua* spp.), which is an unusual lineage of brood parasites. Young males in this group learn to mimic their host species' song while young females learn to prefer features of their host species' nest and conspecific males that mimic the song of their foster fathers (Fig. 4; Payne 1973; Payne et al. 2000). Such imprinting seems to have been the major factor causing recent adaptive radiation in sympatry in this group (Sorenson et al. 2003), although other factors that enhance divergence play a role as well (Balakrishnan et al. 2009). A few other taxa in which learning of parental features by young may influence speciation include Galapagos finches, *Geospiza fortis* (Grant & Grant 2009), Lake Victoria cichlid fish, *Pundamilia pundamilia* and *Pundamilia nyererei* (Verzijden & ten Cate 2007), and sticklebacks (*Gasterosteus* spp.) (Kozak et al. 2011).

Most animals never encounter their parents, and hence cannot acquire sexual preferences across generations. Such animals, however, still have ample opportunities for learning in the context

of mate choice, which could influence speciation. Recent data, mostly from insects (but see King & West 1983; Patricelli et al. 2002; Hebets 2003; Magurran & Ramnarine 2004), indicate that individuals refine their courtship and mate choice based on information about, and feedback from, locally available mates. In fruit flies, male *Drosophila melanogaster* show robust associative learning of the cues associated with receptive females (Siegel & Hall 1979; Ejima et al. 2005). While the males initially indiscriminately court conspecific females and females of the sister species, *Drosophila simulans*, both rejection by the heterospecific females and acceptance by conspecific females cause the males to selectively reduce heterospecific courtship (Dukas 2004; Ellis & Carney 2009; Dukas & Dukas 2012). Similarly, males of the closely related species pair, *Drosophila persimilis* and *Drosophila pseudoobscura*, also initially indiscriminately court conspecific and heterospecific females. Following rejection by heterospecific females, however, the males learn to selectively reduce heterospecific courtship. The selective decline in heterospecific courtship also leads to a lower frequency of heterospecific matings (Fig. 5; Dukas 2008a, 2009a; Kujtan & Dukas 2009; Dukas et al. 2012).

Within-generational learning can also affect mate choice in females. Female fruit flies (*D. melanogaster*) typically prefer large over small males. Females that encounter large males when immature are less likely to later mate with small males than are females that have previously encountered only small males (Dukas 2005). Similarly, in field crickets, *Teleogryllus oceanicus*, females exposed to their preferred songs are later less likely to respond to a reference song than females previously exposed to less preferred songs (Bailey & Zuk 2009). In treehoppers (*Enchenopa binotata* species complex), prior experience with male courtship signals alters females' subsequent selectivity (Fowler-Finn & Rodríguez 2012). Finally, experience influences females' avoidance of heterospecific males in the closely related damselfly species *Calopteryx splendens* and *Calopteryx virgo* (Svensson et al. 2010). All of the above examples suggest that learning from potential mates is common and may have influenced speciation rates. However, there is still no direct evidence linking within-generational learning in the context of mate choice to speciation. Nevertheless, the first population genetic analysis of the effects of within-generational learning in the context of mate choice indicates that learning by females has robust, substantial, positive effects on population divergence while learning by males increases divergence only under a limited set of conditions (Servedio & Dukas, in press).

CONCLUSIONS AND PROSPECTS

All organisms are highly plastic, and plasticity has the potential to promote evolution. Plasticity of neurons allows individuals to record novel information and this can have unique effects on facilitating evolution. However, the magnitude of the effect of learning on evolution, compared to other types of plasticity, has not been examined. Future research should thus quantify the marginal increase in factors such as individual survival, reproduction and speciation rates attributed to learning. Furthermore, it is widely acknowledged that plasticity, including learning, can also hinder evolutionary change. The common explanation for such negative effect is that heritable variation may not affect fitness if plasticity allows individuals to attain the optimal phenotype (Anderson 1995; Robinson & Dukas 1999; Huey et al. 2003; Price et al. 2003; Servedio & Dukas, in press). Future research should thus consider, and attempt to quantify, both positive and negative effects of learning on evolution.

I focused here on three major ways through which learning can influence evolution. First, both the abilities to record novel information and to accumulate experience allow individuals that learn to

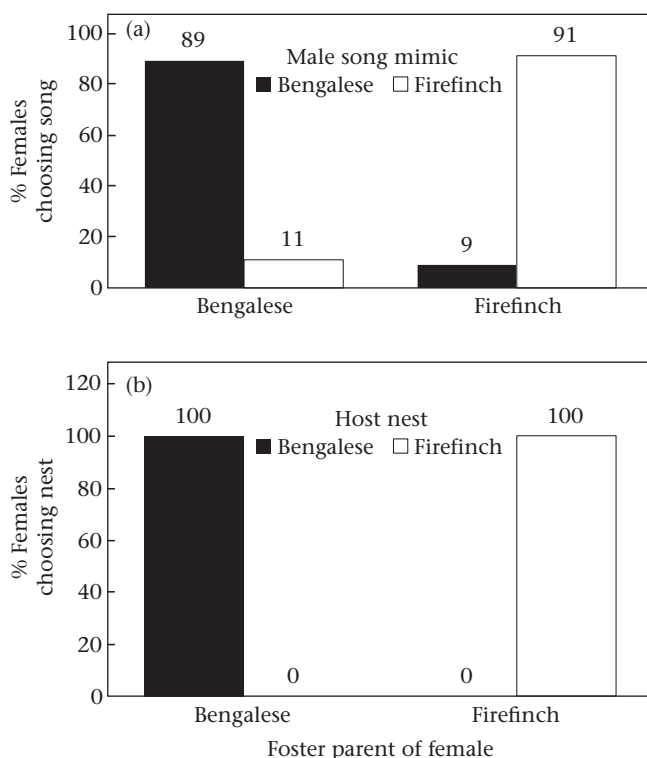


Figure 4. Imprinting in brood-parasitic village indigobirds, *Vidua chalybeata*. Birds were foster-reared in captivity either by their normal host species, the red-billed firefinch, *Lagonosticta senegalensis*, or by an experimental foster species, the Bengalese finch, *Lonchura striata*. (a) In mate choice tests, females preferred conspecific males that mimicked the females' foster host song. (b) In host choice tests, females preferred to lay eggs in nests of their foster host species. Such imprinting to host may have led to rapid adaptive radiation in indigobirds. Numbers above the bars indicate the percentages of females. Data from Payne et al. (2000).

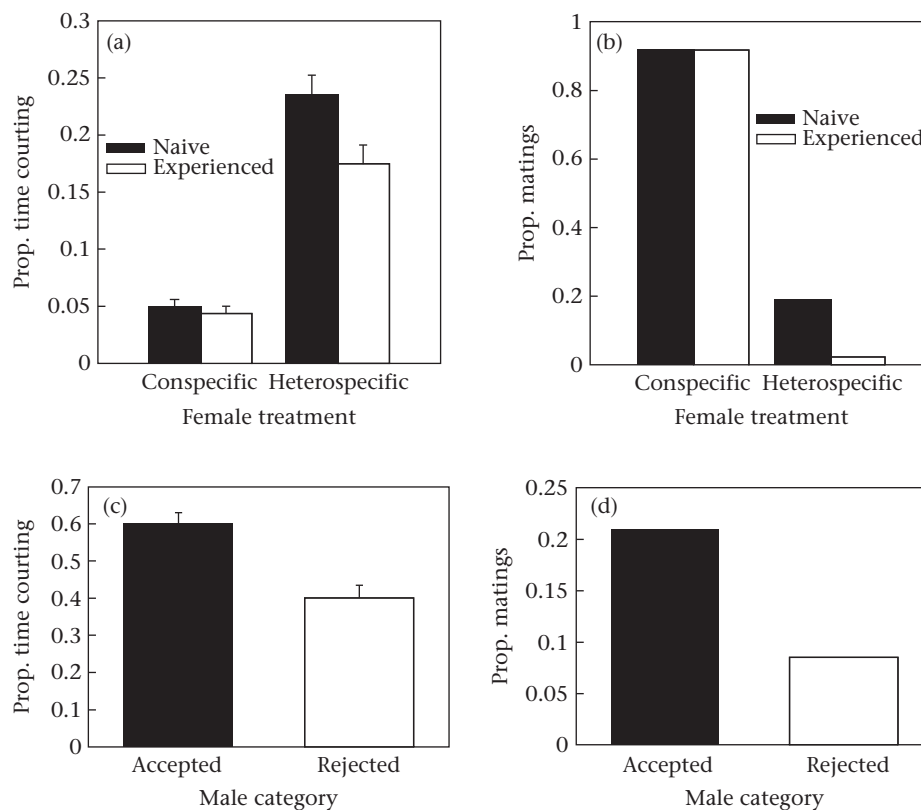


Figure 5. (a, b) Results from a learning experiment where males' experiences were controlled by the experimenter. (a) Proportion of time (mean \pm SE) that male *D. persimilis* that were either inexperienced (black bars) or experienced at courting and rejection by heterospecific female *D. pseudoobscura* (white bars) spent courting either conspecific or heterospecific females, and (b) the proportion of matings by these males (data from Dukas 2008b). (c, d) Results simulating actual encounters in nature, where the experiences of either mating or rejection were determined by the flies. (c) Proportion of time (mean \pm SE) that male *D. persimilis* that had been either previously accepted or previously rejected by heterospecific female *D. pseudoobscura* spent courting heterospecific females, and (d) the proportion of matings by these males (data from Kujtan & Dukas 2009).

be more robust than individuals that do not learn. Of the three topics discussed in the section on robustness, we have intriguing though limited data on the effects of learning on the timing of egg laying in birds, excellent data on learning and nest site selection in birds, and an incomplete understanding of the degree to which indirect cross-generational learning influences substrate choice in either insects or other species where parents and offspring do not overlap (Davis 2008). Significant effort has recently been devoted to examining the effect of global warming on the timing of egg laying in birds. The existing experimental protocols, especially those involving climate-controlled aviaries (e.g. Visser et al. 2009; Schaper et al. 2012) can readily be modified to explicitly test the role of learning in adjusting the timing of egg laying based on experience. Similarly, existing protocols in fruit flies (Jaenike 1983; Barron & Corbet 1999; Stamps et al. 2009b) can be modified to closely examine preference for relevant factors adults encounter upon eclosion. I focused on only three topics in the section on learning and robustness because I am unaware of further examples. It is likely, however, that learning enhances robustness through its effects on other behaviours, and this possibility requires further investigation.

The second way by which learning can influence evolution is through increased innovation, a by-product of the exploration and improvements that are inherent to learning. The comparative data indicate a positive association between innovation and evolution, and human cultural innovations have been shown to lead to genetic changes. Studies providing details about the learning events leading to a specific innovation and how this brings about specific genetic changes in animals other than humans would be highly valuable. Third, learning can influence evolution through increased speciation rate because it has an enormous potential for increasing

the levels of assortative mating leading to population divergence. There are currently, however, no empirical studies directly indicating positive effects of learning on speciation rates. The population genetic model of Servedio & Dukas (in press) suggests that within-generational learning in the context of mate choice is most likely to increase the rate of population divergence in cases where females learn to avoid mating with males from partially divergent populations based on early experience with males from within the females' population. This prediction can be tested in future research involving experimental evolution using a species with short generational times and evidence for female learning in the context of mate choice (Dukas 2005; Bailey & Zuk 2009; Fowler-Finn & Rodríguez 2012).

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