

Learning, evolvability and exploratory behaviour: extending the evolutionary reach of learning

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Abstract

Traditional accounts of the role of learning in evolution have concentrated upon its capacity as a source of fitness to individuals. In this paper I use a case study from invasive species biology—the role of conditioned taste aversion in mitigating the impact of cane toads on the native species of Northern Australia—to highlight a role for learning beyond this—as a source of evolvability to populations. This has two benefits. First, it highlights an otherwise under-appreciated role for learning in evolution that does not rely on social learning as an inheritance channel nor “special” evolutionary processes such as genetic accommodation (both of which many are skeptical about). Second, and more significantly, it makes clear important and interesting parallels between learning and exploratory behaviour in development. These parallels motivate the applicability of results from existing research to learning and learning evolution and to our understanding the evolution of evolvability more generally.

Keywords Evolvability • Learning • Plasticity • Behaviour • Facilitated variation

Introduction

In essence my claims in this paper are relatively simple. We all accept that learning is frequently adaptive for individuals in changeable environments. It can allow organisms to continue to survive and reproduce despite any changes to the environment that occur during their lifetimes. What I highlight here is that this is not all that learning does. Learning can allow populations to respond appropriately to environmental change without the requirement for any genetic change. In doing this, learning allows populations to avoid the potential loss of genetic diversity that comes with directional selection, and thus it preserves the standing variation in populations. This buffers populations from future environmental changes by maintaining their capacity for rapid adaptation in the future. In this way learning (both social and asocial) can be a source of lineage level robustness. This type of robustness is important to evolvability as it allows for both populations and the standing genetic variation within them to persist and contribute to future evolution. Further to this, in the latter part of the paper, I make note of important parallels between the mechanisms underwriting certain forms of learning and recognized developmental

sources of evolvability. In doing so, I offer a novel starting point for the investigation of the evolution of evolvability.

Throughout the paper I use a case study for illustration that serves to highlight both the adaptive value of learning to individuals and its role as a source of evolvability to populations. In particular I explore the differential response of a two native predator populations—the common planigale (*Planigale maculata*) and the red-bellied black snake (*Pseudechis porphyriacus*)—to a toxic invasive species—the cane toad (*Rhinella marina*). Both planigales and red-bellied black snakes prey on cane toads and suffer population losses as a consequence. Importantly for my purposes, both planigale and red-bellied black snake populations are able to persist in cane toad-infested areas despite cane toad toxicity, but the methods via which they adapt to the cane toad threat differ. Planigales learn via taste aversion conditioning to avoid cane toads as prey, while red-bellied black snake populations rapidly evolve of physiological and behaviour adaptations to avoid cane toad ingestion. Consequently, the case study serves to provide an instructive means of comparing the impact of learning upon both individual survival and reproduction and population level evolvability.

To begin I provide some basic background to the cane toad invasion, and then turn to the specifics of the case study.

The adaptive benefit of learning to individuals: the invasion of the killer cane toads

In the early 1900s, sugar cane farmers in the eastern Queensland region of Australia struggled to deal with the impact of cane beetle (*Dermolepida albobirtum*) attacks on their crops. In 1935, in an attempt to control the beetle threat, cane toads, originally native to South and Central America, were introduced into the area to act as a biological control (Lever 2001). Unfortunately, the introduction of the cane toad was ineffectual in mitigating beetle damage to cane crops. Furthermore, cane toads were subsequently revealed to be a far greater ecological problem than the beetles they were introduced to control in the first place. It turns out that cane toads are one of the world's worst invasive species, and in the Australian context they are particularly insidious (Lowe et al. 2000).

Since their introduction, cane toads have successfully invaded regions of the Australian landscape well beyond the location of their initial release. As of 2011, their range extended almost across northern Australia into far north Western Australia and as far south as northern New South Wales (Sutherst et al. 1995; Cameron 2011). In some of these areas they are found in densities of more than 2,000 cane toads per hectare (Freeland 1986). Modeling predicts that cane toads will eventually establish themselves across one-third of the Australian continent (Sutherst et al. 1995; Beeton et al. 2006).

The secret to the successful invasion of cane toads in Australia lies in a “perfect storm” of factors. Firstly, cane toads are very well suited to the climate across a significant proportion of the Australian landmass (Kearney et al. 2008). Thus, their potential range (and consequent impact on the environment) is not limited to a small

area. Second, they have a relatively large reproductive output— cane toads usually breed twice a year, laying between 8,000 and 35,000 eggs at a time (Cameron 2011). This has seen many attempts at cane toad eradication and population control through culling and other means fail (Lampo and De Leo 1998). Third, they have few effective predators and competitors within the Australian context. This is largely because cane toads carry a toxin that is particularly problematic for Australian natives. There is a lack of historic co-adaptation to such toxins in Australian natives, which means that they are highly sensitive to cane toad toxin and the ingestion of cane toads is commonly fatal (Chen and Kovarikova 1967; Lutz 1971; Covacevich and Archer 1975; Llewelyn et al. 2011).¹ Large numbers of cane toad-induced deaths amongst native predators and major population declines across a large range of taxa have been documented following the invasion of cane toads into a new territory; snakes (Breedon 1963; Rayward 1974), lizards (Doody et al. 2006), amphibians (Crossland et al. 2008), crocodiles (Letnic et al. 2008) and marsupials (Burnett 1997).

Surprising resilience: survival in the face of cane toad invasion

The massive rise in cane toad numbers across Australia has had great impacts on native species via displacement, predation and loss of habitat (Phillips et al. 2003). Native predators are particularly vulnerable to cane toad invasion because of the aforementioned potential for population losses due to fatal cane toad ingestion. Although it is reasonable to conclude from this evidence that cane toad invasion will have devastating consequences for the survival of Australian native species, investigations into the long term effects of cane toads have challenged this intuition. In fact, despite the significant initial impact of cane toad invasion on the size of native populations, no evidence of cane toad-induced extinctions has been found. Rather, many native species have been observed to recover their original numbers relatively quickly post-invasion (Freeland 1990). The observed recovery of species via the rapid modification and adaptation of behaviour and morphology to cane toads is an impressive example of the resilience that animal populations can display (Llewelyn et al. 2010b).

Learning is one key source of this adaptation. Two classes of learnt adaptive strategies have been observed. First, modifications to feeding strategies to allow the safe consumption of cane toads have been observed. For example, black rats (*Rattus rattus*) in areas that have long been infested with cane toads have been observed to consume cane toad carcasses but avoid the toxic parts of the body (Fitzgerald 1990). Second, the learned avoidance of cane toads after negative exposure to cane toad toxin is observed. This has been noted in a number of species including, the barramundi, *Lates calcarifer* (Crossland 2001); the native marbled frog, *Limnodynastes convexiusculus* (Greenlees et al. 2010a); and fresh water crocodile,

¹ There are exceptions to this general rule. A small number of native species have been observed to be relatively “immune” to toad toxin (e.g. the keelback snake, *Tropidonophis mairii*). The “preadaptation” to toads in these lineages is believed to be the product of contact between ancestors of these native species and Bufonid toads in Asia (where such species are endemic) prior to migration onto the Australian continent (Llewelyn et al. 2010a, 2011).

Crocodylus johnstoni (Somaweera et al. 2011). The common planigale is an example of a species that has adapted to cane toads via learning. It is also a well-studied case within this system and thus is the focus of the remainder of my discussion.

The hardy planigale: the benefits of learning

The common planigale is a small marsupial “mouse” found in the northern half of the east coast and in areas of the Northern Territory and northern Western Australia. Planigales are primarily insectivorous but also prey on small reptiles, amphibians and birds (Webb et al. 2008; Llewelyn et al. 2010b).

They occupy areas impacted by cane toads and have foraging dispositions that expose them to the consumption of cane toads. They are also highly sensitive to cane toad venom—even mouthing a large cane toad can be fatal to a planigale (Covacevich and Archer 1975). Despite this, populations of planigales have persisted in cane toad-infested areas. The central mechanism for survival is their capacity for conditioned taste aversion when exposed to cane toad toxin (Webb et al. 2008).

Naïve planigales from both cane toad-infested and cane toad-free areas, will kill and eat cane toads, but, if these exposures are not fatal, they learn to avoid them. Planigales given a single negative exposure to metamorph (immature) cane toads in the lab refuse to attack cane toads again on further exposure for up to 28 days (Webb et al. 2008; Llewelyn et al. 2010b).

The learning mechanism here (conditioned taste aversion) is a form of classical (or Pavlovian) conditioning. This is a type of asocial learning; it involves the association of a particular stimulus (in this case, the taste of cane toad) with a negative experience (in this case, illness) and results in the subsequent avoidance of the stimulus (in this case, cane toads) (Shettleworth 2010: 97–98). A number of features are indicative of this type of learning. Firstly, conditioned taste aversion is a rapid form of learning—organisms learn to avoid foods after a single negative exposure (rather than the multiple negative exposures required for most forms of classical conditioning) (Shettleworth 2010: 97–98). Secondly, conditioned taste aversion can occur even with a temporal delay between the stimulus and negative experience (Garcia et al. 1966; Shettleworth 2010: 97–98). Third, the learned response from conditioned taste aversion is relatively fine-grained, as is the case with planigales. Although cane toad-exposed planigales are more likely to avoid eating species that are phenotypically similar to cane toads (such as frogs) after their negative exposure to cane toads, the frog-avoidance-effect is weaker than the cane toad-avoidance-effect and less long lasting. Fourth, the taste aversion generated by this form of conditioning is difficult to override, even cognitively (Shettleworth 2010: 97–98). This is well illustrated in humans. Humans, like most mammals, exhibit taste aversion learning. Most of us will have had the unfortunate experience of getting food poisoning from a late night kebab or poorly refrigerated prawn. You may also have had the (perhaps even more unfortunate) experience of subsequently being unable to eat the same otherwise delectable foodstuff, despite being very sure the food is safe to eat. This is an example of conditioned food aversion in humans and offers a first hand example of how difficult it is to cognitively override taste aversions. Even when we know a food

is safe (and delicious), our conditioned response is to avoid it if it has caused illness previously.

Importantly for our purposes here, conditioned taste aversion is a deep ancestral adaptation that is present across the mammal order (Shettleworth 2010: 97–98). Furthermore, it is a specific example of a more general phenomenon—classical conditioning—that is seen throughout the Animal Kingdom from fruit flies to humans (Tempel et al. 1983; Mery and Kawecki 2002). Consequently, showing how conditioned taste aversion affects evolutionary outcomes in this case can inform us about the broader significance of learning in animal evolution.

One thing the planigale example clearly illustrates is that learning is a powerful and useful adaptation. Even simple forms of learning can confer great benefits to organisms—in this case, for a predator in the face of a toxic novel prey species—by increasing their capacity to behave in a way that suits their environment. Those planigales that are better at learning to avoid eating cane toads are more likely to survive and reproduce than those less adept at learning to avoid cane toads. Although conditioned taste aversion learning is an existing adaptation in planigales, being better at conditioned taste aversion learning (e.g., faster, more accurate, more fine-grained) is clearly an advantage in cane toad-infested areas. Importantly, despite it being the behavioural trait (avoiding cane toad ingestion) that is advantageous, the capacity for taste aversion learning is selected rather than the behavioural trait itself. This is because the learned behaviour is not inherited from parent to offspring (via social learning nor genetics). Planigales that learn to avoid cane toads do not have offspring that spontaneously avoid cane toads (Webb et al. 2008; Llewelyn et al. 2010b). Rather, planigales that exhibit conditioned taste aversion learning to cane toads will have offspring that are likely to also exhibit such learning, and thus will learn to avoid cane toads also.

Caution: learning is not always adaptive

While learning can confer great adaptive benefits on individuals (i.e. it can increase their fitness), it is important to be cognisant of its limitations. In particular, the adaptive benefits of learning are contingent on certain background conditions holding.

First, for learning to be advantageous to individuals, the environment must have a particular epistemic character. Accurate cues and signals of the aspects of the environment that are relevant to the learned adaptive response must be available to the learning organism. In some cases, the appropriate cues required to enable the organism to learn to respond appropriately to their selective environment will not be available.

Sterelny (2003: 20–26) offers a useful terminology for highlighting the epistemic differences between environmental elements. He describes some environments as epistemically “transparent.” In such environments the salient functional features of the environment correspond to reliable perceptual cues; for example, all beetle-shaped things are edible, all cane toad-shaped things are poisonous. There are, however, very few transparent environments. Rather, environments tend to be what Sterelny (2003: 20–26) calls epistemically “translucent” or “opaque.” In such situations the salient features of the environment do not correspond neatly to reliable

cues. For example, the same perceptual cue might correspond to multiple, functionally distinct entities (e.g., some cane toad-shaped things are edible and some are poisonous) or there may be no directly perceivable cues for a feature of the environment at all (e.g., bacteria are too small to see with the naked eye). Unsurprisingly, epistemic translucency (or even opacity) is the norm in the natural world (rather than an oddity), as competition between and within species tends to select for sources of deception such as mimicry and camouflage. When environments lack a clear epistemic structure it is much harder (or even impossible) for organisms within those environments to track salient entities (such as predators and prey) and learn to behave appropriately towards them. This type of epistemic system can effectively neutralise the adaptive benefits of learning to individuals (and thus populations as well) by making learning ineffectual.

Naïve planigales, for example, do not readily discern between cane toads and frogs when foraging (Llewelyn et al. 2010b). One way to interpret this is that the amphibian-food-stuff aspect of the foraging environment is to some extent translucent — there is significant phenotypic overlap between cane toads and frogs and planigales which makes distinguishing between them difficult and this can result in costs to cane toad-exposed planigales in terms of loss of a good food source in frogs if their toad-detection is perceptually coarse-grained. Although in this circumstance it is not a significant problem (the cost is small and relatively short lived as planigales rapidly learn to be more discerning), we can imagine an organism whose diet consisted solely of frogs and who could not distinguish between them and cane toads at all (i.e. they were perceptually indistinguishable to the organism). In such a situation the organism would either avoid cane toads and frogs altogether (and starve), or prey on both indiscriminately (and likely die of toad poisoning).

The adaptive value of learning to individuals (and populations) is not only sensitive to epistemic conditions. It is also sensitive to the cost-benefit structure of the world. In some cases cues are in principle available to organisms but are ultimately too costly to be beneficial. One way that this can be borne out is in the cost of exploration. Although learning allows organisms to modify their behaviour according to their environment, it also requires them to undertake a risky and relatively inefficient period of “training” or “trial-and-error.” For example, a species that learns which foods are appropriate (rather than being relying on solely on a genetic disposition to eat certain foods from birth) has to undertake a potentially risky period of trial and error on unknown foods. If the cost of error is very high then learning will only be beneficial to organisms if the benefits of success are also high. We can see this if we return to the case study once again.

The benefits of conditioned taste aversion learning to native animals in cane toad threatened areas are contingent on the possibility of a sub-lethal interaction with the invading prey. A fatal interaction with a cane toad presents an extreme cost of error. Learning will not always confer an advantage to individuals if a predator can only discern the danger of a particular prey via a lethal interaction with the prey.

The absolute toxicity of any given cane toad depends on both body size and the size of the parotid gland and these vary geographically as a product of climate and history (Llewelyn et al. 2011). Thus, the toxin threat on any given predator depends (at least in part) on the size of the cane toad that the predator is able to ingest.

Another factor that influences the toxin threat of cane toads is the absolute toxicity of individuals in the geographic area. This varies depending on the relative size of the parotid glands to body size of cane toads. If the metamorphs in an area carry large amounts of toxin their invasion will have a broader impact than if the metamorphs carry only small levels of toxin. Consequently, the impact of cane toads on predators is a product of the toxicity of cane toads in their area and also the size of cane toad they can physically consume. The impact of cane toads on the northern quoll (*Dasyurus hallucatus*) illustrates this well.

Although in laboratory trials northern quolls exhibit conditioned taste aversion to sub-lethal doses of cane toad toxin just like planigales, a number of quoll populations have been lost post-cane toad invasion. It is thought that this is because they are bold predators (hence will prey on the large adult cane toads as they tend to sit out in the open) and are able to ingest very large cane toads. Consequently, for many quolls their first encounter with a cane toad is fatal. In contrast, planigales are relatively timid predators and eat their prey headfirst. This is thought to increase the likelihood that they will spit the cane toad out before the ingestion of a fatal amount of toxin (Shine 2010).

While the standard fitness-based analysis of the adaptive benefits of learning to individuals just outlined is relatively uncontroversial, many believe that it unjustifiably downplays the important benefits that learning can confer on populations. This challenge to the status quo has tended to rely on the role that social learning can play as an inheritance channel and in special evolutionary processes such as genetic accommodation (for example, Laland et al. 2003; Laland and Hoppitt 2003; Laland and Janik 2006; Laland et al. 2009). While persuasive, the challenge from evidence of animal cultures and genetic accommodation is controversial. There is significant skepticism of there being any widespread role for learning in influencing evolution beyond its adaptive value that cannot be captured by the Modern Synthesis (Galef 1992, 2009; Heyes 1993; Via et al. 1995; Rollo 2004; de Jong 2005; Tomasello 1994, Hartfelder 2005, Tomasello 2009; Hoekstra and Coyne 2007). This paper is a response to this skepticism, albeit an indirect one.

In the remainder of the paper I defend a role for learning in evolution that is reliant neither on social learning as an inheritance channel, nor its role in genetic accommodation. Rather, I show an aspect of the evolutionary benefits offered by learning that has thus far been relatively ignored by behavioural biology. In short, asocial learning mechanisms—whose existence is widely accepted—affect the evolutionary trajectory of populations because they preserve variation in those populations. This action of learning is not a product of selection and is not adequately captured by the Modern Synthesis. While learning is selected for by allowing individuals to survive and reproduce in the face of environmental heterogeneity, the population level benefits of learning in terms of evolvability are a side effect. This claim has implications both for our understanding of the role of learning in evolution but also of the sources of evolvability.

Learning and evolvability: the benefits of learning to populations

In this section of the paper, I explore the role of asocial learning in evolvability by comparing the evolvability of planigale populations with those of another native predator also impacted by cane toads—the red-bellied black snake (*Pseudechis porphyriacus*). Unlike the aforementioned planigale, red-bellied black snakes do not learn to avoid cane toads via taste aversion learning. Rather, black snake populations have been observed to adapt to cane toad invasion via rapid evolution. As such, they offer a means via which I can illustrate the relative benefits of asocial learning for populations with respect to evolvability.² In what follows, I outline why asocial learning contributes to evolvability and demonstrate that although both planigale and red-bellied black snake populations have successfully adapted to the cane toad invasion, their subsequent evolutionary potential differs in important ways. Red-bellied black snake populations in cane toad-infested areas have undergone a dramatic shift in the nature of the genetic variation within them. Whereas learning has allowed planigale populations to adapt to cane toads and maintain their genetic diversity at the same time, making them more capable of dealing with a broader range of possible future environmental change than the black snake populations. The benefits I discuss here are relevant to any form of adaptive phenotypic plasticity, but learning is particularly powerful, being directed towards adaptation even without pre-adaptation.

Having highlighted this role for learning in evolvability, in the latter section of the paper I discuss the implications of this understanding of the role of learning in evolvability. In particular, not only does it increase our knowledge of the causal factors that contribute to the shape of the tree of life, but the research also has implications for evolutionary developmental biology—more specifically, Kirschner and Gerhart's (2006) theory of facilitated variation.

Rapid evolution in response to environmental change

The red-bellied black snake is a large elapid that is found right along the eastern coast of Australia. They feed primarily on frogs (Phillips and Shine 2006). As with planigales, there are red-bellied black snake populations in regions that have long been infested with cane toads. The snakes in these populations exhibit a number of adaptations to cane toads not seen within snake populations in cane toad-free areas. These adaptations include morphological modifications to the mouth (these limit the size of cane toads that individuals can consume), physiological adaptations (such as tolerance to cane toad toxins) and altered foraging behaviours (for example, the avoidance of cane toads as prey) (Phillips et al. 2003; Phillips and Shine 2004, 2006; Greenlees et al. 2010b). For our purposes here, I will concentrate on the behavioural adaptations and the reduced preference for cane toad consumption observed in red-bellied black snakes.

Unlike the learned response seen in planigales, the behavioural aversion to cane toads in cane toad-exposed red-bellied black snake populations is the consequence of

² Note, red-bellied black snakes are not incapable of learning full stop, they simply do not exhibit learning with respect to cane toads (Phillips and Shine 2006).

rapid evolutionary change due to strong directional selection, rather than learning or any other form of adaptive phenotypic plasticity (Phillips and Shine 2006). Rapid evolution occurs in situations when a population is under strong selection pressure and there is an existing capacity within the population to respond to that pressure. Such a capacity is sufficient to prevent a population being wiped out completely but large initial population losses still occur due the strength of selection. While this carries some costs with respect to loss of genetic diversity (see later discussion), the large population losses can have the positive result of generating a rapid shift in the distribution of phenotypes within the population towards adaptation to the novel selective pressure (Carroll 2007a, b).

In the case of red-bellied black snakes, cane toads present a particularly strong directional selection pressure because of their toxicity to snakes and close phenotypic similarity to other species normally preyed on by the snake (i.e., native frogs). Thus, early in the period of cane toad invasion, we see significant mortality and morbidity in snake populations from cane toad consumption (Breedon 1963; Rayward 1974). Notably, despite the considerable impact of cane toads on naïve snake populations, enough snakes with limited physiological resistance and inherent cane toad aversion survive the initial cane toad invasion to reproduce. During this early period of cane toad invasion, cane toad resistance largely determines survival and reproduction and cane toad resistant snakes disproportionately contribute to the subsequent generations of snakes in the populations. This has the consequence that as snake populations in cane toad-infested areas rebuild their numbers following initial cane toad invasion, there are increasing numbers of “cane-toad-proof” individuals each generation. The change in population composition from majority “cane-toad-sensitive” to majority “cane-toad-proof” is relatively swift, occurring at a fast enough rate for the population to adapt within a few generations (Phillips and Shine 2006).

The capacity for red-bellied black snake populations to persist in the face of the invasion of a toxic prey item without learning is impressive. One thing it serves to highlight is the degree of influence that the supply of variation available to a population can have upon its evolutionary prospects. The survival of red-bellied black snakes was completely reliant on the presence of some individuals with a latent resistance to cane toad toxin. In what follows, I consider the effect that undergoing rapid evolution has on the supply of phenotypic variation and the evolvability of cane toad-exposed red-bellied black snake populations. To do this, I compare the consequences of cane toad adaptation for planigale and red-bellied black snake populations.

While both planigale and red-bellied black snake populations have been able to successfully adapt and persist in the face of cane toads, the distinct routes by way of which this adaptation occurred differentially impacts on their evolvability. I focus, in particular, on the impact that the specific route taken by a population when undergoing phenotypic modification in response to a novel environmental threat has on the amount and nature of standing variation in that population over time. Planigale populations, by learning rather than evolving genetically in response to cane toads are able to maintain standing genetic variation where snake populations cannot. Before I argue for this thesis, I will cover some important background regarding evolvability and the standing within populations.

Evolvability and standing variation

Evolvability is best thought of as the probability of a particular feature or set of features arising at some future time given the non-selection based features of a population or lineage and its environment at some particular starting point (Brown, forthcoming). This probability picks out the influence of features of populations (rather than selection) on the outcomes of the evolutionary process. For our purposes here I am particularly interested in the extent that a property of individuals in a population (the capacity for learning) can alter the probability of the evolution of adaptation for that population over time (above and beyond the mere adaptive benefits that learning confers on individuals). More specifically, I argue that learning is a mechanism that facilitates the maintenance of standing genetic variation within populations, and thus contributes to evolvability.³

The standing genetic variation of a population is the existing (rather than prospective) pool of genetic variation and covariation within that population (Houle 1992). It is important to the evolvability of populations (with respect to complex adaptation) because (as compared to populations with little standing variation but the potential to generate novel mutations) having a large supply of standing genetic variation increases the likelihood that a population will persist over time and can increase the speed and likelihood of the evolution of adaptation (Boyce 1992). In particular, those populations with large amounts of standing genetic variation are more likely to be able to respond to stochastic events in their environments and adapt to any more permanent novel selection pressures that may arise. In other words, they are robust and adaptable. This increases the likelihood that these species will undergo speciation and divergence in the future; as noted by Pfennig et al. (2010), there is strong evidence that plasticity facilitates speciation by protecting the pool of genetic variation in populations such that those populations subsequently are better able to undergo evolutionary divergence when exposed to novel selective regimes. There are a number of reasons for this.

First, the likelihood that a beneficial allele will be immediately present in the population should an environmental change occur is higher when a population carries a large and varied pool of alleles than when a population has a small or homogeneous pool of alleles (Barrett and Schluter 2008). To put it slightly differently, populations with a large supply of standing variation occupy larger areas of genotypic possibility space than less well-endowed populations. Occupying a larger area of phenotypic possibility space increases the chance that a beneficial allele will be in a population when an environmental change occurs. Thus, when a population holds a large amount of standing variation it is less likely to go extinct should the environment change. It is

³ It is important to note that this claim—that learning influences evolvability—is made elsewhere (albeit in passing) within the literature on the contribution of adaptive phenotypic plasticity to the evolvability of populations (in particular, see Pfennig et al. (2010); West-Eberhard (2003); Fitzpatrick (2012)) and also that concerning the Baldwin effect (e.g., Papineau 2005). Here, I am both making the claim regarding learning clearer and more specific but also, as will become apparent, highlighting some novel implications for evolutionary developmental biology.

also less likely to have to “wait” for a beneficial mutation to occur before adaptation to a novel selection pressure can begin.

A second reason why standing genetic variation is important to the evolvability of populations with respect to complex adaptation is that populations with a high level of standing genetic variation are more likely to have multiple copies of beneficial alleles (Teotonio et al. 2009). This is because, although it is theoretically possible for quite small populations to have high levels of standing variation, in general, populations with large standing variation are large and thus many mutational variants are repeated.⁴ To further the genetic possibility space metaphor above, populations with large standing variation not only occupy more of possibility space but also are more likely to occupy that space more densely. Having multiple copies of any beneficial alleles when a novel selection pressure arises, increases the speed at which populations can evolve by increasing the pool of individuals that flourish under selection, and are consequently able to contribute to further mutational events and adaptation. In addition, having multiple copies of beneficial alleles in a population also serves to buffer the population from the impact of stochastic events. “Bad luck” is a potent force in evolution and in situations where populations are reliant on novel mutations for adaptation, and consequently expected fitness is not always borne out in actual reproductive success. All else being equal, having many copies of a high fitness allele in a population increases the likelihood that the fitness of individual alleles in one generation will be borne out appropriately in the distribution of alleles in the following generation.

A third reason that populations with large standing variation are more evolvable with respect to complex adaptation and less likely to go extinct is because the alleles within those populations are more likely to have undergone previous selection (Barrett and Schluter 2008). Previous selection increases the likelihood first, that any alleles in the population be beneficial alleles, and second, that their beneficial effects will be broad. Although pleiotropic alleles that arise *de novo* in populations are highly likely to be lethal, existing pleiotropies found in the standing supply of variation to a population are less likely to be so; existing pleiotropies have shown themselves to be non-lethal (in at least one developmental context) via their persistence in the population. Having beneficial pleiotropic alleles allows populations to make large moves in phenotypic space for very little movement in genetic space and thus allows them to evolve adaptations faster. It is worth noting a small caveat here; while the alleles within populations with large standing variation are in general more likely to have undergone previous selection, where there is significant phenotypic plasticity

⁴ Note that, although there are documented cases of relatively large, but genetically homogeneous, populations, such populations are rare and fragile. To illustrate, prior to 2008, Tasmanian devil (*Sarcophilus harrisi*) populations in Tasmania were very large, but exhibited low levels of genetic diversity at a number of particularly polymorphic parts of the mammalian genome (McCallum 2008). Therefore, this population lacked robustness. Since 2008, devil populations have been decimated by a particularly virulent host-specific pathogen whose transmission is aided by the genetic homogeneity of the devil population. Because of the fragility of populations like this (and thus their rarity), it is a relatively uncontroversial assumption of much of conservation biology that small populations have lower standing genetic variation than larger ones (Boyce 1992; Shaffer 1981).

(for example, learning) within a population the adaptedness of the pool of standing variation is likely to be less than we would otherwise expect. This is because phenotypic plasticity shields the genetic variation in a population from selection.

It is for these reasons that having large amounts of standing variation increases the ability of a population to respond adaptively to future environmental changes and reduces its susceptibility to extinction (i.e., it increases robustness⁵). This contributes to the evolvability of populations by facilitating the persistence and maintenance of the supply of variation ready for selection.

The benefits of learning: learning reduces lethality

Learning is a means through which populations can maintain their standing variation, and thus it alters their evolvability. This is because learning can reduce the lethality of the phenotypic variants within a population in the face of environmental change. As discussed in the previous section of the paper, large populations most often (though not always) will have larger standing genetic variation than small ones. Consequently, one way that the standing genetic variation in a population is preserved over time is via the maintenance of population size. By reducing the likelihood that the genetic variants that exist in a population will be lethal, learning also reduces the likelihood of a population suffering losses, and thus losing diversity.

One factor that can lead to a loss of standing genetic variation in a population is strong directional selection. Such heavy selection results in a discriminate loss of individuals in the population—some individuals do better than others by virtue of the traits they have. This results not only in a loss of population size (at least initially) but also a loss of genetic diversity. If we look at the planigale and red-bellied black snake response to environmental change we see that, while both populations are able to persist in the face of cane toad invasion, red-bellied black snakes have likely lost significant genetic variation in their response while planigales have not. By being able to learn to respond to the cane toads during their lifetimes planigales have been able to survive the initial cane toad invasion in much greater numbers than red-bellied black snakes. Given this, we should expect to see greater standing variation in planigale populations than in red-bellied black snakes just on the basis of size.

Size, however, is not the only feature of a population that contributes to its standing genetic variation. The standing genetic variation of a population captures not just the number of copies of alleles present but also the number of unique alleles (i.e., a large, but genetically homogeneous, population has a low level of standing genetic variation). In principle it is possible to have over-production and soft selection, such

⁵ There is considerable conceptual confusion surrounding the term “robustness” both within the sciences and in the philosophy of science (Wimsatt 2007) but also more specifically in evolutionary developmental biology (this confusion concerns relationship between robustness and evolvability—see Wagner 2005; Wagner 2008; Lenski et al. 2006; Brookfield 2009). As such, note that here I mean “robustness” to refer to the ability of a population or lineage to respond adaptively to environmental change. I take it that, at least with respect to a population’s capacity to evolve adaptation (i.e., their evolvability with respect to adaptation), this type of robustness is not in conflict with evolvability. A population that is robust in this manner is also evolvable with respect to complex adaptation.

that selection does not change population size, just genetic constitution. In such a situation, if the only role that learning played were to protect population size, it would have little effect on standing variation. It is thus important that learning not only serves to maintain population size but it does it in a manner that also retains pre-existing genetic diversity. I return to the planigales and snakes to illustrate this.

In the case of red-bellied black snakes, those individuals fortunate enough to have genes that confer on them a physiological, behavioural or morphological resistance to cane toads survive cane toad invasion. Those snakes that do not have such traits are highly likely to die during the initial period following cane toad arrival. When discriminate losses like this occur in a population we see increases in the alleles that are beneficial to survival and reproduction but also in any alleles that are at loci associated with the beneficial locus. In other words, rapid genetic adaptation to a particular threat reduces variability in traits directly under selection as well as any linked trait. Thus, depending on the degree of linkage in the genome of a given species, strong directional selection reduces the genetic variation in populations. In red-bellied black snakes we expect this to be borne out in reduced genetic diversity in populations in cane toad-infested areas as compared to those in other areas of Australia. This loss of genetic variation is in stark contrast to what we expect in planigale populations. Within these populations losses due to cane toads are relatively indiscriminate with respect to traits. Individual planigales that are unlucky enough to first encounter a large or particularly toxic cane toad die but others who have a sub-lethal first exposure to cane toads are relatively immune to the cane toad threat. As mentioned already, planigale foraging behaviour increases the likelihood of sub-lethal cane toad encounters occurring. Planigales kill their prey by biting them on the heads and then ingesting them headfirst. This means that often planigales reject the cane toad before ingesting a lot of toxin (because they feel nauseous before they get to the highly toxic parotid glands). Because of this, planigales are more likely to have a sub-lethal interaction with a cane toad than snakes (that tend to swallow prey whole) and can learn to avoid cane toads post a sub-lethal interaction, we should see larger numbers of planigales surviving the initial onslaught of cane toads and thus a greater level of standing genetic variation being maintained in the population.⁶

Unlike red-bellied black snake populations, planigale populations are able to respond adaptively to the arrival of cane toads without having to undergo a shift in their genetic diversity. Thus, not only do they maintain population size but also they maintain the diversity of characters within the population. As already explained, having a large amount of standing variation in a population increases its evolvability with respect to adaptation. Thus, we can say that learning has increased the evolvability of cane toad-exposed planigale populations relative to cane toad-exposed red-bellied black snake populations by maintaining standing variation within the population (all else being equal).

When learning is adaptive it also offers a source of evolvability to populations by conferring on them what can be described as “lineage level robustness.” By maintaining the standing variation in populations, learning reduces the likelihood of a

⁶ Unfortunately, I was unable to find any data in the literature on the genetic diversity of red-bellied black snake and planigale populations that I could use to test the hypotheses I make here.

population going extinct and increases the likelihood of adaptation subsequent to a major environmental shift. Were another non-native species to invade the territory of planigales and red-bellied black snakes, planigale populations are more likely to be able to respond to them adaptively than red-bellied black snake populations because they have a greater capacity to respond in the genetic variation they are carrying. Importantly, the lineage level robustness that learning confers is domain general. We expect that the standing genetic variation maintained in populations via learning will be relatively unbiased, and hence, the genetic composition of the population should remain fairly stable over time, despite there being learning-induced changes in phenotype. We see this reflected more generally in the aforementioned research demonstrating that species with adaptive phenotypic plasticity are more likely to undergo speciation and diversification in the future than those without it (Pfennig et al. 2010).

Before I proceed, note that while the emphasis of this paper is on the benefits offered by simple asocial learning, the claims I make about evolvability and learning can be generalised. We should expect both social and asocial forms of learning to result in an increase in evolvability by reducing the lethality of phenotypes. While this is the case, it is also worth bearing in mind that the type of information required for social learning is not always available to organisms. This means that, although social learning and asocial learning are thought to be built on the same core mechanisms (and thus social learning does not necessarily require any particular cognitive adaptations (Heyes 2011)), social learning is not always possible. This can be for many reasons (e.g., life history, ecology or perceptual system) but for the planigale case, the epistemic nature of the system in question is particularly important.

In planigales, no social learning of cane toad avoidance has been observed (Webb et al. 2008; Llewelyn et al. 2010b). For planigales to learn to avoid cane toads from other planigales, the relevant behaviour the naïve planigale must observe in experienced planigales is that they do not use a potential food source (as opposed to using a novel food source, as seen in the cases of stimulus enhancement led social learning of foraging seen in many species). Simple mechanisms of social learning (such as stimulus enhancement and observational conditioning) are not useful in such epistemic circumstance because they rely on naïve individuals observing the behaviour of experienced individuals (and thus learning for themselves the location of a novel food source or foraging technique). In the cane toad case, such social information is not available—individuals that have learned to avoid toads will do so in almost all subsequent cases, and hence, there is little information for the naïve toad to exploit about toad toxicity. While some social learning systems can overcome this problem (for example the “teaching” of scorpion-handling techniques to pups observed in meerkats, *Suricata suricatta* (Thornton and McAuliffe 2006) and the observational learning of food aversions red-winged blackbirds, *Agelaius phoeniceus*, via conspicuous “disgust” responses (Mason and Reidinger 1982)), these sorts of systems are relatively rare. My focus here on the benefits offered by asocial forms of learning highlights the robustness of learning as a source of evolvability even in the face of a lack of socially available information.

As you can now see, learning is very often a beneficial adaptation for individuals. It also offers benefits to populations in that populations of learning individuals can respond to changes in the environment while maintaining their genetic diversity and size. This has consequences for the likelihood of adaptation subsequent to environmental change in learning species, and thus their lineage-level robustness. Furthermore, this role for learning as a source of evolvability is not captured by the Modern Synthesis, which tends to ignore these processes and focus on the role that the environment plays in the direction and nature of evolutionary change. Now, in final sections of the paper, I consider three important implications of this account of the role of learning with respect to the supply of standing variation in populations and consequently their evolvability. The first and arguably most significant of these actually concerns the science of evolutionary developmental biology (or Evo-devo) rather than behavioural biology.

Implications for Evo-devo

It is often the case when applying a set of existing concepts to a new system that we can gain an insight into the systems for which the concepts were originally devised. Here we have a prime example of such a situation. Within Evo-devo there is an existing literature on the role that facilitated variation, exploratory behaviour in particular, plays in evolution (Kirschner and Gerhart 2006; Gerhart and Kirschner 2007). In this section of the paper I draw a number of useful and previously unrecognised and unexploited analogies between asocial learning systems and a set of developmental patterns identified as being generative of morphological evolvability (i.e., “facilitated variation”). These analogies are only become apparent when learning is placed in the context of it being a source of evolvability. I begin by outlining the class of developmental patterns that contribute to morphological evolvability: exploratory behaviours.

Exploratory behaviour and novelty

During development of the vertebrate embryo a large number of axons (significantly more than is ultimately required) grow out of the central nervous system towards the extremities. The actual path these many nerves take as they grow is random. They wind their way down the limbs and into the digits in a meandering fashion. Some of these nerves are “lucky.” By chance they hit muscle or organ tissue. This results in the production of a stabilising protein at that location which encourages the nerve to persist. The majority of the nerves generated are less fortunate and exist only fleetingly. While they too grow forth into the limbs they fail to happen upon muscle or organ. In the consequent absence of the stabilising protein that would be generated if they collided with muscle or organ, they shrink back into the nervous system rather than being maintained.

This two-step process of “variation” followed by “selection” in limb neural development is a source of great adaptive benefit; it allows the system to explore or search the local space of phenotypic possibilities and stabilise upon the most suitable

given the internal environment. In other words, the limb nervous system development is flexible enough to meet the demands posed by changes in the musculature or skeletal system arising from mutation. Limb neural development is not alone in exhibiting this type of behaviour. Other morphological systems such as the growth of the mitotic spindles display a similar pattern of “variation” followed by “selection.” These patterns of development are known within evolutionary developmental biology as “exploratory behaviours” (Kirschner and Gerhart 2006; Gerhart and Kirschner 2007).

The presence of such “exploratory behaviours” in the individuals making up populations is a recognised source of morphological evolvability. This is because exploratory behaviours alter the capacity of populations to generate and maintain novel morphological variation. As already discussed, the supply of variation available to a population and its nature (particularly its breadth and scope) directly effects the directions in which that population can move through phenotypic space and how fast those moves can be made (i.e., their evolvability). In short, because exploratory behaviours are able to alter the capacity of populations to generate and maintain novel variation they influence evolvability.

The case of neural development in the extremities already discussed serves well to illustrate exactly how this works. Exploratory behaviour in neural development in the extremities allows the neural architecture of the limbs to adapt to changes in the internal environment of the organism. This means, for example, that mutations that alter the gross structure of the muscle and skeletal components of the limbs are accommodated without the modification of the developmental systems governing their innervation.

Firstly, this has the effect of reducing the number of mutations required for a stable morphological novelty; rather than requiring alterations to the systems governing both the muscle or organ and neural development, only an alteration to the muscle or organ system is necessary. To put it slightly differently, there is no need for alterations to the genes governing limb neural architecture in response to a change in the genes for musculature or skeleton. Hence, a population where individuals have exploratory behaviour in the neural development of the extremities is (all else being equal) better able to generate large-scale variation in limb morphology than a population without it.

The second effect of exploratory behaviour—the suppression lethality—also concerns the supply of variation. Many alterations to musculature or skeleton, for example, would be lethal if there were no matching modification of the limb neural architecture. By having an adaptive process of limb neural development, the potential lethality of mutation is greatly reduced. The phenotype of the organism is partially buffered against changes in the internal environment, allowing genotypes that would not otherwise persist in the population to survive. This means that the sheer number of variants available to a population is increased. Imagine all the possible genotypes that could occur in a population by a single mutation. Many of these genotypes would code for phenotypes that are non-viable or unlikely to persist to reproductive age. Exploratory behaviour reduces the proportion of such genotypes by facilitating the generation of a viable phenotype. In summary, exploratory behaviours have two key effects:

1. *A reduction in the number of genetic mutations required for phenotypic novelty.* If only a small number of mutations are required for major phenotypic change, then the potential of that population for phenotypic variation is greater than for a population where large change requires many mutations. Being better able to generate phenotypic novelty potentially increases the rate at which the population can “move” through design space and thus their evolvability.
2. *The suppression of lethality (the number of possible mutational variants that are lethal) by buffering the phenotype of the organism from changes in its environment.* If fewer mutational changes within individuals in a population have lethal consequences, then the standing variation in that population available to selection is increased, and thus the evolvability of that population is also increased.

These effects alter the evolvability of populations because they, to use a phrase from Kirschner and Gerhart, “lower the hurdle for generating novelty” (2006: 171). They make it easier for populations to move through phenotypic space.

Similarities between exploratory behaviour and learning

An obvious similarity between asocial learning earlier and the role of exploratory behaviour is a reduction in lethality. Like exploratory behaviour, learning reduces the lethality of phenotypic variants by buffering the genotype from changes in the environment (broadly construed). The key difference between the asocial learning system and exploratory behaviour is the target of the selection process. In asocial learning the operation of the system is directed towards adapting the behaviour of the organism to the external environment; whereas, in the case of exploratory behaviour, the operation of the system is directed towards adapting the internal architecture to changes in the internal environment. For example, adapting the neural architecture to changes in the muscular or skeletal morphology.

Exploratory behaviour and learning generate a fit between organisms and their internal or external environment via feedback. In exploratory behaviour and learning, the mechanisms in question increase the viability of individuals, making it easier for the populations that they are members of to persist and survive over time. This in of itself increases the evolvability of the populations (extinct populations cannot evolve), it also increases evolvability by allowing the accumulation of hidden variation (Kirschner and Gerhart 2006). In both cases, the system modifies itself in response to feedback from the internal or external environment in such a way that it increases the viability of the organism. For this reason, we expect that both populations of individuals with developmental systems that exhibit exploratory behaviour and those with learning individuals will be able to better protect their standing variation. Such populations are more evolvable than populations composed of individuals that do not have these properties.

A key feature of both exploratory behaviour and learning systems is their capacity to detect relevant aspects of the environment and respond adaptively. In both cases, a period of variation is followed by selection using information about success or

failure. In the case of exploratory behaviour in the nerve development of the extremities, the multiple nerves sent out from the central nervous system detect whether they have reached muscle or not and retract or grow further depending on what is the case. For simple asocial learning, the organism acts in its environment on a largely trial-and-error basis with feedback on success or failure modifying further behaviour. As already discussed, in learning, this process has specific enabling conditions.

The environment has to have certain epistemic qualities for learning to be possible. Recall for example that the planigale's success is partly dependent on cane toads and frogs being largely perceptually distinguishable. For learning to be beneficial, the environment must also have a certain cost-benefit structure. Learning cannot be so costly that the costs outweigh the benefits, as is the case with the northern quoll and cane toads discussed earlier. It is likely that similar enabling conditions exist for exploratory learning systems.

Exploratory behaviour requires, first, that signals within the body are accurate and salient. In effect, there must be some available signal for the tracking of success so that selection can be discriminate. We might expect such a signal to be more readily available than in the learning case. Within the internal environment, all the elements of the body have the same evolutionary interests⁷—there is no selection on organisms to increase the opacity of the internal environment. Hence, we might well expect that exploratory behaviour would be easier to establish and maintain over time than learning.

Second, like learning organisms, developmental systems with exploratory behaviour also face a cost-benefit analysis. The costs of the redundant deployment of resources on aspects of morphology that ultimately are reabsorbed into the system must be overcome by the benefits of having a system that is plastic. The costs and benefits of exploratory behaviour have a slightly different structure to those for learning, however, because in exploratory behaviour all the phenotypic options are effectively being produced at once and then pruned, rather than being produced successively. For learning, behaviours are produced successively and beneficial behaviours repeated. I suspect this means that the risk of error in exploratory behaviour is thus lower. If an exploratory system such as the nervous system sends out multiple nerves during development it is in effect having many concurrent bets on its internal environment. In a learning system, each bet must be made successively. In the exploratory case, a poor nerve growth pattern in a nerve is not likely to be fatal as other nerves offer concurrent opportunities for success. In the learning case, the choice of a poor behavioural option early on can result in death or injury and thus cost the learning individual significantly.

Understanding how evolvability arises and is maintained in populations is a key question in Evo-devo (Brigandt, forthcoming). The analogies drawn above between learning and exploratory behaviour are a starting point. I will not go into the details any further here, however, due to the restrictions of time. The take home message for the purposes of this paper is simply that the picture of learning in evolvability that I

⁷ There are certain situations (e.g., chimerism) in which there can be divergence in the interests of the cells within the body but these are rare.

present here is not only useful for our understanding of behavioural evolution and the evolutionary trajectories of learning populations but can offer insights to existing targets of research within traditional Evo-devo. I now turn our focus to two further implications of this picture.

Other implications

Conservation and learning as a source of robustness

In this paper I have argued that learning offers a type of lineage level robustness to populations by increasing their evolvability with respect to adaptation. In doing this I have also claimed that populations with learning individuals are at a reduced extinction risk. It is not just that learning individuals are better able to respond to environmental change than non-learners, but that populations of learning individuals are better equipped to maintain standing variation within their populations over time, and hence, are better able to respond (both behaviourally and in terms of standard genetic evolution) to environmental change over time.

For conservation ecology this may mean that learning needs to be taken into account of our assessment of extinction risk. Standard assessments of extinction risk, known as population viability analyses, take into account both features of a population (such as size, genetic diversity, fecundity, fertility and mortality) as well as features of their environment (such as habitat fragmentation) in order to estimate the viability of populations over time (Begon et al. 1986). I have not found analyses of this type that take into account the influence that learning may have on the capacity of populations to respond to environmental change without loss of genetic diversity.⁸ Given the picture presented in this paper, learning can buffer populations from environmental change, and thus be seen to increase their viability in the long term. Consequently, learning is relevant to the analysis of the viability of populations over time.

Our understanding of evolution

Another implication of the arguments in this chapter relates to our understanding of the tree of life. If, as I argue here, learning plays a role in maintaining the supply of genetic variation to populations, then it may explain the differential response of populations to sequential environmental change. For example, were another environmental shift to occur which had significant selective consequences for cane toad-exposed planigale and red-bellied black snake populations, we would expect that planigales would be better placed to respond than red-bellied black snakes (assuming the threat was not another bufonid prey species). The inability of red-bellied black

⁸ I was able to find some research that is at least related. In birds there is evidence that there is no link between behavioural flexibility and extinction risk (Nicolakakis et al. 2003). Behavioural flexibility and asocial learning are not strictly the same thing, however, though the former may be necessary for the latter. It would be interesting to see if there was a relationship between behavioural flexibility and extinction risk when coupled with asocial learning.

snakes to respond to this new selective regime would be as much the consequence of the nature of the environmental change in question as learning; their earlier inability to respond to a change in selective regime having poorly placed them to respond to future selective variations. Consequently, explaining the differential evolutionary trajectory of lineages in the face of multiple environmental changes may require us to refer to the capacity for learning in those lineages and its influence, not only on their adaptation, but also on the supply of phenotypic variation within those lineages over time.

Conclusion

This paper has ranged over a number of topics including evolvability, the role of the standing supply of genetic variation in evolvability and the role of learning in these. Ultimately, what I have argued is that learning, whether it be asocial or social, is able to contribute significantly to the evolvability of populations composed of learning individuals regardless of whether social learning offers a novel inheritance channel or the theory of genetic accommodation is true. In particular, learning is a means via which the standing supply of variation available to populations can be maintained in the face of environmental change. It offers learning populations a source of lineage level robustness. This picture of learning not only highlights the significant impact that learning can have on the evolutionary trajectory of populations but also the conditions that make such impacts possible. It sheds new light on existing topics in Evo-devo such as Kirschner and Gerhart's (2006) discussion of exploratory behaviour.

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