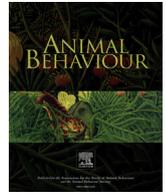




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The role of behaviour in the establishment of novel traits

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It may seem as if behaviour is so plastic that it would not foster the establishment of a genetically determined trait, but under some circumstances, it can greatly influence whether a novel trait, such as a new morphology, spreads in a population. If the behaviours associated with the trait's function already exist, a new variant finds a ready foothold, and selection can act accordingly. Behaviours that are particularly likely to foster novel traits include those that play a role in life history, such as antipredator behaviour, sexual signalling and foraging. Examples of behaviour facilitating novel trait establishment include the spread of a silent mutant in male Pacific field crickets, *Teleogryllus oceanicus*, and the propensity of juvenile fence lizards to show antipredator behaviours towards attacking fire ants, providing a selective opportunity for the evolution of longer limbs. The genetic or physiological mechanisms behind a behaviour can also influence its establishment; for example, learning may generate selection in favour of conspicuous novel traits faster, and for a wider range of traits, than genetically based sensory biases. Just as changes in behavioural traits over evolutionary time may expose populations of individuals to new adaptive zones, behavioural variation within a population may increase the diversity of environments to which individuals are exposed.

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How do new traits arise and how are they maintained? All variation ultimately stems from mutation, but while mutations arise continuously, few become established. Under selection, mutations that confer a benefit to their bearer may be able to persist, and they may become widespread quickly if circumstances allow, resulting in so-called 'rapid' or 'contemporary' evolution (Carroll, Hendry, Reznick, & Fox, 2007). Such contemporary evolution, in which demonstrable genetic change occurs in ecological time-scales, often fewer than 100 generations, is now suggested to be much more common than previously thought (Hendry & Kinnison, 1999; Thompson, 1998). New traits, however, do not arise in a vacuum: they occur in a milieu of other characteristics that may hinder or facilitate their establishment (West-Eberhard, 2003).

At first glance, it may seem as if behaviour would be more likely to hinder the establishment of new genetic variants, because if an animal can respond to a new environmental pressure, say, from a new predator, with a plastic behavioural response, selection

favouring genetic mutations that allow the animal to avoid predation would be diminished. But precisely because behaviour is often plastic and context dependent, it can change within an individual's lifetime to accommodate a new, genetically based morphological or physiological characteristic. Indeed, several authors have suggested that 'behaviour leads the way' in adaptation, or that behaviour acts as a kind of pacemaker for the rate at which evolution occurs (Duckworth, 2008; Hunt, 2012; West-Eberhard, 2003). For example, Hunt (2012) argued that social insect behaviours such as allomaternal care and larval feeding served as precursors for the eventual evolution of eusociality.

Despite this seemingly obvious role for behaviour in what Simpson (1944) famously termed the 'tempo and mode of evolution', behaviour is sometimes seen as superfluous to understanding evolutionary rates. For example, a 2007 special issue of *Functional Ecology* on 'Evolution in Ecological Time-Scales' included behaviour only in a scant handful of its articles. A more recent review similarly focused on population dynamics and other processes above the individual level (Ellner, 2013). We all tend to speak more to those in our own subdisciplines, but we suggest that in this case a consideration of behaviour by those interested in the broader question of how evolution proceeds would be helpful. Which types of behaviours are most likely to aid or hinder the establishment of novel traits? And how common are such links between behavioural

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plasticity and facilitation or hindrance? We explore this relationship here, first by illustrating how behaviour appears to have been important in the rapid adaptive loss of a sexual signal in a field cricket. We address the question of definitions of traits, both in terms of their novelty and the rapidity with which they change. We also discuss situations where behaviour seems to have shaped the acquisition of adaptations, and situations where rapid evolution seems surprisingly rare. We then consider whether behaviour plays a special role in the establishment of new traits, the potentially critical role of mechanisms, and how researchers might merge behavioural biology with evolution in future studies.

CASE STUDY: ADAPTIVE SEXUAL SIGNAL LOSS IN THE PACIFIC FIELD CRICKET

A dramatic example of behaviour influencing the establishment of a novel trait can be seen in the Pacific field cricket, *Teleogryllus oceanicus*, which is widespread in Australia and the Pacific islands and has been introduced to Hawaii (Otte, 1994; Otte & Alexander, 1983). In Hawaii, *T. oceanicus* is parasitized by *Ormia ochracea*, an acoustically orienting parasitoid fly that uses the calling song produced by male crickets to locate its hosts (Cade, 1981; Zuk, Simmons, & Cupp, 1993). Enhanced signalling thus increases both risk from fly parasitism and attractiveness to potential mates (Zuk et al., 1993; Zuk & Kolluru, 1998). Parasitized Hawaiian populations differ in song structure and signalling behaviour from unparasitized populations (Rotenberry, Zuk, Simmons, & Hayes, 1996; Zuk et al., 1993). Most recently, a new male morph that lacks the stridulatory apparatus necessary for producing song has arisen and spread on two of the Hawaiian Islands, Oahu and Kauai (Zuk, Rotenberry, & Tinghitella, 2006). This morph, called flatwing, became prevalent on Kauai in fewer than 5 years, or 20 generations (Zuk et al., 2006).

Although the flatwings are protected from the flies, which cannot localize their hosts without an acoustic signal, the loss of song poses obvious difficulties to the crickets in mate attraction. Yet the flatwings persist, along with some callers on both of the islands where the mutants occur, indicating that these difficulties have been overcome. Field experiments showed that flatwings on Kauai are more responsive to playback, a behaviour that could presumably allow them to act as satellites more easily and encounter females that are attracted to callers (Tinghitella & Zuk, 2009; Zuk et al., 2006).

But how did such a change in responsiveness come about? It is less than parsimonious to suggest that concomitant major changes in the probably numerous genes controlling phonotaxis or female choosiness happened to coincide with the single gene mutation that causes the flatwing phenotype. Instead, perhaps pre-existing behavioural plasticity allowed the wing mutation to spread.

Such plasticity might have been present in the *T. oceanicus* population because their environment is variable, and different mating strategies might be useful under different circumstances. Female crickets would therefore be expected to benefit from operating via simple rules of thumb, such as, 'If only a few conspecific males are calling, move closer to those callers,' or 'If mating opportunities are limited, as indicated by reduced encounter rates, be more likely to accept males that are not producing a courtship song'. An environment with few callers and low encounter rates could occur because of poor habitat, a catastrophic event, or, in the case of the new mutants in Hawaii, the existence of silent flatwings. The behavioural response to a silent environment could thus have served to facilitate the establishment of the silent mutants.

Evidence supporting this suggestion comes from manipulation of the crickets' acoustic environment during development. Male

T. oceanicus reared in song-free incubators are more responsive to playback than those reared in incubators with song (Fig. 1; Bailey, Gray, & Zuk, 2010). The difference between rearing environments was more pronounced in older males, suggesting a cumulative effect of environment on behavioural plasticity (Bailey et al., 2010). Similarly, female *T. oceanicus* reared in silence move towards a playback sooner, move further and are less choosy in their response to variation in elements of the calling song than are females reared in incubators with song (Bailey & Zuk, 2008).

DEFINING 'NOVELTY' AND 'RAPIDITY'

Before discussing the question of how (and whether) behaviour influences the rapid evolution of novel traits, it is useful to clarify the meaning of both 'rapid evolution' and 'novel traits'. Both of these definitions have been the subject of considerable recent discussion in their own right (Ellner, 2013; Peterson & Muller, 2013), so we provide only a brief summary here.

It has become increasingly apparent that evolutionary changes can occur over a timescale that allows researchers to observe their effects (Ellner, 2013; Thompson, 2013). These observations contrast with traditional conceptions of evolution as a gradual process that, at least in complex organisms, results in observable changes only over geological time (Slobodkin, 1961). However, the answer to 'how rapid is rapid?' is not always obvious. Many researchers accept a cutoff value of 100 generations or fewer as a general rule for what defines a 'rapid' change (Carroll et al., 2007; Zuk & Tinghitella, 2008). Others, however, focus on the effects of an evolutionary change on an ecological response variable of interest. Under this definition, an evolutionary change is rapid if the magnitude of its ecological effect is similar to or greater than the magnitude of the effects of the environmental factors influencing it (Ellner, Geber, & Hairston, 2011; Hairston, Ellner, Geber, Yoshida, & Fox, 2005). The unifying theme of most existing definitions of rapid evolution, however, appears to be that an evolutionary change is rapid when it occurs on a short enough timescale that it cannot be ignored when considering what shapes the ecology of a system.

As with rapid evolution, discussions regarding the definition of evolutionary novelty have largely asked some variation of 'how novel is novel?' One intuitive, but narrow, definition of an

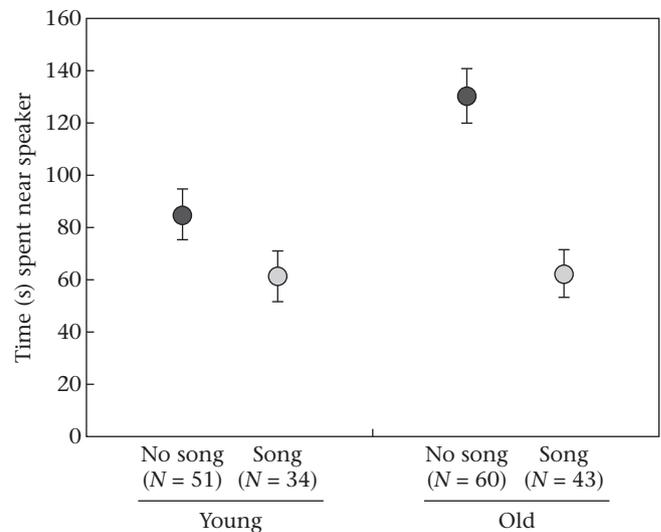


Figure 1. Response to playback of conspecific song by male *T. oceanicus* that were reared in incubators with ('song') or without ('no song') conspecific song. Young males: 6 days posteclosion; old males: 13 days posteclosion. From Bailey et al. (2010).

evolutionary novelty is a phenotype that is clearly nonhomologous to pre-existing phenotypes and positively selected immediately upon arising (Moczek, 2008). However, this definition may exclude traits that many researchers would describe as novel, such as those that result from co-option or reorganization of existing developmental mechanisms (Cebra-Thomas et al., 2005; Emlen, Lavine, & Ewen-Campen, 2007; West-Eberhard, 2005). Other definitions focus on the process by which novel traits arise (Hallgrímsson et al., 2012), but these definitions struggle to deal with traits that are initially nonadaptive (Peterson & Muller, 2013). For our purposes here, we will focus on the ecological functions and effects of traits we characterize as novel (Mayr, 1960; Peterson & Muller, 2013; Pigliucci, 2008). We consider a trait novel if a heritable change in that trait allows for the exploitation of a new behavioural or ecological niche (Moczek, Cruickshank, & Shelby, 2006; Prum, 2005) or allows population persistence in the face of a challenge that the population had not previously encountered (Langkilde, 2009; Zuk et al., 2006).

We thus define both 'rapid evolution' and 'novel traits' in terms of the effect of evolution on ecology (Ellner et al., 2011; Peterson & Muller, 2013). This focus is especially relevant given the increasing recognition of how common and important such effects can be (Carroll et al., 2007). In the remainder of this review, we discuss the extent to which the pre-existing behavioural characteristics of a population may influence the likelihood that novel traits will evolve rapidly within that population. We argue that, when considering how likely a novel trait is to become established in a population, it is crucial to understand the behavioural context in which that trait arises.

WHAT TYPES OF BEHAVIOURS ARE IMPORTANT FOR THE EVOLUTION AND ESTABLISHMENT OF NOVEL TRAITS?

Behavioural plasticity allows organisms to respond to immediate pressure by moving away or changing the way they interact with the environment (e.g. use a new food resource, avoid a new predator, maintain body temperature). That such behavioural plasticity can forestall natural selection by shielding organisms from selection pressure is intuitive (Brandon, 1988; Huey, Hertz, & Sinervo, 2003; Losos, Schoener, & Spiller, 2004; Wake, Roth, & Wake, 1983). An excellent example of this is behavioural thermoregulation. Body temperature has important effects on fitness-relevant traits, especially in ectotherms, including digestive efficiency, development and growth rates, and locomotor performance (Huey & Stevenson, 1979; Wieser, 1973). Therefore, the ability of ectotherms to maintain their body temperature, often within a very precise range, in the face of variable environmental temperatures, such as those resulting from global climate change, can be highly adaptive (Gvozdić, 2012). Several recent studies suggest that plasticity in thermoregulatory behaviour is more likely to inhibit evolutionary change and buffer populations from novel selective pressures (Huey et al., 2003). Preferred body temperature in hatchling side-blotched lizards, *Uta stansburiana*, appears to be influenced, via maternal effects, by the mother's preferred body temperature as an adult (Paranipe, Bastiaans, Patten, Cooper, & Sinervo, 2013). Juvenile estuarine crocodiles, *Crocodylus porosus*, exposed to cold or warm water temperatures adjusted their preferred body temperatures in the direction of the temperature change and also showed changes in their thermal performance curves, such that their physiological performance was not affected by changes in the thermal environment (Glanville & Seebacher, 2006). Similar plasticity occurs in tiger snakes, *Notechis scutatus*, reared in captivity in different thermal environments (Aubret & Shine, 2010).

It is worth emphasizing that the plastic behaviour in this case is considerably less complicated than many of the other behaviours we describe as likely to affect the direction or speed of adaptation, such as antipredator behaviour or mate choice (Dukas, 2013; Snell-Rood, 2013). Behavioural thermoregulation by ectotherms often involves little more than movement among microhabitats over the course of the day (e.g. from sun to shade; Huey et al., 2012), something that they do remarkably precisely, allowing them to maintain consistent body temperatures across extremely variable environmental conditions (Andrews, 1998).

That behavioural flexibility can enhance the evolution of novel traits is less obvious. However, behavioural change within an individual's lifetime in response to its internal and/or external environment can shift the selection pressures to which additive genetic variance is exposed, leading to the evolution of novel traits (Duckworth, 2008; Hunt, 2012; West-Eberhard, 2003). This role of behavioural plasticity was first articulated by Baldwin (1896), who argued that more plastic individuals within a population were the most likely to live long enough for selection to act positively on their genetic variations. Do all behaviours affect evolution equally? We argue that behaviours that are more flexible or plastic should have the greatest influence on the evolution of new traits.

Behaviours that are typically most plastic are those that play an important role in life history, as it is critical that they be able to respond (continue to function) if conditions change. Below we describe some examples where such plasticity has promoted the establishment of novel traits.

Predator Avoidance

Predation threat can be variable, predator identities can change between populations, and antipredator defences can be costly; for example, there is often a trade-off between foraging and predator vigilance behaviour (Harvell, 1990; Levins, 1968; Skelly, 1992). Flexibility of antipredator behaviour allows animals to respond quickly to changes in predation environment (Lima & Dill, 1990). Behavioural responses to novel predation threats can lead to the establishment of novel traits by allowing populations to persist long enough for evolutionary adaptations to take place, and/or by exposing populations to novel selection pressures.

Native fence lizards, *Sceloporus undulatus*, have become behaviourally responsive to attack by invasive predatory fire ants, *Solenopsis invicta*, performing vigorous body twitches and fleeing from attack, behaviours that are rare in naïve populations (Langkilde, 2009; Fig. 2a, b). This plastic shift in behaviour increases survival by reducing encounters with fire ants (Freidenfelds, Robbins, & Langkilde, 2012) and by removing fire ants in the case of an attack (Graham, Freidenfelds, McGormick, & Langkilde, 2012; Langkilde, 2009; Langkilde & Freidenfelds, 2010). Fence lizards from fire ant invaded sites have also evolved longer hindlimbs, which increase the effectiveness of this behaviour in removing attacking fire ants (Langkilde, 2009; Fig. 2c, Fig. 3). *Anolis* lizards on small Caribbean islands alter their habitat use following the introduction of ground-dwelling predators, moving off the ground and into trees (Losos et al., 2004). Although in the short term these predators select for larger females and longer-legged males, which can run faster and/or are harder to consume, this change in habitat reverses the selective pressure on limb length, favouring shorter limbs that increase locomotor efficiency on the narrower substrates provided by this new arboreal habitat (Irschick & Losos, 1999; Losos, 1994).

In both cases, the ability to adjust behaviour to avoid predation during an individual's lifetime has led to the evolution of increased hindlimb length, either as a result of selective pressure to increase the effectiveness of the behaviour, in the case of the fence lizards

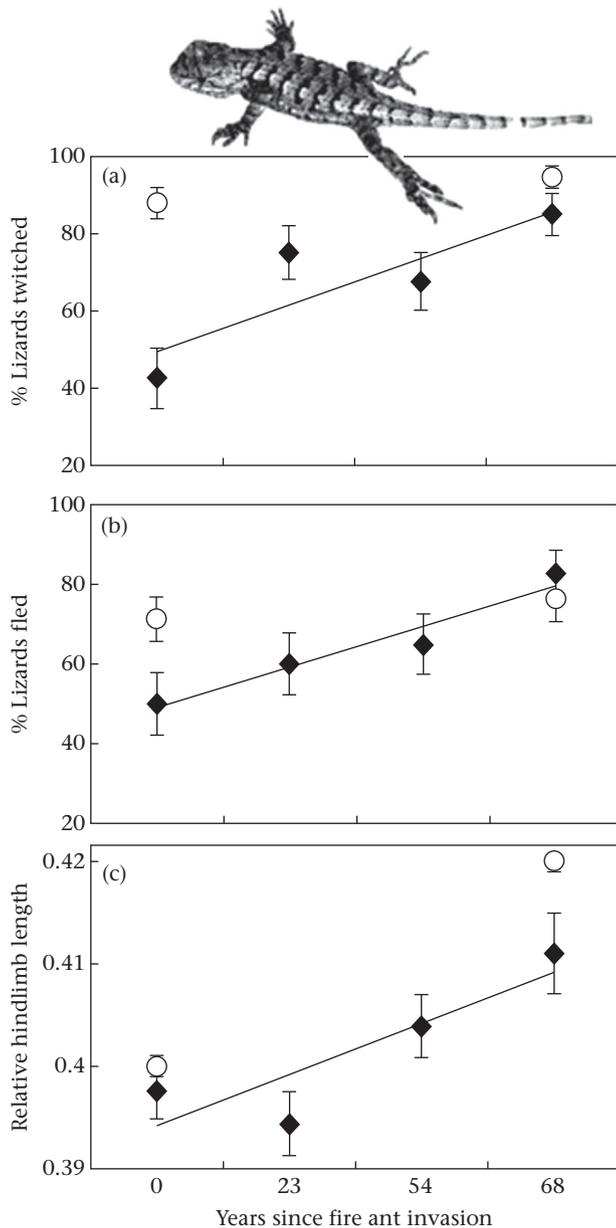


Figure 2. Change in use of (a) body twitch and (b) flee defensive behaviour, and (c) the relative hindlimb length (shown as hindlimb length/snout–vent length, SVL) of adult (solid symbols) and juvenile (open symbols) fence lizards, *Sceloporus undulatus* (inset), across sites with different histories of fire ant invasion. Sexes are pooled for all panels; values for adults represent mean \pm SE for 20 male and 20 female lizards from each site; values for juveniles represent mean \pm SE for 157 juveniles laboratory-born to 16 females (at 0 years since invasion), and 128 juveniles laboratory-born to 18 females (at 68 years since invasion). From Langkilde (2009).

(the same environmental trigger as for the behaviour itself; Langkilde, 2009), or, in the case of the anoles, as a result of pressure imposed by new habitat (a different environmental trigger; Losos et al., 2004).

Foraging and Food Preference

Plasticity in foraging tactics, prey choice or food preference can allow animals to survive periods during which their preferred food is rare or absent, to take advantage of new food resources and to avoid feeding on novel unpalatable food items. For example, translocated Arctic charr, *Salvelinus alpinus* L., that fed on a different

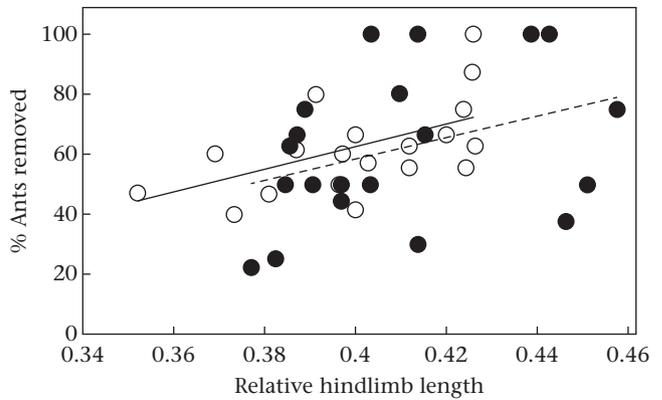


Figure 3. Relation between relative hindlimb length of a fence lizard, *Sceloporus undulatus* (hindlimb length/snout–vent length, SVL) and effectiveness of behaviour (body twitch: open circles, dashed line; flee: solid circles, solid line) for removing attacking invasive fire ants, *Solenopsis invicta*. From Langkilde (2009).

diet from that of the source population became piscivorous at a later age, after approximately six generations (25 years) of divergence from the source population (Michaud, Power, & Kinnison, 2008). Translocated fish showed concurrent inherited changes in morphology, including having a smaller gape size relative to body length, which constrains foraging ability of these morphs and is associated with inherited differences in dietary preference (Adams & Huntingford, 2002). The change in diet occurred despite the fact that the ancestrally preferred prey item was still available in the new habitat, suggesting that the behavioural shift in prey choice preceded morphological evolution.

Mating and Mate Attraction

Reproduction is a critical component of fitness, and plasticity in mating behaviour allows animals to find and attract mates, and therefore maximize reproductive output, under changing conditions. As a result, we expect to see plasticity in mating and mate attraction behaviour leading to the evolution of novel sexual traits. This is demonstrated by the previously mentioned spread of a new obligately silent morph of Pacific field cricket, despite the cost of signal loss to mating, potentially because pre-existing behaviours alter phonotaxis and choosiness depending on acoustic rearing environment. We provide some additional examples below.

Many species use calls as the primary mechanism for attracting and selecting mates. One of the less considered impacts of anthropogenic activities is loss of acoustic space. Songbirds alter their vocalization in noisy urban environments, singing more loudly (Brumm, 2004), at higher frequency (Potvin, Parris, & Mulder, 2011; Slabbekoorn & Peet, 2003; Fig. 4) and/or at quieter times of the day (Fuller, Warren, & Gaston, 2007; Nemeth et al., 2013; Warren, Katti, Ermann, & Brazel, 2006). Similarly, native white-banded tree frogs, *Hypsiboas albomarginatus*, alter their calls when exposed to recorded calls of the invasive American bullfrog, *Lithobates catesbeianus*, calling at higher frequencies and decreasing signal duration (Both & Grant, 2012). Changes in call structure can be adaptive by optimizing call transmission (Morton, 1975). However, such changes could expose native species to novel selection pressures. Females use male calls to choose mates, and changes in calls may cause them to select suboptimal mates, imposing selection on female call preference. Altered calls may impose fitness costs on males if they are less likely to attract females, are more energetically costly, or expose males to detection by predators that are attracted to the new calls (Bee, 2009; Bee & Swanson, 2007; Both & Grant, 2012; Ryan, 1988).

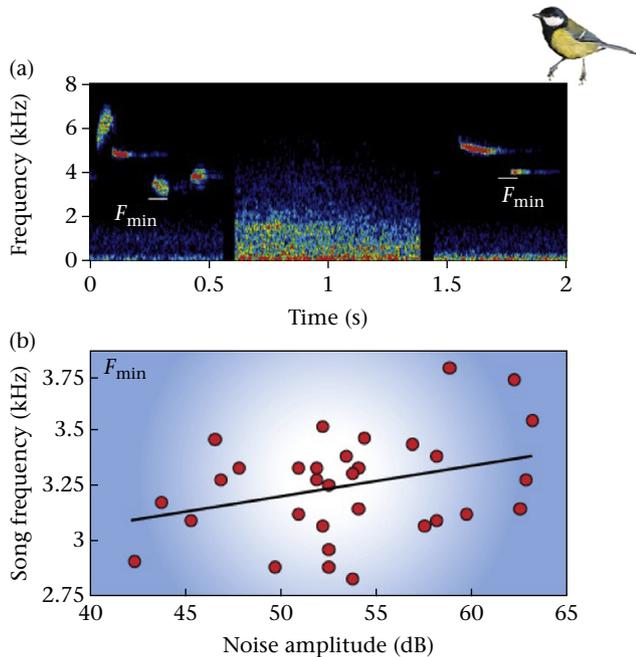


Figure 4. Song frequency versus ambient noise in urban great tits, *Parus major*. (a) Songs from birds in a low-noise territory (left) have a lower minimum frequency than do songs from birds in a high-noise territory (right) recorded at a quiet moment. The centre shows the typical spectrum of urban noise. (b) Owners of territories with higher average noise amplitude have higher average minimum frequency songs. From Slabbekoorn and Peet (2003).

Female dark-eyed juncos, *Junco hyemalis*, from a small population that moved to a new environment breed longer, and this timing is more variable; likely a plastic response to the milder climate (Price, Yeh, & Harr, 2008). This extended breeding season allows for multiple clutches, more than are possible in the more hostile environment of the source population. Within just eight generations, the birds experienced a 22% reduction in the white portion of the tail feathers (signals of dominance; Yeh, 2004). This appears to be the result of mortality-driven selection against white-tailed juveniles. The longer breeding season means that late-hatching juveniles are likely to find themselves in competition with larger, early-hatching juveniles. Late-hatching individuals that signal as subordinate (i.e. have reduced tail white) in aggressive interaction with early-hatching individuals may be at an advantage relative to stronger signallers.

Sexual selection is often supposed to lead to rapid changes in morphology, given its role in reproductive isolation. Surprisingly, however, we see few cases of plasticity in mating and mate attraction behaviour leading to the rapid evolution of novel traits. A literature search by Svensson and Gosden (2007) found relatively few cases of sexually selected traits that had exhibited substantial evolution in fewer than 100 generations. Svensson and Gosden (2007) suggested several possibilities for the paucity of examples compared with the results of similar searches for examples of changes in naturally selected traits, including a bias in the literature, but we propose an additional explanation relevant to the idea that behavioural flexibility can help in establishing new traits. Proper functioning of sexually selected traits such as ornaments or weapons require not only the signals themselves, but also the physiology and morphology necessary to produce and recognize the signal, as well as the behaviours associated with delivering and receiving the signal (Zuk & Tinghitella, 2008). A new colour that is not recognized, or a tail extension that is not incorporated into an existing display, will have no evolutionary traction if, for example,

females do not respond to longer tails because tails are not used in courtship.

Movement Patterns

Movement patterns of populations and individuals can be categorized as continuous (i.e. how far an individual will disperse from its natal grounds), or discontinuous (i.e. whether or not a population exhibits migration). The distance, direction and speed with which animals disperse are often plastic and can have adaptive benefits (Johnson & Gaines, 1990). Environmental factors can influence an organism's dispersal, driving it to move to areas of higher resource availability, avoid climatic extremes, and find mates. Organisms also show plasticity in whether or not they migrate; this again is often determined by changes in the environment and subsequent shifts in the relative costs and benefits of making these long journeys (Alterstam, Hedenstrom, & Akesson, 2003; Grayson & Wilbur, 2009; Olsson, Greenberg, Bergman, & Wysujack, 2006). These behavioural changes can expose organisms to novel selection pressures, and thus facilitate the evolution of novel traits.

In the decades following their introduction to Australia, cane toads, *Rhinella marina* (previously *Bufo marinus*) have been dispersing ever-more rapidly (Phillips, Brown, Webb, & Shine, 2006; Fig. 5). Toads achieve this faster dispersal by marching along relatively obstacle-free highways (Brown, Phillips, Webb, & Shine, 2006). Faster dispersing toads likely get a fitness advantage, as being ahead of the dispersal front reduces competition with conspecifics, particularly amongst tadpoles in breeding ponds (Phillips et al., 2006). These rapid dispersers show physiological and morphological adaptations that aid in dispersal: greater locomotor endurance (Llewelyn, Phillips, Alford, Schwarzkopf, & Shine, 2010) and longer limbs (Phillips et al., 2006). The evolution of these traits is likely the direct result of plasticity in movement patterns ('spatial sorting'; Shine, Brown, & Phillips, 2011): assortative mating between the fastest-dispersing toads at the invasion front results in an evolutionary increase in traits associated with increased dispersal rates (the 'Olympic Village Effect'; Phillips, Brown, & Shine, 2010). However, some of the traits associated with dispersal behaviour are not keeping pace with these rapid changes. 'That incredible increase in toad speed has put enormous pressure on the toads' bodies – bodies that had evolved to sit around a swamp in Brazil and eat flies, not sprint across Australia like an Olympic long-distance athlete.' (T. Shine, www.canetoadsinoz.com). Toads that are adapted to rapid dispersal (large body size, relatively long legs, move frequently) have high rates of spinal arthritis, providing evidence for costs of behaviourally mediated rapid evolution (Brown, Shilton, Phillips, & Shine, 2007).

HOW DOES MECHANISM MATTER?

Our understanding of why behaviour would facilitate the establishment of a novel trait is enriched by a consideration of the mechanisms by which both the novel traits and the behaviours that favour them arise. We define 'mechanism' as the set of processes by which traits arise, including within- and among-individual components. Within-individual components include the genetic underpinnings of traits and developmental mechanisms. In the case of behaviours, these also include the hormonal and neural underpinnings of the activation of behaviours, as well as learning, the addition of adaptive behaviours to the repertoire based on previous experience (Adkins-Regan, 2012; Real, 1994). Between-individual mechanisms include the inheritance of genetically controlled behaviours and cultural transmission (Duckworth, 2008). The mechanisms by which behaviours arise and are transmitted between

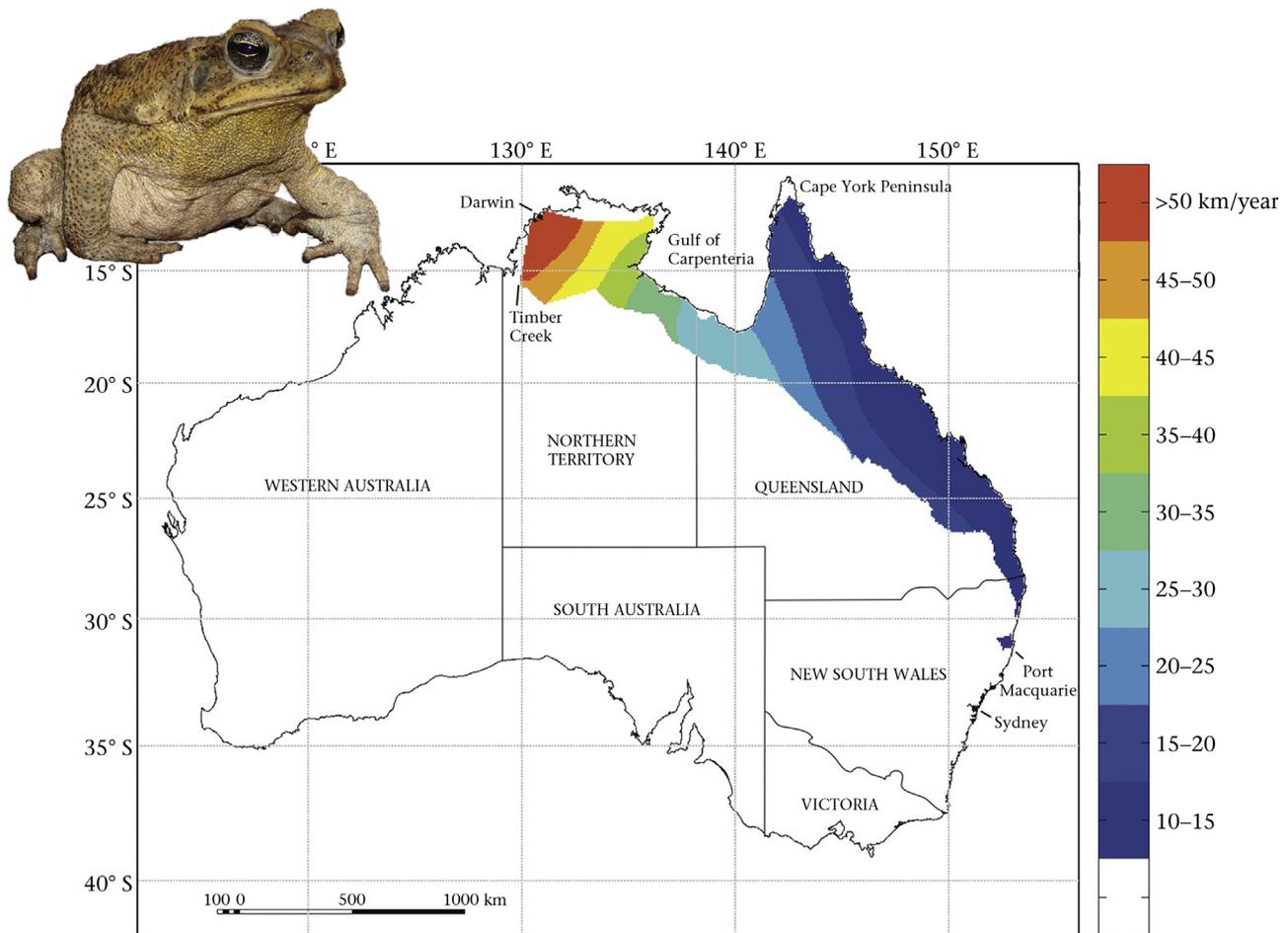


Figure 5. Invasive cane toads, *Rhinella marina*, are moving faster and faster through tropical Australia. Toads at the invasion front are moving further (~ 100 m/day, shown in red) than those near the sources of introduction (~ 10 m/day, shown in dark blue). Graph: Mark C. Urban.

individuals in turn determine the timescale on which behaviours arise. Whether a behaviour that could facilitate the establishment of a novel trait actually does so depends in part on whether the behaviour arises in the same generation as the novel trait.

Behavioural Mechanisms and Behaviour as a Source of Selection

For behaviour to have an evolutionary effect, in this case, the establishment of a novel trait, it must occur on a long enough timescale and frequently enough within a population to generate stable selection (Duckworth, 2008). Novel traits often occur infrequently in a population, whether they represent the tail ends of a distribution of continuous variation or are rare mutants with discrete phenotypic differences. For a behaviour to generate a selective environment that favours a rare novel trait, it should fulfil the following criteria: first, it must occur within the same generation as the novel trait. For a behaviour to generate selection on a trait, individuals that possess the trait must express behaviours that render the trait adaptive or interact with others that do. Second, the behaviour should be sustained across generations. If positive selection for the novel trait is not sustained over time, the novel trait may be lost even if it is initially favoured.

Some mechanisms are more likely than others to produce selection that occurs rapidly enough and is consistent enough in both time and space that the trait becomes established. Learning allows animals to acquire nongenetically programmed behaviours

specifically in response to novel stimuli, potentially allowing animals to express a wider range of responses to previously unencountered variation in phenotype (Dukas, 2009, 2013). This makes learning a potentially powerful mechanism for rapidly generating adaptive responses to novel trait variation. For example, female collared flycatchers, *Ficedula albicollis*, with previous experience of males with an artificial, unfamiliar red forehead patch were more likely to pair with ornamented males than with control males lacking the novel forehead patch (Qvarnström, Blomgren, Wiley, & Svedin, 2004). Theoretical results show that song learning accelerates speciation: Lachlan and Servedio (2004) compared models of songbird signal divergence in which male signals and female preferences were either wholly genetically based, or resulted from genetically based predispositions to learn (or prefer) particular songs. In the purely genetic models, rare alleles were selected against because rare males failed to find mates with matching preferences, and rare females failed to find males whose signals matched their preferences. In the learning models, however, rare male and female variants were more likely to learn the common signal, and common male and female variants were more likely to learn a novel signal, ultimately reducing selection against rare genotypes. Cultural transmission allows selection to persist between generations, causing continued selection in favour of the novel trait. Learning may generate selection in favour of conspicuous novel traits faster, and for a wider range of traits, than might genetically based sensory biases (Dukas, 2006, 2013; Hebets & Sullivan-Beckers, 2010).

Genetic Mechanisms and Response to Selection

The strength of selection, in this case, generated by a behavioural response to a novel trait, is one determinant of whether a trait becomes established. Another determinant of how a trait responds to selection is the genetic basis by which it arises. This includes, among other things, the number of loci contributing to the trait and their relative effect sizes and the amount of standing genetic variation (Barrett & Schluter, 2008). A key consideration is the relationship between the magnitude of selection pressure and the effect sizes of genes responding to selection: strong selection may be more likely to act on major genes, whereas weaker selection may be more likely to influence a larger number of relatively minor genes (Thompson, 2013).

Many examples of rapid trait evolution are underlain by genes of major effect (Reznick & Ghalambor, 2001). Genetic architecture may play a key role in the evolution of the flatwing morph in the *T. oceanicus*–*O. ochracea* system: among-island differences in calling behaviour (e.g. changes in the diel patterning of calling) suggest that some components of calling behaviour have responded to selection by *O. ochracea* (Zuk et al., 1993), and calling behaviour responds to experimentally applied directional selection (Cade, 1981). The simple genetic architecture of the flatwing trait, which is inherited as a single-locus, sex-linked trait (Tinghitella, 2008), may have facilitated a rapid response to strong selection because it is a mutation of large effect rather than a polygenic trait such as frequency of calling behaviour. There are many examples of traits controlled by a few major loci spreading rapidly in response to strong directional selection. Resistance to commercially used pesticides is often underlain by a few genes of large effect (Roush & McKenzie, 1987), as is heavy metal toxicity resistance in plants (Macnair, 1993). A single gene of large effect seems to be responsible for the ability of garter snake, *Thamnophis sirtalis*, populations to evolve complete resistance to the toxins of their newt (*Taricha* spp.) prey (Hanifin & Brodie, 2008). These examples are in line with the theoretical prediction that the genetic architecture most likely to respond to strong directional selection, as opposed to weaker selection over the long term, comprises few mutations of large effect.

Hormones, Adaptive Suites and Adaptive Change

Hormones are one of the key mechanisms governing behaviour and are often involved in the development of a well-integrated phenotype (Adkins-Regan, 2006). The regulation of suites of traits by a relatively small number of hormones often means that these traits do not evolve independently, and this is often regarded as a constraint on the range of phenotypes that can evolve (Ketterson & Nolan, 1999). However, if hormones result in a suite of traits that are collectively adaptive in a new environment, they can result in dramatic fitness increases relative to a suite of physiologically and genetically unlinked traits. If directional selection on a novel trait variant also acts on endocrine systems in ways that result in a well-integrated adaptive phenotype, the trait may become established very rapidly.

This appears to be the case in the ability of soapberry bugs, *Jadera haematoloma*, to adapt rapidly to novel host plants. Soapberry bugs feed on the seeds of fruiting plants, and their beaks (mouthparts) have repeatedly evolved rapidly to match the size of the fruits whose seeds they feed on (Carroll & Boyd, 1992; Carroll, Klassen, & Dingle, 1998). A selection experiment revealed high standing genetic variation in beak length, which likely influences the species' ability to adapt rapidly to the availability of local hosts. Lines selected for long beaks show differences in several life history traits mediated by juvenile hormone, including a higher proportion

of long-winged, potentially migratory morphs, and differences in egg size (Dingle, Carroll, & Famula, 2009). The life histories of the local host species suggest that a correlation between beak morphology and life history traits may be adaptive: the host that selects for long beaks, the balloon vine, develops few fruits and does so asynchronously with other nearby balloon vines (Carroll & Boyd, 1992; Carroll et al., 2005). Sparse, asynchronously available resources should favour the ability to migrate (i.e. the long-winged morph) and other life history traits mediated by juvenile hormone (Dingle, 1972; Dingle & Winchell, 1997). Hormonal coordination of an adaptive suite of traits may be an important determinant of the population response to selection.

IS BEHAVIOUR DIFFERENT?

Considerable research into the effect of behaviour on the trajectory of evolution has focused on the effects of behavioural traits on diversification rates, often by comparing the diversity of higher-order taxa that differ in some behavioural trait (Barraclough, Harvey, & Nee, 1995; Kraaijeveld, Kraaijeveld-Smit, & Mann, 2011; Panhuis, Butlin, Zuk, & Tregenza, 2001). Both theoretical and empirical work have also considered the question of whether the magnitude of phenotypic plasticity within a population could influence the speed or direction of subsequent evolution, especially in response to a changing environment (Draghi & Whitlock, 2012; Price, Qvarnström, & Irwin, 2003; Price, Yeh, & Harr, 2008; West-Eberhard, 2005). In this section, we discuss the relationship between how behavioural traits appear to affect macroevolutionary diversification and the ways they may affect the evolution of novelty at the microevolutionary scale. We will also consider whether behavioural plasticity differs from phenotypic plasticity more generally, as well as whether any of those differences may be relevant for its propensity to influence the rapid evolution of novel traits.

Behaviour Influences Macroevolutionary Diversification

The hypothesis that greater behavioural complexity or plasticity could increase diversification rates at the among-taxon level has received both theoretical and empirical support (Dukas, 2013; Price et al., 2003; Snell-Rood, 2013; Sol, Stirling, & Lefebvre, 2005; Wcislo, 1989). Several nonmutually exclusive mechanisms could account for this pattern. Behavioural differences among partially diverged populations may reduce gene flow between them, thereby accelerating speciation (Panhuis et al., 2001; West-Eberhard, 1983; Zuk & Tinghitella, 2008). Species in which individuals show alternative behavioural tactics, or in which all individuals show generalist strategies, may exploit wider niches than species that are more specialized. These wider niches could insulate them against extinction in changing environments (Clavel, Julliard, & Devictor, 2010; West-Eberhard, 1986). Finally, changes in behaviour may prompt diversification by exposing individuals to new abiotic, biotic or social environments in which they are subject to novel selective pressures (Sol, Stirling, et al., 2005).

The Relationship between Diversification and Innovation

Diversification and evolutionary novelty are closely connected. Traits described as 'key evolutionary innovations' are often used as synapomorphies to define clades and are frequently invoked to explain the diversification of particularly successful or speciose taxa (Bond & Opell, 1998; Hunter, 1998; Liem, 1973; Maia, Rubenstein, & Shawkey, 2013). Many of the arguments regarding how behaviour may promote macroevolutionary diversification, therefore, also apply to the question of how behaviour may

promote the evolution of novel traits within populations (West-Eberhard, 2005). If behavioural plasticity allows a population to persist in the face of a threat that might otherwise lead to population extinction (Fig. 6), novel selective forces in this new environment may drive the evolution of novel traits (Baldwin, 1896; Crispo, 2007). Changes that are initially environmentally induced may eventually become heritable through genetic assimilation, especially when plasticity itself is costly (Crispo, 2007; Price et al., 2003; West-Eberhard, 2003). Just as changes in behavioural traits over evolutionary time may expose populations of individuals to new adaptive zones (Sol, Stirling, et al., 2005), behavioural variation within a population may increase the diversity of environments to which individuals are exposed. When individuals within a population are collectively exposed to more forms of selection, the probability may be greater that some of them will possess a trait variant that is both novel and adaptive in at least one of these environments (Snell-Rood, 2013).

Behavioural Plasticity versus Plasticity in General

Many of the arguments regarding the effects of behavioural plasticity on diversification among populations or the evolution of novel traits within populations have been framed as being about phenotypic plasticity more generally (Draghi & Whitlock, 2012; Price et al., 2003, 2008; West-Eberhard, 2005). Phenotypic plasticity has been observed in virtually every category of trait, including morphology, physiology, life history and demography (Miner, Sultan, Morgan, Padilla, & Relyea, 2005). Many of the examples cited to explain how phenotypic plasticity may drive diversification or the evolution of novelty refer to behavioural traits (Miner et al., 2005; Moczek et al., 2006; Sol, Stirling, et al., 2005), but it is not clear whether this represents a true difference between behavioural plasticity and plasticity in other traits. Instead, the preponderance of behaviour examples in the discussion of phenotypic plasticity's effects on evolution may represent a bias in research or a tendency of review authors to select intuitively appealing examples.

The parallels between the discussions regarding the evolutionary effects of phenotypic plasticity in general and behavioural plasticity specifically therefore prompt two related questions. (1) Is behavioural plasticity quantitatively or qualitatively different from plasticity in other traits in some way that makes it unusually likely

to promote the evolution of novel traits? (2) Do any of the putatively unique characteristics of behavioural plasticity tend to speed up the rate at which novel traits become established?

Few studies have explicitly compared the degree of plasticity in behavioural traits versus other trait categories, although the limited evidence that exists (Fig. 7) suggests behaviour may show greater plasticity than morphology in a few species (Relyea, 2001). However, behavioural plasticity may exhibit unique characteristics that differentiate it from other categories of plasticity. Behavioural traits represent the integration of all levels of organization within an organism, including morphology, physiology, neurology and genetics (Kappeler & Kraus, 2010; Rendall & Di Fiore, 2007). Changes in behaviour therefore expose entire suites of other traits to novel abiotic, biotic or social environments. The role of the social environment is particularly important to a discussion of behavioural traits, since a social environment cannot exist without behavioural interactions. Also, changes in an individual's behaviour often occur on shorter timescales than changes resulting from plasticity in morphology or physiology, and they are often more reversible (Dukas, 2013; Relyea, 2001; Snell-Rood, 2013).

This final difference between the ways in which behaviour is plastic relative to other plastic traits may contribute an answer to question 2, providing a mechanism by which behavioural plasticity promotes not only the evolution of novel traits, but also their rapid evolution. It seems intuitive that, if behavioural changes occur more quickly and can be reversed more easily than changes in other plastic traits, they could facilitate more rapid evolutionary changes. Several studies have supported this effect in the specific case of learning as an example of behavioural plasticity (Dukas, 2013), including the evolution of the ability to digest lactose into adulthood in populations of humans that learned to domesticate cattle (Tishkoff et al., 2006). However, at least one modelling study complicates the idea that adaptation occurs more rapidly when phenotypic plasticity (behavioural or otherwise) 'primes the pump'. Ancestral (2000) modelled the approach of both phenotypically plastic and nonplastic populations to a new phenotypic optimum. She found that, while plasticity shortened the initial 'search' for the optimal phenotype, the plastic population reached that optimum faster than the nonplastic population only when the initial genotype distribution of a population was distant from the optimal distribution. Behavioural traits such as dispersal and migration (Pearse et al., 2009; Phillips et al., 2006) may introduce populations to conditions very different from those to which they are adapted, exposing those populations to particularly strong selection and thus potentially causing them to evolve rapidly in response.

Behavioural Plasticity as a Buffer

The case for behaviour as a promoter of rapid adaptation or evolutionary novelty is not universal. Indeed, it may be more intuitive to expect that a population that can respond to a selective force by plasticity would be less likely, rather than more likely, to undergo evolutionary change (Kappeler & Kraus 2010; Price et al., 2003). This effect has been called 'behavioural inertia' or 'behavioural inhibition' (Huey et al., 2003; Sol, Stirling, et al., 2005), and empirical evidence supports its importance in some cases. For example, populations of the lizard *Anolis cristatellus* distributed along an altitudinal gradient show behavioural plasticity in thermoregulatory strategy, which appears to have buffered them from evolving differences in thermal physiology (Huey et al., 2003).

Both behavioural plasticity and other categories of phenotypic plasticity appear to slow evolution and inhibit innovation in some cases (Huey et al., 2003). Also, the questions of whether behaviour speeds up evolution and whether it promotes novelty are often considered separately (Ancestral, 2000; Huey et al., 2003; Lister, 2013;

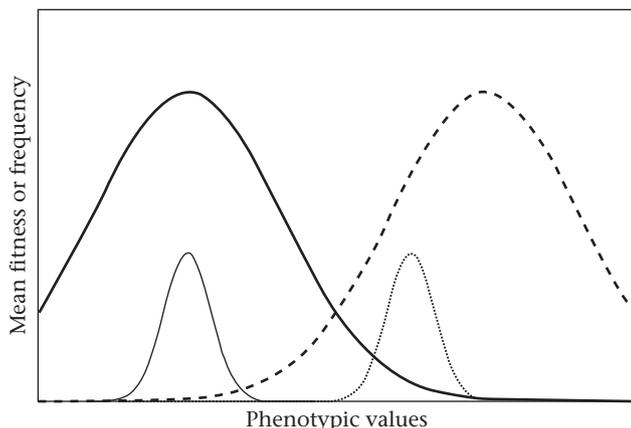


Figure 6. Plasticity may allow populations to persist long enough in a new environment for a peak shift to occur (from Price et al., 2003). Heavier lines represent population mean fitness in old (solid lines) and new (dashed lines) environments. The thinner lines represent the trait frequency distributions in each environment. Under this scheme, plasticity brings the population onto the lower 'slope' of the new adaptive peak, whereas a lack of plasticity would lead to population extinction.

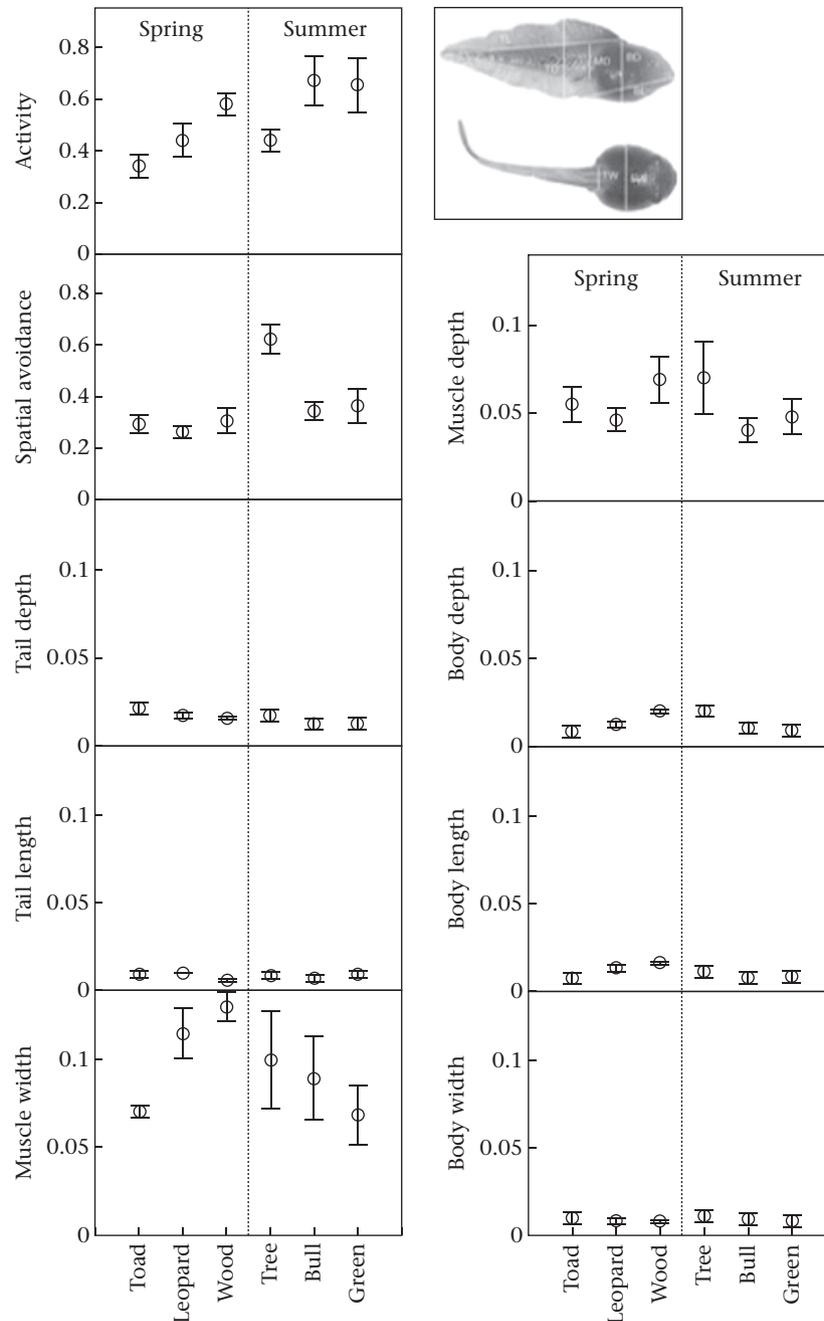


Figure 7. Relyea (2001) exposed larvae of several anuran species to four natural predators and a control treatment during development. Behavioural traits (spatial avoidance and activity) were more plastic than morphological traits, as measured by the coefficient of variation (from Relyea, 2001).

Moczek, 2008; Sol, Duncan, Blackburn, Cassey, & Lefebvre, 2005; Sol, Stirling, et al., 2005). In some instances, the questions clearly are separate: rapid changes in allele frequencies may occur within populations even if no novel traits are involved (Carroll et al., 2007). Similarly, novel innovations are sometimes established as part of a gradual process (Lister, 2013; Prum, 2005). However, cases in which novel traits evolve rapidly are of particular interest, both because they provide an opportunity for researchers to observe evolutionary innovation and because anthropogenic influences on many species' environments may make the question of which populations are most likely to evolve novel traits crucial for conservation rapidly (Kinnison & Hairston, 2007; Schiffrers, Bourne, Laverne, Thuiller, & Travis, 2013). The factors determining the magnitude and direction of behavioural plasticity's effect on evolution and the

extent to which behaviour's tendency to accelerate evolution occurs under the same circumstances as its tendency to facilitate the evolution of novel traits may be fruitful directions for future research.

MOVING FORWARD

How does an explicit consideration of the role of behaviour in the establishment of novel traits influence the study of animal behaviour? Below we suggest how certain behaviours, including predator avoidance, movement patterns, foraging and food preference, and mating and mate preferences, may be particularly likely to result in the establishment of novel traits. We also discuss how studies of populations and/or taxa whose recent ecological or

evolutionary histories are known can be useful: when recent evolutionary changes are documented, researchers can test whether behaviour played a key role.

What Sorts of Behaviours Expose Their Bearers to Novel Selection Pressures?

The types of behaviours that are most likely to facilitate the establishment of novel traits include predator avoidance, movement patterns, foraging and food preference, and mating behaviours and mate preferences. Researchers studying these behaviours should do so with particular attention to whether and how they expose their bearers to new selection pressures.

For example, as discussed above, [Losos et al. \(2004\)](#) examined behavioural responses of *Anolis* lizards to novel predators and found that lizards that moved into arboreal habitats to avoid predators experienced selection for longer limbs (in males) and larger bodies (in females). Because behaviour represents the integration of multiple levels of organization ([Kappeler & Kraus, 2010](#)), attention should be paid to selection that results from phenotypic changes associated with the behavioural shift itself. When behavioural mechanisms can be explicitly connected to other phenotypic traits, selection on those phenotypic traits should also be measured. Patterns of antipredator behaviour in barn owls, *Tyto alba*, covary with stress response and patterns of melanin-based coloration ([van den Brink, Dolivo, Falourd, Dreiss, & Roulin, 2011](#)), any or all of which may be subject to differential selection pressures, given exposure to a novel predator. The approach of quantifying adaptive behavioural responses to novel environments and resulting selection gradients on associated traits ([Brodie, Moore, & Janzen, 1995](#)) should yield insight into how plastic behaviours influence evolutionary trajectories and rates.

Several of the examples given above are well-documented invasions in which invaders (e.g. cane toads) or native species coping with invaders (e.g. fence lizards and fire ants) evolved rapidly ([Langkilde, 2009](#); [Llewelyn et al., 2010](#); [Phillips et al., 2006](#)). Such cases offer an opportunity to ask which behaviours facilitate rapid evolution. Comparisons of the behaviours of 'ancestral' populations, those that did not move to a novel habitat or cope with a novel threat, to the 'derived' populations can yield insight into which behaviours facilitated persistence in the face of novelty.

One might expect individuals that have invaded new habitats, or descend from those that did, to differ behaviourally from individuals that have not. They may be more exploratory, more likely to disperse or disperse longer distances (as in dispersing cane toads), or more likely to exploit novel resources. Also, in populations that have recently evolved novel traits, behaviours that may have facilitated these traits can be investigated either in the wild or in the laboratory. For example, female Pacific field crickets become less choosy when reared in a silent environment, potentially relaxing sexual selection pressure against silent flatwing males ([Bailey & Zuk, 2008](#)). (Interestingly, a higher frequency of flatwing males will result in a quieter environment for females, which means the phenotype induced by the mutation makes the environment more favourable for its spread.)

The above suggestions would yield insight into how behaviour facilitates the evolution of novel traits within populations. The question of behaviour's role in evolutionary trajectories can also be considered at the interspecific level ([Barraclough et al., 1995](#); [Kraaijeveld et al., 2011](#); [Panhuis et al., 2001](#)). One approach to investigating whether especially plastic behaviours result in the establishment of evolutionary novelty at the interspecific level is to use phylogenies to establish ancestral and derived states. If plasticity in the behaviours discussed in this review facilitates novel trait evolution, taxa that show more plasticity should also have

higher overall rates of evolution. Theoretical work also suggests that learning is more likely to be associated with evolutionary novelty at the interspecific scale ([Lachlan & Servedio, 2004](#)).

Behavioural Mechanisms and the Evolution of Novelty

Behavioural ecology increasingly focuses on integrating the role of behavioural mechanisms in evolution. We have highlighted some mechanisms of the acquisition and/or coordination of behaviour that might be more likely than others to promote the establishment of novel traits: first, learning allows individuals to interact adaptively with previously unencountered components of their environment. This might facilitate flexibility in behaviours associated with exposure to new selection pressures, such as persistence in the presence of a novel predator. Second, because the hormonal mechanisms that coordinate behaviour often have pleiotropic effects, a consideration of how behaviour, novel traits, and other ecologically relevant aspects of phenotype are integrated may yield new insight into which traits become established and which do not.

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