CHAPTER 4

Experience and learning in changing environments

Culum Brown

➲ **Overview**

This chapter examines how animals use learning to adapt to environmental change. It focuses on the consequences of anthropogenic activities for learning and the adjustment of animal behaviour. First, I introduce learning and its role in the development and evolution of behaviour. In particular, I identify the circumstances under which learning is likely to play a key role in the adaptation to novel environments and rapid environmental change. I then provide a number of examples of the way in which animals adapt to human induced habitat change, using urbanization and climate change as case studies. From this, we should be able to draw some general conclusions about the characteristics of species that enable them to cope with rapid environmental shifts.

4.1 Introduction

Over the years the ethology and comparative psychology paradigms have merged to form a modern synthesis that recognizes the role of both genes and the environment in shaping animal behaviour. The approach recognizes that animals display a large degree of phenotypic plasticity in response to variable environments and that much of this is mediated via learning. Learning is described as a change of behaviour induced by experience, which provides animals with an opportunity to adapt their behaviour to suit contemporary environments. It is the primary mechanisms animals use to cope with shifting environmental variables. Changes in behaviour as a result of experience can also be induced through mechanisms other than learning, for example by physiological shifts, but here we are primarily concerned with cognitive changes induced by neural plasticity.

In the modern world, the environment that animals are adapting to is more often than not the product of human disturbance. Human affected landscapes are characterized by large-scale land clearance for farming or mining, and by urbanization as human populations increasingly consolidate in cities. More recently, it has become clear that human impacts can operate at a global scale as evidenced by human induced climate change and acid rain. Rapid changes in the environment are typical of modern human activities and such changes often occur too rapidly for evolutionary processes to respond. Thus, in many circumstances, learning may provide the only avenue for animals to track environmental variation.

4.2 Learning and its role in the development of behaviour

The development of animal behaviour is controlled by two underlying mechanisms. The first is an automated response to specific stimuli within the environment that is entirely predetermined by specific genes. These innate behavioural responses are the result of natural selection acting over many

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generations. The second mechanism involves modification of behaviour through experience and interaction with stimuli in the environment during an individual's lifetime. Learning has the added benefit in that animals can change their response to specific cues or respond to new cues during ontogeny. Like innate behavioural responses, learning ability may also evolve over evolutionary time and there are multiple examples of differences in learning ability between closely related species and populations within species (e.g. Brown and Braithwaite 2005).

Whilst these two mechanisms (genetic inheritance and learning via experience) are often portrayed as polar opposites (the Nature–Nurture debate), in reality this is a false dichotomy as most behaviour is determined by some mixture of the two. Animals may have evolved an innate predisposition to perform a certain behaviour in a given context or pay attention to certain stimuli, but these behaviours or the response to the stimuli are then modified as a result of experience to produce an optimal response specific to local conditions. For example, innate predator recognition may result in a response to a generalized predatory threat (e.g. any large moving object), but the response is fine-tuned by learning as the animal comes to recognize which large objects are especially associated with danger in the current environment and which are not. In this manner the innate and learned responses interact to produce an adaptive response such that the animal will only display an antipredator response when it is appropriate to do so (Lima and Dill 1990).

It is important to recognize that both learning and innate responses contribute to animal behaviour. Even if predator recognition were entirely innate, the prey animal would still alter its behaviour when presented with a generalized predator cue, for example by seeking cover. Learning, however, provides an opportunity to fine-tune the response and enables the animal to choose from an infinitely larger set of behavioural responses to suit any given context (e.g. the animal may recognize that the predator is satiated and thus does not presently represent a risk; Licht 1989).

There are a number of criteria that must be met in order for learning to occur. First, animals must be able to determine which environmental cues are associated with important biological events. This is in fact a daunting task given the seemingly infinite number of cues and events that occur in the natural world. Much of the information emanating from the environment is effectively noise and has no relevance to the animal. Thus, determining the relevant cues in the environment must be one of the most important constraints on the learning process. Second, they must be able to determine the consequences of their behavioural response to environmental cues. In this regard, the immediate reward of performing the response is measured by reference to a change in internal state (e.g. hunger or fear level). A large number of studies have shown that if the gap between the animal performing an action and the consequences (reward or punishment) is separated by too long a time period then no association will be drawn (e.g. trace conditioning; Shettleworth 1998).

The combination of innate and learned behaviour that best tracks environmental change will result in the optimal behavioural phenotype. This will depend on the degree to which the environment is stable and, hence, predictable through space and time. Let us first consider spatial heterogeneity. When we consider spatial heterogeneity, we must examine it at several scales. At the individual level, the appropriate spatial scale is that of the home-range. That is the environment in which the individual operates and where the fitness benefits associated with performing certain behaviours are relevant. At the population level, we must also consider the potential for immigration and emigration from local microenvironments, where individuals may experience a range of alternative environmental variables. At the species level, the appropriate spatial scale is the entire species distribution. As we proceed through larger spatial scales it becomes apparent that the environment is less likely to be homogeneous and behaviour will need to be increasingly plastic to cope with this variability. Thus, learning plays a larger role in shaping the behaviour of species that occupy large geographical areas that encompass a variety of environmental conditions.

When we are dealing with temporal heterogeneity there are essentially two important levels to

consider. Firstly, the degree to which the environment is temporally stable during the lifetime of an individual. If the environment is highly stable there will be little need for the individual to display behavioural plasticity and innate behaviours should dominate. At intermediate levels of temporal heterogeneity, learning should prevail since innate responses will not be sufficient to track environmental variability. Secondly, the intergenerational scale concerns the degree to which the environment is stable from one generation to the next. In circumstances where the environment is temporally stable over many generations, behavioural traits can become genetically fixed in the population. But, if there is temporal environmental variance between generations then plasticity will be favoured. Because environments are variable in space and time, no given phenotype will ever be consistently optimal and some degree of phenotypic plasticity is required. Thus learning tends to be a ubiquitous trait in virtually all animals. It is important to note that the relevant temporal and spatial scales will vary depending on the species we are concerned with.

The temporal and spatial dimensions may also interact when we are concerned with dispersal over multiple generations (see also Chapter 5). High dispersal rates will result in behavioural (and genetic) panmyxia at the species level, whereas low levels of dispersal will generate population diversity. In the former case, innate behavioural responses will be highly generalized because they will have to encapsulate the total environmental variance experienced by the species. In this context, behavioural plasticity would be best generated via learning to fine-tune behaviour to suit the specific location an individual finds itself in. In the latter case, innate behavioural responses may be more specific and closely match local ecological conditions and learning would be less important. Indeed, isolated populations on the fringe of the species range are more likely to develop novel behavioural phenotypes (Cassel-Lundhagen et al. 2011). However, behaviour is commonly controlled by multiple loci each with a small effect. Therefore, even small amounts of gene flow will likely erode local adaptations and, once again, learning would be favoured.
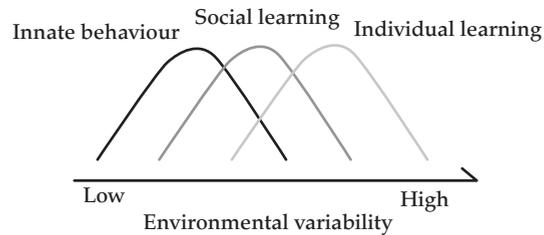
Figure 4.1 The relative contributions of three forms of plasticity generating mechanisms at varying levels of environmental variability.

To summarize, if the environment were completely homogenous then there would be no need for learning at all and innate behavioural responses would dominate. At the other extreme, the environment could be completely heterogeneous and there would be no opportunity to learn, because environmental cues would become too unstable to be of any predictive value. Needless to say, in the real world, the environment is never completely stable nor is it completely unstable so some degree of plasticity is required. We might generally predict that at low levels of heterogeneity, innate behaviours would dominate but as the environment becomes increasingly heterogenous learning would prevail (Fig. 4.1).

4.3 Social learning

Learning can occur both through individual trial and error learning (sometimes referred to as asocial learning), through social learning, or some mix of the two (Brown and Laland 2003). Social learning can be defined as incidences where individuals acquire new information about their environment or adopt a new behaviour as a result of observing or interacting with another individual or its products (Brown and Laland 2003). Individual learning requires the animal to interact directly with the environment and make associations between cues and events. It may take a considerable amount of time before individuals make appropriate associations and, therefore, individual learning can incur multiple costs as outlined below. In contrast, social learning enables animals to take short-cuts by using cues emanating from conspecifics, so called public information, to focus on particular cues or locations

(stimulus or local enhancement) or to reproduce the outcome of the conspecifics' behaviour (goal emulation) (Boyd and Richerson 1985). In some species, individuals may even adopt new behavioural patterns by direct imitation (e.g. birds; Zentall 2004). Moreover, social learning may expose individuals to novel conditions or focus their attention on novel stimuli, after which individual learning can then act to generate novel behavioural repertoires. Thus, social learning can lead to the rapid adoption of novel behavioural phenotypes that are likely to be locally adaptive and potentially produce behavioural innovations.

Unlike individual learning, social learning enables information to be passed on through generations via vertical transmission. In this respect, it has similarities with innate behavioural responses. Thus, local behavioural traditions can form which are themselves subject to natural selection. Unlike heritable traits, however, behavioural traditions can rapidly transform via copying error or the introduction of novel behavioural patterns into the population within an individual's lifetime. Social learning can also incur costs if the environment shifts and the cultural norm becomes disconnected from current environmental conditions. For example, Day et al. (2001) trained guppies *Poecilia reticulata* to utilize one of two coloured doors to access a feeding site. When new individuals were added to the school, they continued to follow the trained demonstrators even when the food patch was moved closer to the alternative door. Thus social learning can favour the maintenance of maladaptive behavioural patterns if individuals do not sample the environment for themselves. Recent studies suggest, however, that most individuals rely on a mixture of private and public information to make decisions (van Bergen et al. 2004), which means that maladaptive behavioural traits are soon extinguished (Brown and Laland 2003).

In a broader context, individual learning is most beneficial in conditions subject to higher levels of environmental heterogeneity. Even though social learning can speed up the learning process, it is better suited to lower levels of environmental heterogeneity because local behavioural traditions are more likely to be out of date at high levels of environmental variability (Fig. 4.1).

4.4 Interaction between innate and learnt responses

The interaction between innate and learned behavioural responses is an interesting topic worthy of closer scrutiny. It is likely that the manner in which the two mechanisms interact is more than just additive. Innate mechanisms often act as filters to focus the attention of the animal on environmental cues that are likely to be biologically meaningful. Learning then enables the animal to make associations between cues or outcomes through classical or operant conditioning. It is important to note that in cases where a single cue may have different predictive outcomes in different environments or contexts, it is vital that the animal is flexible in the way it can respond. Similarly, displaying a given behaviour can have various outcomes depending on the context in which it is performed. For example, an animal may respond to a predatory cue (e.g. olfactory cues) by seeking cover in dense vegetation, but this would not be an appropriate response if the particular predator detected is commonly encountered in vegetation.

There are many examples of the interaction between innate and leant responses in the animal world. During operant conditioning experiments, for example, rats *Rattus norvegicus* are more likely to associate gastric illness with olfactory cues rather than mechanical ones (e.g. electric shock or flashing lights) (Garcia et al. 1974). Many fish have a strong preference for red coloured objects because red is associated with high quality foods. Guppies can be taught to find a food reward hidden behind a red partition far more quickly than if the partition is any other colour (C. Brown unpublished data). This preference for red has been secondarily adopted as a sexually selected trait to attract mates, thus, the colour red may be of predictive value in multiple contexts (Rodd et al. 2002).

One might view the interaction between innate and learned behaviours in different ways. To some extent, a predisposition to pay attention to some cues in favour of others may be viewed as a

constraint because it limits the possibility that an animal will pay attention to novel cues when they become available, thereby limiting the development of innovative behavioural patterns. On the other hand, there is little doubt that paying attention to specific cues in the environment dramatically reduces the time it takes to learn associations between environmental cues and important biological events, thereby dramatically reducing the cost of learning. The problem with these combinations of innate dispositions acting in concert with individual learning is that the system breaks down if the environmental cues upon which the innate response depends shift, perhaps as a result of habitat disturbance or climate change. A good example of this is the historically strong connection between the leaf sprouting time of trees, the emergence of caterpillars, and the breeding time of insectivorous birds such as the great tit *Parus major* (Both et al. 2009). This mismatch is a reflection of the fact that the various different trophic levels are responding to different environmental cues to adjust their phenologies (see Chapter 6 for more detail). Thus, as the environment gets progressively warmer, there is a growing gap between the timing of the emergence of caterpillars and the hatching time of the birds, which leads to rapid population declines in the bird population. Similar observations have been made between migrating cuckoos and their resident hosts (Møller et al. 2011). In many ways an over reliance on genetic predispositions greatly enhances that probability that a species will fall victim to an evolutionary trap from which it is unlikely to emerge (see Chapter 16 for more information).

4.5 Costs associated with learning

It is quite apparent that animal behaviour is not infinitely plastic and learning is constrained by certain costs. The fact that we see differences in learning ability between different populations of the same species, or even between sexes, suggests that the evolution of learning depends on the relative costs and benefits of enhanced learning ability. While the costs associated with learning have been predicted by a range of models, there is still relatively little experimental evidence.

One obvious source of costs is that associated with the development and maintenance of neural tissues. There is no doubt that brain matter is by far and away the most expensive tissue in the body to maintain. Of course this argument relies on the fact that there is a link between brain size and learning ability. This is still a highly controversial topic, but there are a number of direct and indirect lines of evidence that suggest it may well be true. In terms of direct evidence, butterflies that have a high capacity to learn the location of host plants have larger mushroom bodies in their brains (Snell-Rood et al. 2009) and comparative studies have revealed that a larger hippocampus is associated with improved spatial learning in mammals and birds (reviewed in Sherry et al. 1992). Both of these brain structures are intimately associated with spatial learning. Indirect evidence also comes in many forms. Firstly animals reared in enriched environments tend to have larger brains and a higher capacity to learn. Salmon *Salmo salar* par reared in enriched environments, for example, are better able to generalize between food types and thus learn to forage on novel prey items more quickly than those reared in impoverished conditions (Brown et al. 2003). Secondly, changes in brain sizes have been observed in animals when they no longer require their high capacity for learning. One very nice example is that of the male meadow vole *Microtus pennsylvanicus*, whose brain size increases during the breading season in line with the increasing size of his territory. Similarly, black-capped chickadees *Poecile atricapillus* increase their brain size during autumn when they are busy caching food items for the coming winter. Moreover, there is some evidence that larger brained species are more likely to develop behavioural innovations through their higher capacity for learning, both socially and asocially (Reader et al. 2003; Sol et al. 2002).

As alluded to above, there are two ways in which brain size can be enhanced. The first is a congenital (inherited) investment in brain size that arms the animal with a high capacity for learning. But this approach has the potential to incur a high cost because the energetic investment is made before learning occurs, thus the cost may be borne even if the animal doesn't fully utilize its learning capacity

(Dukas 1998). Alternatively, investment may be made in brain size during ontogeny as the animal faces particular environmental challenges (e.g. learning tasks; Clayton and Krebs 1994). In this instance, brain growth can be specifically targeted to those areas that are needed when required, and would greatly reduce the chances of learning capacity redundancy and associated costs. Reducing the costs of learning would encourage the persistent use of learning, both by individuals during ontogeny, and by species over evolutionary time.

Another cost of learning is often referred to as the cost of being naïve. Naïve individuals must first sample the environment to determine what the contemporary conditions are and the information they gather may not be entirely accurate. A small amount of environmental variability can generate a degree of uncertainty. Thus, during the following period of trial and error learning it takes a considerable amount of time for associations to be formed, and behaviour is therefore sub-optimal during this time. During both of these phases, there is a cost in terms of time that would otherwise be available to perform other behaviours, the energetic cost of performing the sub-optimal behaviour, as well as the costs associated with making errors. Some of the costs of being naïve are actually associated with picking an appropriate behaviour from a potentially large behavioural repertoire rather than the process of learning itself. Thus, the costs of being naïve can be dramatically reduced by enhancing learning speed. Even innate behavioural responses may incur a cost of being naïve because it is unlikely that the present environmental conditions are exactly the same as those over the proceeding generations, during which the innate behaviour was shaped. Naturally, the costs associated with a genetically fixed trait are huge should the animal find itself in an inappropriate environment.

There are a number of good examples in the literature that clearly illustrate the cost of being naïve. In fishes, it has been demonstrated that the handling time of novel prey items is relatively high and, in combination with the development of a new search image, represents a considerable cost to switching to novel prey items (Warburton 2003). Moreover, it is apparent that fish are aware of this

cost. Thus, fish may delay the switch from their preferred prey item to a novel prey item even when the latter becomes increasingly abundant. Similar observations have been made in bees *Apis mellifera* (Laverty and Plowright 1988). Thus, the cost of being naïve can impede optimal foraging.

4.6   Learning and evolution

One intriguing question that is often fiercely debated is the extent to which learning facilitates or inhibits the evolution of novel behavioural phenotypes. This is particularly important in the context of rapid environmental change associated with human activities. To address this question, we must consider the interaction between innate predispositions and learning. After all, natural selection can only act on the heritable components of behaviour, which may include the heritability of plasticity or general learning ability itself.

A number of arguments suggest that learning would inhibit natural selection in response to environmental change. First, the interaction between innate and learnt behaviours may inhibit behavioural innovation by limiting the cues to which animals pay attention (see Section 4.4). This effectively restricts the animal's ability to respond to novel environmental stimuli and thereby prevent the production of behavioural innovations. Second, learning allows animals to fine-tune their innate behavioural responses and thus learning may act as a buffer against selective forces. This would have the effect of reducing selection on the underlying innate behavioural traits, thereby slowing down their evolution.

On the other hand, a number of models have suggested that learning increases the probability of invading novel habitats (Thibert-Plante and Hendry 2011; Chapter 14). Exposure to new environments may generate novel selective forces that then act by shifting the underlying genetic architecture by natural selection. Thus, learning, by facilitating invasion, may ultimately result in the rapid movement of innate behaviours towards a new optimum in novel environments (Price et al. 2003; Fig. 4.2). If this is the case, learning is likely to result in rapid shifts in the evolution of behaviour in response to large shifts in
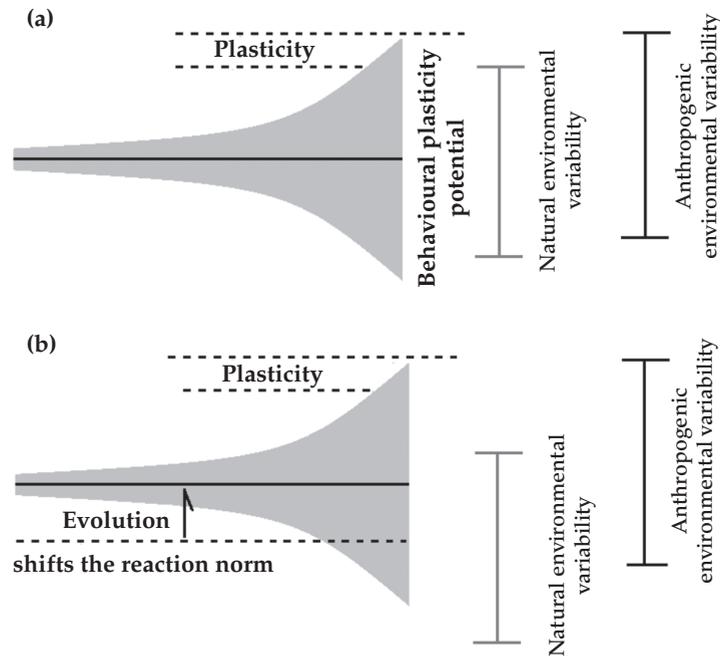
Figure 4.2 Degree of plasticity (y axis) displayed by a range of individuals in a population in response to a given environmental variable (x axis). Individuals with low levels of plasticity (left end of the x axis) cannot respond to environmental changes. An individual with a high degree of behavioural plasticity primarily mediated via learning (right end of the x axis) is confronted with a sudden environmental change. If the environmental change is small (a), these individuals will be able to cope by changing their phenotype. Alternatively, if the shift is large (b), then some of the required change in behaviour will be generated through plasticity, but this will need to be accompanied by an underlying, elevated shift in the reaction norm via selection on innate traits, perhaps via the Baldwin effect (arrow). Natural selection would ensure this new reaction norm spreads through the population.

environmental variables brought on by human activities. One such method by which this might occur is via the Baldwin effect (see also Chapter 1). However, quantitative genetic models suggest that the conditions under which learning facilitates evolution are highly restricted (Lande 2009).

Many of these models, however, do not consider the source of individual behavioural plasticity, but take as their starting point that some degree of plasticity exists. Plasticity itself may be heritable and can also be generated by physiological changes in addition to cognitive changes (i.e. learning). As mentioned above, innate behavioural responses can only generate limited plasticity but this is significantly enhanced through learning. The interaction between social learning and individual learning, however, may expose individuals to novel situations or direct attention to novel cues. Wilson (1985)

suggested that through high rates of social and individual learning, individuals expose themselves to novel selective pressures, which can then act as a driver for evolution. In both birds and primates, there are correlations between the propensity to learn and rates of behavioural innovation (Sol et al. 2002; Reader 2003). But, innovative species and individuals are also characterized by high rates of neophilia. Thus, a combination of high learning capabilities generating plasticity and exposure to novelty likely plays a key role in the evolution of novel behavioural types.

4.7 Learned responses to human induced environmental variation

There is little doubt that humans are creating a degree of environmental change at a rate that has

rarely been witnessed in Earth's geological history. Much of this damage has been inflicted by a few key processes including land clearing, urbanization, overharvesting of prey species, and pollution. Some of these processes have resulted in rapid and irreversible damage to the environment, providing species with little opportunity to adapt, whilst others, such as climate change, are more insidious.

Some of the less obvious examples of human induced environmental change are brought about indirectly. Whilst pollution has a very direct influence on species behaviour and survival, indirect effects include climate change (see subsection 4.6.2) and acid rain. In apparently undisturbed streams in North America, acid rain can have surprising effects on animal behaviour and the learning process in particular. Many young salmonids rely on chemical cues to recognize predators through associative learning, but acid rain has changed the configuration of key components of the alarm cues to the extent that fish no longer respond to them (Leduc et al. 2006). Changes in ocean acidification associated with climate change have also interrupted the chemosensory ability of clown fish *Amphiprion percula* both during settlement and during predator encounters (Munday et al. 2010). We do not know if these fish shift their behaviour to rely more on alternative cues (e.g. visual or auditory) to compensate, nor do we know if they will be able to adapt their chemical recognition capabilities to suit the new environment.

The commercial overharvesting of animals has also had a large impact on animal behaviour. Although much of this effect in terrestrial habitats occurred hundreds of years ago, this process is ongoing in the marine environment. Systematic hunting of cod has led to changes in a wide range of traits including size at maturity, fecundity and migration routes, the latter of which is likely maintained via cultural traditions (Ferno et al. 2006). The overharvesting of large marine fish species by commercial fishing operations has also significantly altered the behaviour of prey species both directly and indirectly. In both terrestrial and aquatic ecosystems, the systematic removal of predatory species (so called apex predators) or other key stone species can have flow-on effects throughout the food web (Crooks and Soulé 1999). Fish communities that are varyingly exposed to commercial fishing pressure differ in their predation risk, as large piscivores are removed, which, in turn, affects the foraging behaviour of multiple small, prey fish species (Madin et al. 2010). These changes are brought about by a mixture of immediate learned responses by individuals and long-term shifts in selective pressures.

I have argued that the key to responding to environmental variation is behavioural plasticity, primarily mediated via learning. In disturbed environments, generalists maintain their numbers (some may even flourish) whereas specialists rapidly decline. The success of generalists has been correlated with their high degree of behavioural flexibility and a lack of neophobia (Reader 2003). Habitat generalists can adjust their movement patterns and resource use to make the most of the modified habitat. Most strikingly, they are able to change their foraging behaviour, use of shelter, and so on to incorporate novel resources that are available in human environments, which helps mitigate against the loss of natural resources. It should come as no surprise that the characteristics of species likely to respond favourably to human induced environmental change match very closely those of invasive species (i.e. short generation time, rapid growth, large fecundity potential, etc: Sol et al. 2002).

Innovation frequency is a decent surrogate for behavioural flexibility, including learning and problem solving (Webster and Lefebvre 2001), and has been implicated in the invasion potential of birds (Sol et al. 2002). The blackbird *Turdus merula*, for example, is often portrayed as a successful invader and colonizer of a range of habitats around the world. Over 23 foraging innovations have been reported for this species, including hawking for insects and attacking skinks (Sol et al. 2002). This species was the fastest learner in comparative tests (Sasvarï 1985) and has low levels of neophobia (Marples et al. 1998). A lack of fear when operating in new environments or in the presence of novel objects, combined with high rates of learning, is likely to lead to the discovery of new resources, such as novel prey items. Indeed the response of birds to urban environments is one of the most well

studied examples of how animals adapt to human induced environmental changes.

4.7.1 Learned responses to urbanization

As one moves along the urbanization gradient from native bushland to cities, species richness tends to decline (Clergeau et al. 1998). The homogenization process of urbanization is similar all over the world, thus, the same species tend to be present in cities around the globe. The fauna is often dominated by a small number of non-native, urban specialists (Blair 1996). For most native species, living in urban areas is a stressful business, as these species are either not pre-adapted to live in urban environments or are not able to adapt. Indeed, recent evidence suggests that some species, which have been traditionally thought of as urban specialists, are not coping as well as it first appeared. For example, despite incorporating human food sources into their diet, urban starlings show reduced food provisioning at the nest, resulting in lower nestling weight compared to starlings in nonurban areas (Mennechez and Clergeau 2006).

The key question is what characterizes successful urban adapters? The potential list is long and includes: high sociality, the utilization of human resources, a lack of fear, tendency to be sedentary, and broad diet (Clergeau et al., 1998). Many of these traits, however, are likely to be pre-adaptations and have little to do with learning and behavioural plasticity *per se*. For example, birds that have a tendency to nest in trees are worse off in the cities than those that nest in crevices, such as pigeons *Columba livia*. Kark (2007) added another trait to this list: behavioural flexibility.

Foraging innovation, including the introduction of novel behaviours and the utilization of new food sources, appears to be one of the key characteristics of urban specialists. Urban adapters must be able to feed on a wide variety of prey items and readily adopt new resources. Thus, scavengers or generalist omnivores tend to do quite well in cities (Courtney and Fenton 1976). There are numerous accounts of feeding innovations in urban bird species (Lefebvre et al. 1997). Starlings picking off insects plastered to the front of arriving trains, sparrows operating bus

station doors by setting off the motion censor, and birds entering shopping centres by waiting for the automated doors to open as shoppers pass through, providing them with access to food. It is unclear how these behaviours develop, but they are likely to be opportunistic in the first instance and reinforced by operant conditioning, and then spread through the population via social learning (e.g. Hinde and Fisher 1951).

A number of studies have reported significant shifts in the temporal and spatial activity patterns of urban animals, many of which occur via learning. In some instances, activity is extended because of a reduction in natural predators. In other instances, activity patterns are moved to avoid urban predators, such as cats or humans, or to benefit from new resources. For instance, black bears *Ursus americanus* in urban areas that have access to garbage have significantly different time budgets. They have also shifted to becoming nocturnal, are 30% bigger, have sex ratios skewed towards males, and increased female reproductive success (Beckmann and Berger 2004). Thus, it is apparent that shifts in activity times and diets associated with urban environments may have flow on effects on life history traits.

The increased availability of food in landfills and trash cans can increase local population densities. Animals soon learn the location of these stable food sources and are attracted to them. For example, the distributions of gray squirrels *Sciurus carolinensis* and chipmunks *Tamias striatus* in urban areas are determined by the proximity to artificial food sources rather than by other habitat characteristics (Flyger 1970; Ryan and Larson 1976). In urban areas, insectivorous bats spend a significant amount of time hunting around street lights, and subsequently densities are higher than elsewhere (Jung and Kalko 2009). Clumping around artificial food sources can have several secondary influences on urban animals. Increased social interactions can result in risk of disease/parasite transmission and changes in social structure. Raccoons *Procyon lotor* in urban areas have smaller and more stable home ranges than rural individuals (Prange et al. 2004). House geckos *Lepidodactylus lugubris* outcompete other native gecko species, but only when prey patches are clumped around lights (Petren and Case 1996).

Animals typically tradeoff foraging opportunity with predation risk. This balance can be affected by a large number of factors, including competition for food, perhaps mediated by conspecific densities, and perceived risk of predation. Thus, risk assessment in urban animals is influenced by a range of factors that are likely to vary from those experienced in the wild (Blumstein 2002). As populations habituate to humans, as part of their adaptation to urban environments, it is plausible that they equally reduce fear towards predators in general. Squirrels in urban environments show reduced responses to humans, compared to suburban and rural squirrels, as well as reduced responses to hawk and coyote vocalizations (McCleery 2009). McCleery (2009) suggested that this is evidence of a generalized decrease in antipredator behaviour, but it may also be indicative of behavioural plasticity, since both hawks and coyotes are rare in urban settings. Comparative analyses have shown similar processes in a wide range of birds, where shorter flight distances to approaching predators characterize urban species (Møller 2008). Like other behavioural adaptations to urban environments, it is not clear if these changes stem from phenotypic plasticity operating through individual habituation to humans, or from evolutionary responses over multiple generations (Diamond 1986).

Urban animals need to successfully communicate with one another, which is a relatively difficult task in a noisy environment. For passerines, this is highly problematic because the urban environment interferes with the transmission of their calls. There is plenty of evidence that urban birds respond to background noise in a number of ways, including shifting the frequency of their songs (see Patricelli and Brickley 2006 and Chapter 2 for reviews) or changing the time at which they sing (Fuller et al. 2007). Similar observations have been made in a variety of animals, ranging from whales to frogs (Parks et al. 2011; Sun and Nairns 2005). To date, however, it is unclear how animals achieve these shifts. Bermudez-Cuamatzin et al. (2011) found house finches *Carpodacus mexicanus* to instantaneously alter their song to avoid the dominant frequencies in the background noise, indicating high plasticity in song. Shifts in song characteristics of

passerine birds might also be culturally inherited, because song is vertically transmitted from parent to offspring during a sensitive period early in ontogeny. If male urban birds are singing higher frequency songs, then young male birds in the vicinity are likely to produce high frequency songs (Luther and Baptista 2010). Noisy environments also exist in the wild (e.g. near streams, or in windy areas), so it should not surprise us that animals can adapt to a noisy urban environment (Dubois and Martens 1984). Nevertheless, behavioural plasticity in communication seems to be part of the urban dweller's survival kit (see Chapter 2 for full discussion).

4.7.2   Learned responses to climate change

It is widely accepted that recent changes in global climate have had numerous effects on the behaviour of animals. These changes include direct changes in phenology with respect to migration, development and reproduction (see Chapters 6 and 8). To date, observations of shifts in phenology dominate the climate change literature when it comes to animal behaviour. But, there are also far more subtle behavioural changes, which are induced by climate change indirectly, such as those resulting from shifting food availability or predator density. For example, during years of high snowfall, snowdrifts accumulate in Antarctica, allowing giant petrels *Macronectes giganteus* to safely crash land and feed on the Antarctic petrel's *Thalassoica antartica* chicks and eggs (Van Franeker et al. 2001). However, observations of behavioural innovations brought about by learning in response to climate change are very rare. Fortunately, we can rely on observations of animals that have undergone large shifts in climate in the past, such as prolonged droughts, to provide an insight into how animals are likely to react to future climate change scenarios.

Shifts in behaviour as a response to global warming are expected, given that behavioural adjustment is often a first means of coping with environmental variability. One of the basic underpinnings of behavioural ecology is that even short-term changes in climate can dramatically alter animal behaviour (Krebs and Davies 1991). Flying foxes *Pteropus poliocephalus* spend significantly more time fanning

themselves in their roosts during hot days, rather than sleeping, which has significant implications for energy expenditure (C. Brown unpublished data). Similarly, during drought, impala *Aepyceros melampus* need to drink and their movement patterns become restricted to water courses where predation risk is high (Jarman and Jarman 1973). Both examples illustrate the typical behavioural flexibility illustrated by animals in response to climate variation.

Much of the evidence of behavioural shifts influenced by climate change involves movement in phenology. Mammals, for example, emerge from hibernation earlier in response to global warming, which has several impacts on their behaviour (Stirling et al. 1999; Inouye et al. 2000; Reale et al. 2003). While there is no doubt that changes in behaviour are occurring, far less is known about the mechanisms by which these changes arise. As discussed above, there are essentially two ways behaviour can track climate change: (1) microevolutionary responses via natural selection or (2) phenotypic plasticity, which may be mediated by learning. Recent studies have found evidence of both microevolutionary and plastic responses to climate change (Reale et al. 2003; Bradshaw and Holapzfel 2006). In an analysis of a long-term data set on great tits in the UK, Charmantier et al. (2008) used an individual mixed modelling approach to examine the reaction norms of individual females to changes in spring temperatures. She found the population to have closely tracked environmental change associated with global warming over the last 50 years, and much of this was due to individual plastic responses.

In these examples, the plastic response observed in animals is largely a direct physiological response to environmental cues. There is little suggestion that shifts in the behaviours are generated by learning, or that they cascade to other behavioural patterns that are influenced by learning or other cognitive decision making processes. Nevertheless, since the different members of an ecological community vary in their responses to climate change, multiple trophic interactions will become disconnected in space and time, and new relationships will be born. Thus, behaviour will have to alter accordingly. The development of novel behaviours will be particularly obvious in long lived species

and in those that show range shifts to keep up with climate change, such as migratory birds. Highly mobile species will head polewards (or to higher elevations) at a far greater rate than less mobile species. As these animals encounter new communities, they will inevitably have to adjust their foraging and antipredator responses via learning (Walther et al. 2002). Bluefin tuna *Thunnus thynnus*, for example, migrate across the ocean searching for suitable prey species, which can be directly influenced by climate induced changes in upwelling and current circulation (Polovina 1996). If there are cultural elements to migratory patterns, shifts in migration patterns may be further exacerbated by human exploitation, if the largest and most knowledgeable individuals are selectively removed from the population (Ferno et al. 2006).

Long lived animals may be able to rely on previous experience and retreat to refugia during tough times, the location of which may be culturally inherited. Elephants *Loxodonta africana*, for example, are long lived and maintain a variety of traditions within family groups. During extreme drought events, large numbers of juveniles perish, but calves with mothers that had previous experience of extreme drought were more likely to survive (Foley et al. 2008). Similarly, elephant seals *Mirounga leonina* show a high degree of foraging site fidelity, even though the productivity of their preferred foraging site varies from year to year. It's thought that this long-term strategy ameliorates fluctuation in food availability in response to climate variables (Bradshaw et al. 2004).

The social organization of animals can also vary depending on the availability of prey items, the abundance of which is influenced by climate variation. As prey availability increases, the competition of food resources within the group is reduced and, thus, animals can afford to form larger social groups (Lusseau et al. 2004; Western and Lindsay 1984). Observations of Alaskan red foxes *Vulpes vulpes* show large changes in breeding behaviour during poor seasons brought about by El Nino. In good years (La Nina), the foxes breed polygynously. Males have many mates and female helpers at the den. But during El Nino, food supplies drop and the breeding system reverts to monogamy, because

fewer females are in suitable breeding condition (Zabel and Taggart 1989). Such shifts in group size and breeding behaviour are active decisions made by the animals.

Similar indirect influences on mating behaviour will occur if shifts in climate lead to changes in operational sex ratio. A large number of reptiles show temperature dependent sex determination. In painted turtles *Chrysemys picta*, for example, the sex ratio is linked to mean July temperature, with the sex ratio becoming increasingly female biased as temperatures increase (Janzen 1994). Mitchell et al. (2008) speculate that some of the sex bias in tuatara *Sphenodon guntheri* could be offset by behavioural decisions to nest in shaded areas or laying deeper in the soil. The Australian water dragon *Physignathus lesueurii*, for example, uses both techniques to compensate for higher temperatures in the warms regions of its distribution (Doody et al. 2006). It is unknown if this is an active decision making process or an example of local adaptation. It is likely that females are choosing nest sites based on soil temperature and are therefore making active decisions where to nest. To confirm this, one would have to follow the nesting behaviour of individuals over time to show that they respond in a plastic way.

To summarize, there has been a big emphasis on describing phenological responses to climate change, but the vast majority of these responses are simple physiological responses to environmental cues. Whilst it is clear that these changes must also be associated with the corresponding emergence of novel behavioural patterns or innovations, such observations are rare in the primary literature. We can, however, resort to previous examples where animals have been observed responding to natural environmental perturbations (e.g. extended drought periods) and thereby make some predictions about how animals will respond to future climate change scenarios. In future, closer observations of behavioural responses to climate change and accounts of behavioural innovations will come to light.

4.8   Conclusions

While much of the modelling and theoretical evidence suggests that learning will play an important role in how animals cope with shifts in environmental variables induced by human activities, there is surprisingly little empirical evidence of this. In both case studies explored here, urbanization and climate change, there are a very large number of observations that show that animals do indeed adapt their behaviour to suit novel environmental circumstances, but we are still very much in the descriptive stage of the scientific process. Very few experimental or manipulative studies have been conducted. Perhaps the only exceptions being the documentation of birds responding in real time to background levels of noise (Bermudez-Cuamatzin et al. 2011) and evidence of foraging innovation in urban birds. In most cases, we simply can't say if the changes in behaviour are brought about by natural selection or via phenotypic plasticity. Modern statistical approaches will enable us to disentangle the relative contributions of genes and phenotypic plasticity in shaping animal behaviour (e.g. mixed modelling and reaction norms).

The potential relationship between brain size, cognitive ability and behavioural plasticity is certainly worthy of further investigation, in a broader range of species, especially given the link with the propensity for behavioural innovation. It is likely that those animals that have these traits will show the greatest resilience to environmental changes induced by human behaviour. The potential for innovation also seems to be associated with other factors such as a lack of neophobia. Investigations of the traits linked with invasive potential will also likely shed further light on those characteristics that enable animals to respond positively to environmental change.

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