BEHAVIOURAL RESPONSES to a CHANGING WORLD

mechanisms & consequences

Edited by
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UC dedicates this book to her daughters, Erika and Heidi, whom she loves more than words can say.

BBMW dedicates this book to his parents, Steven and Lesley, who supported his interests and nurtured his dreams.

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Foreword

Nicholas B. Davies

Our generation will surely be the last to take the natural world for granted. When I was a young boy, I thought there would always be skylarks singing and cuckoos calling to greet the spring, and on hot summer days swifts would forever scythe the skies in search of their insect prey. But populations of these and many other familiar species have declined alarmingly during my lifetime. What can behavioural ecologists do to help?

This inspiring book makes a powerful case that we can contribute through a better understanding of how organisms adapt their behaviour to a rapidly changing world. A change in behaviour is often the first response. Sometimes an individual's flexible behaviour (for example: earlier breeding, hiding from predators) is sufficient to adapt it to new conditions. Or a behavioural change will expose the organism to new selection pressures and hence promote the genetic changes necessary for adaptation. So behaviour can often play the lead in evolution.

Organisms have evolved in response to environmental change ever since life began, with changes on the grand scale of shifting continents and ice ages. For thousands of years they have been faced with human-induced changes, too, as our ancestors cut trees, burnt grasslands, or flooded and drained the land. Indeed, skylarks were likely beneficiaries of some of these changes. But the current scale and pace of change is unprecedented, involving: climate change, habitat destruction and fragmentation, ever more intensive farming and fishing, urbanization, and a new biotic environment of invasive species, pathogens and parasites. Can organisms adapt fast enough to avoid extinction?

Many chapters describe examples of rapid behavioural changes to suit the new conditions. Birds, frogs, and whales have adapted their vocal signals for more efficient transmission in a noisy human environment on land and in the seas. Some bird populations, like the blackcap, have changed their migration routes in response to milder temperate winters; their shorter journey to western Europe rather than tropical Africa not only saves on the stress of a long journey but also enables them to arrive on their breeding grounds sooner, to claim the best breeding territories. Furthermore, different arrival times on the breeding grounds also leads to assortative mating by wintering area, and hence restricted gene flow, which has likely contributed to the rapid evolution of the new migration behaviour.

However, in other cases species are suffering in a new world. Changes in water chemistry are impairing the responses of fish to alarm and sex pheromones. Increased water turbidity is obscuring fish visual signals and leading to increased hybridization. Some migrants now arrive too late on their breeding grounds to catch the earlier springs, perhaps because there are no corresponding environmental changes in winter quarters to cue an earlier departure. In Greenland, the migration of caribou has not advanced sufficiently to match the earlier spring plant growth on the calving grounds, so reproductive success has declined. Some species are caught in 'ecological traps', because the stimuli used to guide their behaviour are no longer reliable cues to habitat quality; so some birds are settling in non-native vegetation with poor food and insects are ovipositing on tarmac roads, fooled by the reflective surface.

The book shows that changes in behaviour can also lead to unexpected broad scale community changes. With the return of wolves, elk have become more cautious in feeding close to cover, so thickets are regenerating and affecting populations of other species, too. Range shifts in response to climate change are exposing communities to new predators (shell-breaking crabs in Antarctica, for example) and hence influencing food webs. Our agricultural monocultures are affecting bee behaviour and hence pollination in the wider countryside.

In many ways, this volume is a cry for help. Few studies have identified whether the changes in behaviour reflect genetic change or phenotypic plasticity. If the latter, then is the behavioural repertoire sufficient to adapt to the full range of environmental change? Some studies have shown that species with more flexible behaviour, and with larger brains, are better able to cope with novel environments. Nevertheless, long-term studies are revealing some surprising differences even between populations of the same species. Some populations of great tits, for example, have advanced their breeding entirely through phenotypic plasticity, to keep track of earlier spring food supplies, while others have not adapted and their populations are declining. Why do populations differ in their responses? The book points to the need for new theory to identify whether evolutionary change can be sufficiently rapid for populations to avoid extinction. In some cases, strong selection on individuals to maximize their fitness in changing environments can lead to a lower carrying capacity for the habitat, and hence drive a population closer to extinction.

The book also raises many new questions. As the environment changes, will individuals simply disperse to search for their old habitats or will they stay and adapt? What cues will they use to determine whether they leave or stay? Answering these questions will influence whether we try to conserve species by land-sharing, namely getting biodiversity into our fields, or land sparing, namely keeping biodiversity and our crops separate, with corridors to aid dispersal. The plea in the closing chapters is for behavioural ecologists to join more in conservation efforts to help save our natural world in the face of change, so there will continue to be skylarks and swifts in our skies, both for their own sakes and to inspire our future generations.

Preface

Humans have left an indelible mark on the planet. From the Arctic tundra to the desert outback of central Australia, the reach of human activities has touched even the most remote places on Earth. The changes entrained by such activities are having a profound impact on the natural world. For animals, survival in rapidly changing environments comes down to three options: disperse, adjust through phenotypic plasticity, or adapt through genetic changes. Although environmental changes have been taking place long before the arrival of humans, changes linked to anthropogenic activities are resulting in conditions that many species have never before encountered. Worsening the situation, evolutionary processes are seldom able to keep pace with the sudden ecological changes that humans are causing. Instead, the survival of populations—and ultimately, species—hinges on the plasticity of traits that have evolved under past conditions. The faster the changes are, and the more the conditions differ from those experienced during a species' evolutionary past, the greater the risk of population decline and, in the worst case scenario, extinction. Here, behavioural responses can play an important role in helping individuals to rapidly adjust to new conditions, and to survive and reproduce in the altered environment.

Behavioural adjustments often represent the first response to changing conditions. A bird, for instance, may adjust its vigilance in response to the presence of humans, or a butterfly may have to move to a different patch in search of host plants for laying its eggs. With such responses, animals attempt to increase their probability of survival and reproduction in the changing environment. In addition to these direct responses, environmental changes can also affect behaviours by interfering, for example, with the sensory systems or physiological processes needed to mount an appropriate response. The behavioural alterations that follow (if any) can be adaptive or maladaptive, depending on how they influence fitness. If the responses of individuals alter key demographic parameters (e.g. birth, death, or migration rates of the population) then the dynamics of the population will also change—sometimes for the better; other times not. Changes in the demography of one species can, in turn, influence others and, eventually, the whole community to which it belongs. This can result in further changes to the environment through feedback loops that can, ultimately, impact the entire ecosystem.

Behavioural responses can also have important evolutionary consequences. Responses that help counter drastic population declines can give the population additional time for accruing genetic changes (evolutionary rescue). This is particularly crucial when the behavioural response does not fully rescue the population, and genetic adaptation is required for persistence in the longer term. On the other hand, changed conditions that differ drastically from those experienced by populations during the course of their evolutionary history can constitute major obstacles to persistence that are unlikely to be surmounted by behavioural responses alone. They can also trigger maladaptive behavioural decisions. These so called 'evolutionary traps' can be quite common under human-altered conditions, potentially driving populations into decline.

This book aims to provide insights into the behavioural responses of animals to human-induced environmental change and how—by impacting on ecological and evolutionary processes—such responses can affect the fate of individuals, populations, and ecosystems.

The book is organized into three interrelated parts. Part 1 focuses on the mechanisms underlying behaviour. It discusses how behavioural responses are dependent on the environment, and provide an important context for understanding how anthropogenic changes can modify the way in which animals respond. This section begins with a theoretical framework for understanding how environmental change can affect behaviour at the population level. It then considers the impact of environmental change on animal communication and the endocrine system, as well as the role of experience and learning as potential mechanisms for coping with human-altered conditions. Part 2 explores behavioural patterns and processes under anthropogenic change, including dispersal, migration, foraging, reproduction, social behaviour, and species interactions. Part 3 considers the implications of behavioural responses for populations, ecosystems, and biodiversity. This section begins by exploring the potential role of behavioural plasticity in changing environments and then discusses the impacts of altered behaviours on population dynamics and ecosystem function, as well as the effects of invasive species. Evolutionary implications are further explored in the context of sexual and natural selection, and the potential for plastic and evolutionary responses to rescue populations from decline. The section concludes with a discussion of the importance of behavioural research in conservation science and the role that behavioural scientists can play in providing insights into the impact of anthropogenic activities.

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This book began as an idea conceived in Ithaca during the International Society for Behavioral Ecology Congress. We mulled over it during the poster sessions, discussed it on our coffee breaks, and by the end of the conference dinner had decided that this was a book that needed to be written.

Since that fateful meeting, we have had the opportunity to work with an amazing bunch of people to bring our idea into fruition.

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PART I

Mechanisms

CHAPTER 1

Understanding behavioural responses and their consequences

Andrés López-Sepulcre and Hanna Kokko

➲ Overview

How do populations respond to environmental change? We aim to provide a conceptual overview using the Price equation, which decomposes the mean change exhibited by a population into four components: viability selection, within-individual changes over their lifetime, fecundity selection, and parent–offspring differences. Mechanisms such as phenotypic plasticity, learning, genetic adaptation, maternal effects and cultural evolution can all be understood via their influences on these components. However, we also highlight the fact that population size effects should often be considered more explicitly than this breakdown of components achieves. For example, phenotypic plasticity may help or hinder adaptive evolution, and adaptation does not necessarily lead to a better maintenance of large population size.

1.1 Introduction

Since the very inception of evolutionary theory, animal behaviour has been seen as a trait upon which selection can act. Darwin's theory of sexual selection, exposed in the *Descent of Man* (Darwin 1871), sparked some of the earliest research on the adaptive value of behaviours (e.g. Noble and Bradley 1933), yet the modern synthesis of the 1940s didn't pay much attention to traits that one would nowadays call behaviours (Birkhead and Monaghan 2010; Kokko and Jennions 2010). It took close to a century before the adaptive framework began to dominate the study of behaviour—thanks to the work of Niko Tinbergen and Konrad Lorenz (Tinbergen 1963). This solidified the link between evolutionary biology and the behavioural sciences that Charles Darwin had suggested. Like organs, behaviours represent adaptations to the environment. Tinbergen, for instance, demonstrated that the sticklebacks' fierce reaction against the colour red represents an adaptation to exclude attractive sexual competitors (Tinbergen 1963), while Lorenz studied the impulse of goslings to follow the first object they see after hatching, which ensures they remain safe with their mother and learn how to be adult geese. These landmark studies sparked decades of search for the adaptive function of different behaviours (Owens 2006), which later translated into the behavioural ecologists' modern obsession with fitness consequences of behaviour, ideally in the real ecological context. Behavioural ecology was born (see Birkhead and Monaghan 2010; Kokko and Jennions 2010).

There is, however, some irony in the images that these early studies of adaptation convey. There are famed pictures of geese, which happened to be imprinted on Konrad Lorentz's boots on hatching, courting the ethologist as if they were conspecific adults; and stories of Niko Tinbergen's sticklebacks wasting energy on aggressive displays towards the reflection of red cars which would pass by the window next to their tank. It is hard to see the adaptive value of those behaviours. Naturally, we all know that humans are rarely present when goslings hatch,

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and red car reflections do not represent a frequent sight for most sticklebacks. Perfectly adaptive behaviours can become maladaptive when taken out of context, and we can only expect organisms to adapt to what has been relevant for a substantial part of their evolutionary history. But history changes. In an era of massive human-induced environmental change, goose anthropophilia and stickleback paranoia are the least of our conservationist worries. While behavioural ecologists argue about the 'optimality' of behaviour (Fox and Westneat 2010; Gardner 2010; Kokko and Jennions 2010), entire species are disappearing as they fail to adapt to rapid changes in their environments. The catastrophic population consequences of island birds' inability to escape introduced predators represent a clear example (Blackburn et al. 2004). The list of catastrophic behavioural maladaptation is long. A fatal attraction to lighthouses can claim thousands of seabird lives per night (Jones and Francis 2003), human use of tactical sonars or seismic surveys appear to cause whales to strand on beaches (Weilgart 2007), and dragonflies lay eggs on the tarmac which, under their polarized vision, looks just like the best of ponds (Horváth et al. 1998).

Other organisms seem to adapt to change much better, and this might allow them to mitigate any negative population consequences, sometimes to the extent that the change proves beneficial. Trinidadian guppies *Poecilia reticulata* can evolve their escape ability upwards within a few years of changing their predatory environment (O'Steen et al. 2002). Quolls *Dasyurus hallucatus* in Australia have increased their survival by learning to avoid eating introduced toxic cane toads *Rhinella marina* (O'Donnell et al. 2010). Torresian crows *Corvus orru* have gone beyond learning and survival, and have spread—through cultural transmission—their ability to feed on cane toads by turning them on their bellies and eating their non-toxic innards (Donato and Potts 2004).

Behavioural ecologists often argue about the likely population consequences of behavioural change (or the lack of thereof) when environments are changing. If bird migration timing becomes mismatched regarding weather and the consequent peaks of food availability, will the consequences be dramatic or mild (Jones and Cresswell 2010, Chapter 6)? Will mutualistic relationships between corals and their photosynthesizing symbionts break down or will coral hosts be able to switch to zooxanthellae partners that tolerate thermal stress better (Kiers et al. 2010)? Given such a diversity of examples, how and when do we expect the behaviour of populations to adapt to a novel environment?

The intention of this chapter is to lay the conceptual framework necessary to understand how changes in behaviour occur at the population level and mention the tools we have in hand to predict it. Throughout the chapter, we make a deliberate effort to understand behaviour as a phenotypic trait that can have a genetic basis while also depending on the environment. Fitness-related behaviours will, by definition, have consequences on birth and death rates, which means they will have an impact on population dynamics. The importance of this can be illustrated by a study on Seychelles magpie robins *Copsycus sechellarum*, where competition for territories and mates was shown to strongly influence the demography and extinction risk of this endangered species (López-Sepulcre et al. 2009).

These links between fitness and demography will allow us to refer to tools of analysis common in evolutionary and population biology. Behaviours are not always like any other trait, however; they possess a high degree of plasticity derived from a diversity of mechanisms (learning, conditioning, genetically determined reaction norms, etc.). Consequently, they have the potential to change at a much faster rate than many other traits of an organism, which causes a perhaps richer set of potential evolutionary trajectories than offered by many other suites of traits.

1.2 What causes changes in the average behavioural phenotype of populations?

The behaviours that a population exhibits can be described as a set of phenotypes. In evolutionary biology, our understanding of phenotypic change can be captured by the Price equation (Price 1970), a simple representation of the necessary and sufficient conditions for inter-generational phenotypic change. Although the Price equation has no predictive power beyond one generation nor, in its simplest form, does it explicitly account for all possible mechanisms of change, it is nevertheless a good starting point to structure one's thoughts on the mechanisms responsible for phenotypic change. One of its most common formulations reads,

$$\Delta\,\bar{z} = cov\left(w_i, z_i\right) + E\left[w_i \Delta z_{i,j}\right]$$

In prose, the equation states that the change in the average phenotype z in a population between one generation and the next (Δz) is the sum of two quantities: the covariance between an individual's trait z_i and its fitness w_i as quantified in the parental generation (first term on the right hand side), plus the expected (mean) trait difference between parents i and offspring j (second term on the right hand side). The former change captures selection, and the latter describes the bias in the transmission of the trait from parent to offspring (i.e. how consistently different the offspring are from their parents). Note than in the latter term, the average difference between parent and offspring $\Delta z_{i,j}$ is weighed by the fitness of the parent (i.e. that difference will be represented more often in parents which sired more offspring).

For example, in a migratory bird, the very earliest arriving birds might enjoy better breeding success than they would have before the onset of climate change. If we choose to measure the arrival date as an integer of days after January 1, such that early arrivals are expressed as low values of z_i, we expect a negative covariance between z_i and fitness. This, by itself, tends to make Δz negative, predicting that birds of future generations will arrive earlier. However, it may also happen that the arrival time of an offspring has little to do with the arrival time of the parent, for example, because arrival timing is influenced by weather, rather than a genetic disposition to arrive early, and offspring experience a colder year than their parents (which makes them arrive later and thus have higher z_i). In this case, the early parents with an unusually low z_i, whose fitness w_i is high in the second term of the equation, will tend to have offspring who arrive later, hence $\Delta z_{i,j}$ is positively biased. For those parents with later arriving times, their offspring may arrive earlier than them, creating for those parents a negative $\Delta z_{i,j}$. Is $E(w_i\,\Delta z_{i,j})$ then zero, given that the population features both positive and negative biases $\Delta z_{i,j}$? No: because the fitness w_i of the latter type of parents is low, they have less weight on the mean, and the net effect is a positively biased $E(w_i\;\Delta z_{i,j})$. In other words, offspring are arriving later than they would if the covariance between fitness and trait value was the only factor at play. This outcome means that the fitness advantage of parents with early times is diluted by a low fidelity of trait transmission, and thus the phenotype does not change in an adaptive manner. The net change in arrival timing is small or null when most variation is environmentally, rather than genetically, determined.

By describing inter-generational change, this formulation of the Price equation does not explicitly account for changes in the trait within generations. Since many of the examples of interest involve organisms with overlapping generations, we need to make this explicit and rewrite the equation:

$$\Delta\bar{z} = \overbrace{\underbrace{\mathrm{cov}\left(s_i, z_i\right)}_{\text{viability selection}} + \underbrace{E\left[s_i \Delta z_{i,i}\right]}_{\text{individual change}}}^{\text{intra-generational change}}$$

$$+ \overbrace{\underbrace{\mathrm{cov}\left(r_{i+}, z_i\right)}_{\text{fertility selection}} + \underbrace{E\left[r_{i+} \Delta z_{i+,j}\right]}_{\substack{\text{parent-offspring}\\ \text{differences}}}}^{\text{inter-generational change}}$$

The first two terms represent changes *within* a generation (intra-generational change), which are described as the covariance between survival s and the trait (viability selection, $\mathrm{cov}(s_i z_i)$) plus the expected change between one time step and the next in the trait values of survivors (individual change $E(s_i\;\Delta z_{i,i})$). The second two terms determine the change *between* generations (inter-generational change), which consists of the covariance between the reproduction of surviving individuals $r_{i\,+}$ and the trait (fertility selection, $\mathrm{cov}(r_{i\,+}\;z_i)$) and the expected parent–offspring differences among reproducing individuals (parent–offspring differences, $E(r_{i\,+}\;\Delta z_{i,j})$). It is good to check that this equation reduces to the first one for non-overlapping generations: there is simply no survival (the first two terms of inter-generational change are zero) and fitness is determined entirely by reproduction ($r_{i\,+} = w_i$).

Our intention in this section is not to suggest that all research conducted in the field should use the four components of Equation 1.2. However, we do find it useful to let this breakdown of components help organise thoughts on whether phenotypes will change as environments change, because any combination of mechanisms that we claim to cause a population change in a given phenotype represent a combination of those terms. Each of those terms should be accounted for when arguing about changing populations (see Fig. 1.1), which means that focusing on one is only sufficient if the others can be convincingly argued to be negligible. Considering the Price equation thus ensures that our discussion on mechanisms of behavioural change is logically complete. We now discuss the different biological mechanisms governing each component of the equation.

1.2.1 Covariance between trait and fitness: viability and fertility selection

Unsurprisingly, given the attention that behavioural ecologists pay to adaptive functions of a trait, selection has been the main focus of both theoretical and empirical studies of behavioural ecology (Owens 2006). The first and third terms of Equation 1.2, viability and fecundity selection, capture this line of thought. In principle, documenting selection is easy: individuals with 'better' traits have improved survival or reproduce more effi-

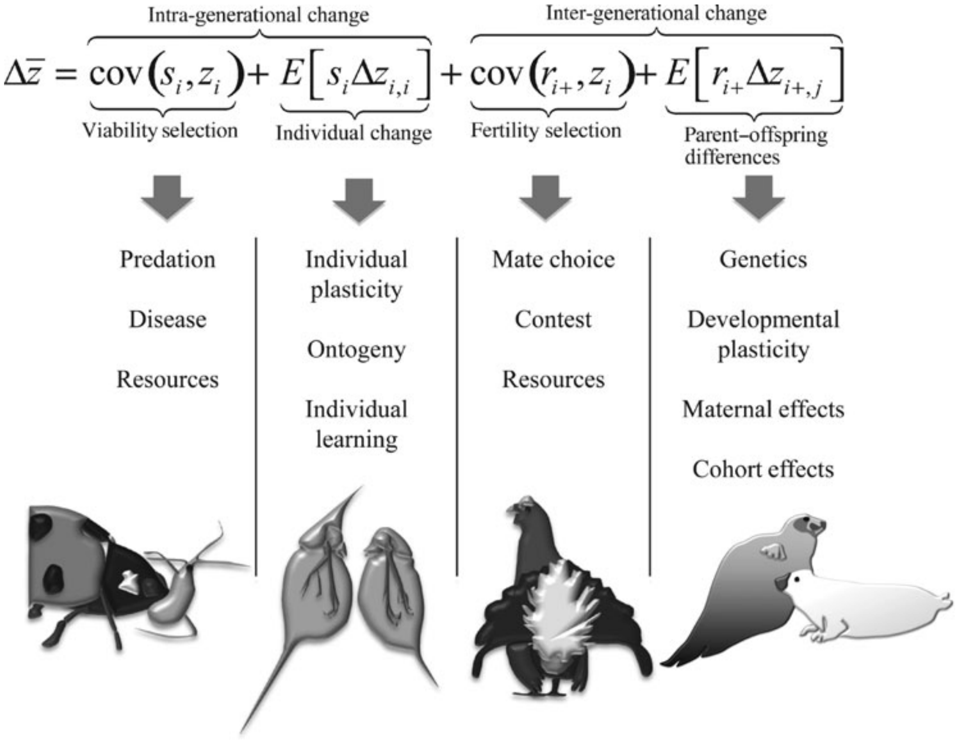

Figure 1.1 Decomposition of phenotypic change using the Price equation for overlapping generations, showing examples of mechanisms that affect each component.

ciently. It is rare, however, to see the full covariance between fitness and the phenotype calculated. Often only survival or reproduction is correlated with the trait. This can mislead, since survival and reproduction may trade off each other.

For example, in the presence of novel predators, some individuals might exhibit better antipredatory behaviour than others. All else being equal, one might expect these individuals to now have higher fitness than before the predator was introduced, but strictly speaking this argument implies that the survival advantage does not trade-off with reproduction. This would allow us to argue that the covariance between the trait of surviving individuals and reproduction is zero, but in reality, an individual constantly hiding in a refuge may not have high mating success (yet see Jennions et al. 2001 for the lack of evidence for such a trade-off). What is true is that, all else being equal, the arrival of a new predator probably does shift fitness in the direction that favours timidity more now than it did before. Parameterizing the Price equation to answer such short-term questions is, as such, not difficult, given that it merely involves the calculation of means and covariances. The difficulty lies in obtaining such comprehensive data. It is here —where one appreciates the enormous value of intensive individual-based field studies—that traits, survival, reproduction and parentage relationships are tracked (Clutton-Brock and Sheldon 2010).

It is important to highlight here the conditional nature of the reproductive term in Equation 1.2. The fertility selection component in this formulation is only the covariance between the trait of surviving individuals and their reproductive output: it does not include those individuals that do not survive (hence the notation $i+$). Survival obviously indirectly affects reproduction because dead individuals do not reproduce (in fact, when considering evolutionary change, survival is only relevant as a means to reproduction), but to avoid double accounting, this is assigned to the survival component.

1.2.2 Between and within individual variation

While behavioural ecology devotes much attention to the study of selection, the remaining two terms of Equation 1.2 are less often explored. The second term describes the degree of trait variation within individuals over their life time, while the last term describes differences between parents and offspring analogously to the second term in Equation 2.1. It is possible, but in reality not very likely, that both values equal zero. This requires that individuals do not change the behavioural trait in their entire lifetimes (e.g. they always display to mates with the same intensity), and that the trait is perfectly inherited such that parents and offspring are identical. If these conditions are not met, we must consider alternative routes to phenotypic change.

Let us first consider individual variation on the phenotype of individuals throughout their lifetimes (second term in Equation 1.2). Behavioural traits are often highly labile. If there is either adaptive or non-adaptive plasticity (reaction norms), we can expect environmentally driven changes in a population from one year to the next (Chapter 11). For example, if individuals tend to flee from predators, then years of predator abundance will see more movement than years when predators are scarce. Similarly, individual learning (see Chapter 4) or ontogenetic (developmental) change can produce differences in behaviour over time.

Such changes can be usefully classified according to their degree of reversibility. Some behaviours respond to immediate environmental conditions: fleeing from predators can function in this way. But antipredatory behaviour can also change with age or prior experience in a unidirectional way. Unidirectional changes are common among morphological traits such as the size of an organism that show either determinate or indeterminate growth. Ontogenetic changes in animal behaviour constitute one of the four big questions posed by Tinbergen (1963), and potential examples include the onset of breeding (which may be a plastic trait with respect to the social situation, Carrete et al. 2006), irreversible effects of early experience on future habitat choice (Stamps 2006), and the increase in helping behaviours at senescing ages (Richardson et al. 2007). Understanding the effect of directional developmental change on changes in the mean phenotype requires tracking the population's cohort or age structure (for a Price equation approach expanded to account for the component of age-structure, see Coulson and Tuljapurkar 2008).

Consider the most extreme case: completely reversible environmental plasticity where individual behaviour is instantly and completely determined by the environment, and the environment varies over time but is experienced in the same way by all individuals. In such a case, individual phenotypes vary over time but no individual differs from another (because they respond to environmental variations in an identical trait). Consequently, all selective components (covariances) disappear. The observable change in behaviour is now completely determined by plasticity tracking the environment (second term in Equation 1.2). Note that this scenario does not say anything about whether the behaviour is adaptive.

Finally, behavioural ecology must consider the last term in Equation 1.2, parent–offspring differences. There are several reasons why this component is important; above we already discussed parent–offspring differences as a source of variation that can counteract selection in the context of migratory bird arrival times. These differences are impacted by several different biological processes. Maternal effects can be important in determining offspring traits such as dispersal (Massot et al. 2002) and territorial behaviour (Stapley and Keogh 2005). Similarity between parents and offspring (i.e. a diminishing of parent–offspring differences) can also occur for habitat choice through imprinting on the natal habitat (Davis and Stamps 2004) or, more simply, by common environmental effects due to spatial heterogeneity and low dispersal. Social learning is another common route to similarity (as may happen with cultural evolution, e.g. Bentley et al. 2004; see also Chapter 4).

Of course, the most commonly studied mechanism of parent–offspring similarity in evolution is that which arises through genetic factors. For genetic factors to be of great importance, parent–offspring differences arising via other mechanisms should be small, leading to a dominating assumption in much of behavioural modelling that the mode of inheritance is not a constraint for evolution in the long term (Parker and Maynard Smith 1990). This is justified in models predicting broad patterns of evolutionary outcomes in the long term (e.g. to answer questions such as whether higher relatedness promotes the evolution of cooperation across species, Cornwallis et al. 2010), considering that parent–offspring similarity is high in the long run even though environmental fluctuations may swamp it when viewed over short periods of time.

However, this justification for adaptation breaks down when we are concerned with population persistence under acute environmental change. In this case, our interest shifts from studying the long-term ability of natural selection in solving problems to estimating the rate of evolutionary change over a much shorter timescale when the population is unlikely to be at evolutionary equilibrium. In such a context, the question is often: will the behavioural response be adaptive in the timescale of the environmental change, or will it be maladaptive (Gomulkiewicz and Houle 2009; Futuyma 2010)? For this, deviations from zero in the last term in the Price equation play a key role. Behaviours display heritabilities similar to other phenotypic traits (Stirling et al. 2002), but they are simultaneously susceptible to an unusually diverse plethora of mechanisms governing parent–offspring similarities, including learning, imprinting, and cultural transmission. The relative role in each factor diminishing or heightening parent–offspring differences could be fruitfully studied in a more integrative fashion.

1.3 When does behaviour change adaptively?

The breakdown of components presented above serves as a framework for understanding how different mechanisms affect a mean change in population behaviour, but it also helps us to reason whether such change will be adaptive. For a change to be adaptive it must go in the direction indicated by the selective components (i.e. the two added covariances in Equation 1.2). However, simultaneously, a population can also manage to persist in novel environments without adaptive change. For example, if all individuals are able to respond to, and flee, from a novel predator, phenotypic tracking without adaptive change can be sufficient to rescue a population.

In general, there is no guarantee that all components of the Price equation will point in the same direction (have the same sign). According to the idea of counter-gradient selection (Conover and Schultz 1995), selection and genetic change may oppose an environmental effect, leaving no net phenotypic change. A non-behavioural example of this is the orange hue of Trinidadian guppies, which shows marked differences across populations sharing the same diet, but due to variation in food availability, most differences vanish in the field (Grether et al. 2005). This example highlights that a lack of phenotypic differences does not exclude genetic population differences.

The genotype–phenotype map has an interesting relationship to selection. Selection can only act on variation that is expressed at the phenotypic level, but it cannot result in an evolutionary response unless the differences in phenotypes have a genetic basis. Hence, highly plastic traits can experience strong selection but, due to their low heritability, little evolutionary response.

Adaptive plasticity, however, has been argued to favour evolution in a different manner: it brings the phenotype closer to the adaptive peak, increasing population size and, consequently, the opportunity to display genetic variation closer to the optimum (Ghalambor et al. 2007; Fierst 2011, also see Chapter 11). In the context of learning, this is known as the Baldwin effect, whereby learning to cope with a new selective pressure allows the population and its genetic variation to persist, allowing future selection and evolution on the learned trait (Baldwin 1896; Chapter 4).

The amount of additive genetic variation present is indeed a strong predictor of how well populations manage to evolve to new adaptive peaks. Heritabilities of traits can only become high if there is ample additive genetic variation. This results in high parent–offspring similarity, and phenotypic changes under these conditions are more closely dictated by selection. Interestingly, life history theory predicts that heritabilities should only remain high for traits that are not strong predictors of fitness due to higher genetic variation (Bulmer 1989; Charmantier and Garant 2005). This prediction arises because selection in the past should have weeded out inferior genotypes if these recurrently, generation after generation, give rise to individuals displaying poor fitness; yet a review of empirical studies showed that the low heritability of fitness-related traits is due to higher environmental variation, rather then lower genetic variation (Houle 1992).

In the context of environmental change, lower heritabilities can be a worrying result: it means that those traits that matter most to how well individuals perform might be the first ones to run out of genetic variation should a changed trait value suddenly become optimal. Horizontal transmission of traits will also tend to increase parent–offspring differences and therefore slow down adaptive change (Helanterä and Uller 2010). For example, if individuals learn new foraging techniques from their peers, the underlying genetic differences in foraging ability will be smaller, and the response to selection will be weaker. Under such a scenario, genetic adaptation will not happen at the same pace as one would see without plasticity and learning.

We have, above, concentrated on the factors that facilitate or hamper genetic adaptation. In a conservation context, the hidden assumption is often that only genetic adaptation can rescue populations in the long term (see discussion on evolutionary rescue in Chapter 16). However, our earlier example of individuals fleeing from predators shows that behaviour can also change (more fleeing) without genetic evolution. Likewise, if individuals are not genetically adapted to, say, urban environments, but can compensate by learned behaviours passed on vertically and horizontally, the population is just as likely to persist. Indeed, plasticity, when not too excessive, has been shown to buffer populations against environmental variability in a way that can enhance population stability (Reed et al. 2010).

A different and graver concern is that not all change, whether genetic or non-genetic, occurs in an adaptive direction. Maladaptive behaviours might be horizontally transmitted. There is, for example, evidence that individuals may choose their habitat based on conspecific attraction. If some individuals make sub-optimal choices, these can become perpetuated (Stamps 2001; Nocera et al. 2006). Distinguishing between mechanisms of genetic and cultural inheritance in models of social evolution has been shown to yield markedly different evolutionary predictions (Lehmann et al. 2008). In the following section we will have a more detailed look at maladaptation and adaptation by making the population-level response explicit in terms of population size. This shows that while maladaptation is often bad news for the persistence of a population, fitness changes can become masked by density dependence. More paradoxically still, there are scenarios where even adaptive evolution can hamper population size.

1.4 Demography as a cause and consequence of behavioural adaptation

For all the beauty of the Price equation approach, it is not exempt from drawbacks. Population change can be decomposed in many ways, and unsurprisingly, the attention of a researcher subsequently becomes focused on what the method singles out. The equation remains true when, say, population size varies over time, but since the approach does not contain explicit terms for such changes, it does not encourage thinking about population sizes *per se* (Rice 2008). The reason to focus on this is that changes in behaviour are likely to affect demography and population size while, at the same time, population size can be an important factor influencing adaptation (Kokko and López-Sepulcre 2007).

A relatively popular avenue of theoretical work is to examine whether adaptation can proceed fast enough to avoid extinction when the environment changes to a state where the original phenotypes perform so poorly that extinction will follow unless there is evolutionary change (Chapter 16). Among such modellers, Gomulkiewicz and Holt (1995) were the first to point out that it is not sufficient to predict a deterministic trajectory where a population first declines after the environmental change occurs and then gradually bounces back (growth now occurs as the remaining individuals are those whose traits allow them to survive and reproduce in the novel environment). The reason why this is not guaranteed to avoid extinction, even if some individuals possess traits that allow them in principle to form a new source population, is that populations can be driven to very low sizes during the dangerous maladapted phase, and small populations are known to be vulnerable to extinction through demographic stochasticity (the factor considered by Gomulkiewicz and Holt 1995) as well as many other stochastic factors (Traill et al. 2010 and references therein). The milder the initial maladaptation, and the larger the initial population, the better the prospects of an evolutionary rescue (the continued persistence of the population that relies on adapting to the new environment, Gomulkiewicz and Holt 1995).

Recently, Chevin and Lande (2010) have investigated the general question of both plasticity and genetic evolution in density-regulated populations; they also assume that the degree of plasticity can either be constant or can, itself, evolve. Again, the environment is assumed to shift abruptly, and then the population either experiences evolutionary rescue or, failing to do so, goes extinct. They show what Gomulkiewicz and Holt (1995) in their Discussion already suspected: the density-independent scenario investigated by Gomulkiewicz and Holt (1995) is a best-case scenario, because density dependence tends to depress population growth. Chevin and Lande (2010) however also pointed out that if we include phenotypic plasticity, it keeps populations afloat much better than mere genetic evolution is able to.

This can be exemplified with a specific scenario. In the context of habitat choice, it has long been known that environmental change can produce 'ecological traps' (Schlaepfer et al. 2002). In a trap situation, individuals use out-dated cues of habitat quality and prefer habitats that have become worse than the (non-preferred) alternatives, or prefer to reside in places that have not previously existed (manmade habitats) and that pose unanticipated dangers (also see Chapter 5). The population dynamics of such cases are interesting. If the population remains large, then many individuals will be forced to breed in the non-preferred but safe B habitat. But if for any stochastic reason (say, a harsh winter) the population falls to low levels, then most survivors can follow their maladaptive preference for A and the entire population may become a sink—followed by extinction via an Allee effect (Kokko and Sutherland 2001). In this setting, there is clear scope for evolutionary rescue. Kokko and

Sutherland (2001) showed that either genetic adaptation or learning can rescue populations, but a very simple rule of phenotypic plasticity works much better than all alternatives. If individuals simply imprint on the type of habitat in which they were born, and preferentially breed in similar habitats, then populations almost immediately switch to near-optimal habitat use. This is because most individuals that are alive at any point in time must have been born in habitats that allow for successful breeding.

We do not know at present, however, how general such findings are. Theoretical effort on this important topic appears relatively scattered, with no systematic effort yet existing to work out precisely what kind of phenotypic change (or lack of change), or which kind of population regulation, should impair population persistence under environmental change. Simple rules of thumb may often work well: large population sizes not only buffer species against the demographic processes that cause vulnerability, but also create a more optimistic outlook for coping with new evolutionary challenges. Reflecting such principles, birds inhabiting large landmasses have been shown to have faster rates of molecular evolution than those confined to islands (Wright et al. 2009), and in the realm of microbial evolution there is even direct empirical support for the role of initial population size and genetic variation in promoting evolutionary rescue (Bell and Gonzalez 2009). The issue of evolutionary rescue is dealt with more extensively in Chapter 16.

1.4.1 Does adaptation always enhance persistence? No

There is one more point that is as intellectually exciting as it is worrying: adaptation itself might not always be in the best interest of a species when environments change. To understand this somewhat counterintuitive point, it is important to remind oneself that selection is much stronger at the level of the gene, or individual, than at higher levels. A population-detrimental behaviour can spread if there is no active policing against it, and if the behaviour causes a relative fitness advantage for its bearer (Rankin et al. 2007). Sexual conflict is a clear example (see Chapter 15), and one does not even have to think about the damaging consequences of extreme male behaviours (that sometimes kill females that males are attempting to fertilize, Reale et al. 1996, Shine et al. 2001; for evolutionary and population dynamic predictions see Rankin et al. 2011) to understand that adaptation can lead to a decline of the population. For example, male–male competition often favours large males, and this can place a large energetic burden on the females that raise male offspring as well as reducing equilibrium population sizes if these large males continually eat more food per capita than the females do. This reduction of what is available for the reproductive fraction of the population then effectively decreases the carrying capacity of the habitat (Kokko and Brooks 2003). Thus, as interesting as the ability of adaptation to rescue populations, is the possibility that strong individual-level selection drives the population closer to extinction.

Conspecific competition can make the consequences of adaptation surprising, and this is not confined to the realm of male–female interactions. Consider, once again, migrant birds, and now assume that there are two behavioural options that are genetically determined: a bird might migrate or it might attempt overwintering at the breeding grounds. The advantage of migrating is that this allows the bird to escape the harshest conditions in midwinter, and thus (despite the dangers of covering large distances) presumably migration improves survival. The advantage of year-round residency, however, is that the bird will gain prior access to the best territories. This means that the best strategy is not simply determined by what balances the survival prospects: a bird may benefit by using a strategy that yields lower survival (the overwintering attempt), because it is balanced by better breeding prospects if it survives. Depending on exactly how severe the winter is, this type of a situation can yield full migration, partial migration, or full year-round residency (Kokko 2011), even if migrants always survive better.

If populations adapt to climate change that makes winters milder and more survivable, one expects the evolution of more residency. This indeed happens in the model of Kokko (2011), and at first sight, one might imagine that such adaptation would improve population performance too. Yet the opposite is predicted to happen: populations can dramatically decline once birds maximize their fitness by abandoning migration. How can there be such a decline in a model that, for once, is focused on a case where climate change is assumed to have only favourable effects (wintering at the breeding grounds is assumed to become easier, while migration mortality is assumed to remain unchanged)? The reasoning goes as follows. The basic trade-off in the model is between survival over the winter (this is better for migrants) and good breeding prospects (this is better for residents). If the relative difference between surviving in different locations diminishes—which is plausible, given that climate change is expected to have its largest effects nearer the Arctic—then birds will increasingly choose the resident option *even though it is still the more dangerous one*. They are rewarded for it during the summer season, which makes this choice fully adaptive, but in the summer season the success of one individual comes at the expense of another since not everyone can occupy the best territories (Kokko 2011). One way to express this is that territorial competition is a zero-sum game, and when individuals evolve to invest more in such games (the expected outcome when the relative importance of survival diminishes relative to intraspecific competition for territories), the population as a whole is expected to perform worse than it did with less investment in outcompeting conspecifics (Rankin et al. 2007). Birds battling climate change might thus, in some cases, decline not because they fail to adapt, but because they do!

1.5 Conclusions: beyond changes in the population mean of a behaviour

We have here encouraged readers to consider that there is more to behavioural change than mere adaptation. The degree to which parents and offspring resemble each other varies because of a multitude of factors, and a change from one generation to the next does not always reflect adaptive evolution. Nor should we expect populations that adapt fastest to necessarily fare best on a changing planet: sometimes plastic responses to new situations are more adequate than adaptive evolution, and sometimes adaptation itself can lead to population decline.

While we have aimed to be comprehensive in decomposing population change to all relevant categories, it is important to repeat that any categorization tends to focus one's attention to specific factors at play, sometimes at the expense of other features that can prove important. Our examples are phrased in terms of a mathematical construction that describes the change in the population mean of a single behavioural trait. For long-term population and evolutionary dynamics, it is important to consider changes in the variance of the trait (see Chapter 12; for the relevant mathematical analysis see Coulson and Tuljapurkar 2008). Sex-specific behaviours are a clear example where a single mean does not capture what is going on: males can be larger or smaller, behaviourally dominant or subordinate, and more or less numerous than females, with obvious consequences for population dynamics and selection (Chapter 12); likewise the degree of variation among males can impact female behaviour (Chapter 15). Entire suites of behaviours may evolve in interdependent ways, a scenario that can be represented by multivariate extensions of the Price equation and which has spurred the study of behavioural syndromes (Dingemanse et al. 2010). Finally, a simple iteration of the Price equation does not allow us to visualize a likely important phenomenon: the evolution of plasticity and behavioural reaction norms. In essence, this would involve allowing the individual change term in Equation 1.2 to evolve: that is to be itself subject to selection, parent–offspring differences, and within individual variation. This important topic is discussed in Chapter 11.

Acknowledging these omissions should not take away from our main point that behavioural ecologists should be open-minded about the mechanisms underlying the change in a trait—or lack thereof. The following chapters present exciting examples where learning, plasticity, genetic inheritance and other modes of trait transmission determine what happens when populations experience novel conditions. Simultaneously, we strongly encourage explicit consideration of population size, density, and sex ratio in behavioural contexts. These are not mere outcomes that a conservationist is interested in (see Chapter 17), but also feed back to impact, and coevolve with, further behavioural change.

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CHAPTER 2

Environmental disturbance and animal communication

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➲ Overview

Even seemingly benign anthropogenic influences can profoundly change animal communication. Human impacts have the potential to alter the dynamics of communication at every stage of the process, from the production of signals to their transmission and ultimately their evaluation by receivers. In many cases, disturbance reduces the efficacy of communication by weakening signal production, distorting or attenuating signals as they travel to the receiver, or hampering their perception. More insidiously, changes to the environment can modify the distribution of signals in the environment or the modalities that receivers use to evaluate signallers. Alterations to communication systems can have far-reaching evolutionary consequences, particularly given communication's role in maintaining reproductive isolation among species.

2.1 Introduction

Communication, which we define following Rendall et al. (2009) as an individual's use of signals to influence the behaviour of a receiver, is fundamental to the well-being of individuals and populations. Social signals are ubiquitously used in finding food, avoiding predators, resolving conflicts, and selecting mates. Interference with communication, therefore, can seriously alter survival patterns, change the magnitude and direction of natural and sexual selection, and impinge on basic evolutionary processes like reproductive isolation and hybridization. Even seemingly innocuous disturbances can impact communication in surprising ways, wreaking havoc on social systems and generating irreversible evolutionary consequences.

The ecological effects of anthropogenic disturbance on communication are often insidious; in many cases, subtle alterations to the environment are only brought to our attention because of changes in animal behaviour. The evolutionary effects of impairing communication can reach far beyond disturbed areas in space and time, particularly if reproductive barriers among species are breached (Servedio 2004).

At its simplest, communication can be abstracted as an interaction between a signaller and a receiver. First, the signaller produces a signal, either by directly generating energy or, notably in the case of visual patterns and colours, modifying the distribution of energy from an external source. Second, the signal is transmitted through the environment, where it inevitably deteriorates in magnitude and quality, and it is finally perceived and processed by the receiver, who may produce a behavioural response (Bradbury and Vehrencamp 1998).

In this chapter, we describe how human impacts can alter communication, which we divide into three phases: signal production, transmission, and reception (Fig. 2.1). Where possible, we also address the ecological and evolutionary consequences of altered communication. The vast majority of relevant studies have involved auditory, visual, and chemical communication; we discuss possible effects on other modalities at the end of the chapter.

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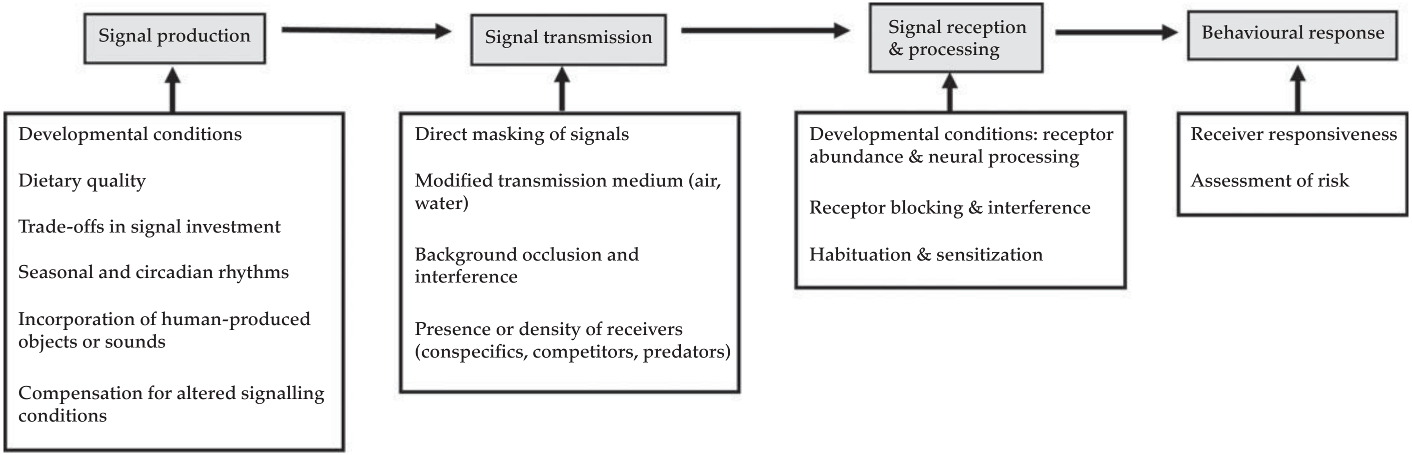

Figure 2.1 Phases of the signalling process (grey boxes) and major factors affecting each phase that have been shown to be modified by anthropogenic disturbances.

We focus on effects of anthropogenic disturbance on interactions among non-human animals, particularly conspecifics, and do not address the phenomenon of human–animal communication. In some cases, human impacts on animal communication are quite deliberate, as in the widespread use of pheromone traps for control of insect pests (Ridgway et al. 1990), and, more recently, invasive lampreys *Petromyzon marinus* (Li et al. 2007) or the use of simulated acoustic signals by hunters and birdwatchers. However, most such effects are unintended consequences of pollution, habitat degradation, or species introductions.

2.2 Signal production

One of the primary ways in which human alteration of the environment impacts signal production is via physiological effects on signal development and expression. In particular, contamination of the environment by metals and chemical pollutants can influence the development and production of signals via their impact on gene expression, endocrine function, and a range of other cellular processes. Perhaps the best documented effects of anthropogenic activities on the expression of animal signals involve endocrine disrupting chemicals (EDCs). EDCs encompass a wide variety of chemicals used in agriculture and industry, which, as their name suggests, affect the endocrine system. Their effects on behaviour and signalling are covered in Chapter 3. In this section, therefore, we focus on the potential effects of chemical and metal pollutants in general, as well as light pollution, on production of acoustic, visual, and olfactory signals. We also discuss situations where novel properties of the environment, such as artificial objects and mechanical sounds, may be incorporated into animal signalling repertoires. Finally, we note that signals are generally matched to local environmental conditions. Changes to signal expression often occur to enable effective signalling under altered environmental conditions, and can thus be a secondary consequence of environmental effects on signal transmission. We discuss these in the subsequent section on signal transmission, focusing here on changes to signal expression caused by physiological changes associated with various forms of pollution.

2.2.1 Acoustic signals

Pollutants such as chemicals and metals can affect many aspects of acoustic signal production. These include developmental processes, such as neural development important for song learning and memory (see also Chapter 4), resource allocation to signalling, and dietary quality affecting signal expression. Although empirical evidence is currently limited, a few recent studies have shown negative effects of pollutants on bird song. Great tits *Parus major* inhabiting sites with high levels of metal pollution have smaller song repertoires, and sing significantly less, than birds from less polluted sites (Gorissen et al. 2005). By contrast, European starling *Sturnus vulgaris* males produce longer and more complex songs when exposed to EDCs (Markman et al. 2008). However, EDC exposure also leads to immune suppression. By preferring males with more complex songs, females choose males in poorer health, suggesting possible population fitness consequences, especially in populations where males provide paternal care (Sandell et al. 1996).

As the previous example highlights, the effects of anthropogenic activities can be profoundly counterintuitive. Even well-intentioned interventions can have unintended consequences. For example, supplementing the diet of adult song sparrows *Melospiza melodia* results in increased clutch size, but male offspring have smaller song repertoires once mature (Zanette et al. 2009). Provisioning parents can thus make males less attractive to females, potentially facilitating heterospecific matings or inducing females to mate with males that produce less-fit offspring.

Apart from chemicals and metals, industrialization and urbanization generate noise and light pollution. We discuss noise in the section on transmission effects. Light pollution is likely to affect multiple aspects of communication, but its effects on the timing and expression of acoustic signals have been well-documented. Light pollution affects animal physiology and behaviour, thereby influencing signal production. This is unsurprising given that many animals show marked physiological changes in relation to both seasonal and circadian variation in natural light cycles (Navara and Nelson 2007). Bright city lights have induced widespread disruption of these natural light cycles.

Constant or changed exposure to light, even at levels comparable to the brightness of moonlight, can have major effects on circadian rhythms in a wide range of hormones, particularly melatonin (reviewed in Longcore and Rich 2004; Navara and Nelson 2007). Effects are exacerbated by the violet/blue wavelengths characteristic of artificial light. Melatonin has well documented effects on reproduction, protection against oxidative stress, and metabolism (Navara and Nelson 2007). Artificial light-induced reduction in melatonin has been implicated in the global increase in metabolic disorders and obesity in humans (e.g. Fonken et al. 2010). Clearly, light pollution has the potential not only to affect the timing of communicative behaviours (e.g. Kempenaers et al. 2010) but also the expression of sexual signals in animals. For example, frogs *Rana clamitans melanota* exposed to artificial light produce fewer advertisement calls (Baker and Richardson 2006). Despite recent recognition of the potential ecological consequences of light pollution (reviewed in Longcore and Rich 2004; Navara and Nelson 2007), we currently do not know how altered lighting regimes affect metabolism or trade-offs between signal investment and other physiological processes in natural populations.

2.2.2 Visual signals

An ever-growing number of studies have shown the harmful effects of human activities on visual signals, particularly secondary sexual ornaments. The development and expression of ornaments is often condition dependent and reflects an individual's level of, and ability to cope with, physiological stress (Buchanan 2000). Developmental stress from exposure to pollutants can influence a range of processes affecting the expression of signals. For instance, in the goodeid fish *Girardinichthys metallicus*, embryonic exposure to low concentrations of the organophosphorus insecticide, methylparathion, reduces male ornament size, colour, and courtship display rates (Arellano-Aguilar and Garcia 2008).

During adulthood, continued exposure to toxins can affect resource allocation, at the expense of signal expression. For example, animals experiencing higher levels of oxidative stress may allocate more antioxidants to reducing damaging effects of free radicals. This may compromise the expression of carotenoid-based visual signals, which is often correlated with levels of circulating antioxidants (Dauwe et al. 2006). For instance, yellow-legged gulls *Larus michahellis* fed a diet containing fuel oil from an oil spill had higher plasma levels of two types of antioxidant, vitamin E and carotenoids, and smaller red bill spots (Pérez et al. 2010a). Additionally, in free-living gulls exposed to an oil spill, the size of the red bill spot was positively correlated with body condition and negatively correlated with aspartate aminotransferase (AST), an enzyme indicative of liver damage in birds (Pérez et al. 2010b).

Several studies have similarly found that the intensity of yellow coloration on the breasts of great tits is negatively correlated with levels of metal pollution (Geens et al. 2009). In this species, however, there appears to be no relationship between total antioxidant capacity and carotenoid-based signal expression. Rather, Geens et al. (2009) propose that the differences in carotenoid coloration along the pollution gradient reflect pollution-induced differences in diet composition and quality. As this example highlights, various mechanisms could account for the relationship between pollution and signal expression. As is the case for acoustic signals, these mechanisms remain poorly understood in natural populations.

2.2.3 Chemical signals

Just as for visual signals, there is extensive evidence for disruption of chemical communication by a wide range of pollutants, in addition to endocrine disruptors. These pollutants can affect chemical information transfer, both within and between individuals, with potentially far-reaching consequences (Lurling and Scheffer 2007). However, it is often more difficult to distinguish which aspect of the signalling process (signal production, transmission, or reception) is being affected. Pollutants can alter chemical communication in three ways: (1) by affecting the quality and quantity of chemical signals (production); (2) by binding to the chemical signals themselves, reducing the quantity transmitted (transmission); or (3) by binding to receptors and influencing receptor function (reception).

The majority of studies on pollution and chemical signalling have focused on the effects of pollutants on receptor function (reviewed in Lurling and Scheffer 2007); however, a few have clearly shown that pollutants affect the production of chemical cues rather than their reception. For example, Ward et al. (2008) showed that exposure to the widely used surfactant 4-nonylphenol (4-NP) does not affect the ability of banded killifish *Fundulus diaphanus* to detect chemical cues but does affect their chemical signals. Similarly, exposure to nitrates, which are used extensively in agriculture, affects the properties of olfactory signals rather than their chemoreception in palmate newts *Lissotriton helveticus* (Secondi et al. 2009). Unexposed females preferred unexposed males over exposed males in olfactory—but not visual—mate choice tests.

Overall, a consistent conclusion of studies on the effects of pollutants on animal behaviour is that levels of exposure considered to be low (substantially lower than those causing mortality, mutation, or cancer) can have major effects on behaviour, including communication. In the most serious cases, this can cause 'behavioural castration' and population decline (Lurling and Scheffer 2007).

2.2.4 Signals acquired from the human environment

Animals can sometimes use features of human origin in their signal repertoires. For example, avian vocal mimics are frequently observed to incorporate mechanical sounds, like car alarms, into their acoustic repertoire (Clark 2001). Human activities can also affect the extended phenotype, such as external structures (e.g. nests and bowers) constructed by individuals to attract mates. For example, bowerbirds decorate their nests with both natural and artificial objects (e.g. coloured plastic and glass) that they collect from the environment (Marshall 1954). Colour preferences for bower decorations, both natural and artificial, have been extensively studied (e.g. Madden and Tanner 2003; Patricelli et al. 2003). Novel objects increase the range of potential signal innovations (see Endler et al. 2005) and their availability can affect both female preferences and male behaviour, such as rates of decoration stealing and destruction of the bowers of competitors (Hunter and Dwyer 1997). In black kites *Milvus migrans*, meanwhile, nest decorations including plastic and other scavenged items serve as territory-defence signals (Sergio et al. 2011).

Anthropogenic effects on nest design and building behaviour are not limited to birds. Three-spined stickleback *Gasterosteus aculeatus* males decorate their nests with coloured algae and, in a laboratory setting, will also use artificial objects such as colourful, shiny foil and 'spangles'. Females are more attracted to nests decorated with artificial objects than those without (Ostlund-Nilsson and Holmlund 2003), suggesting that availability of such objects in the wild could influence male nest decoration and female choice. In this species, changes to water flow regimes have also been shown to result in modified nest structure and building behaviour, with potential consequences for mate choice and sexual selection (Rushbrook et al. 2010). In general, human introductions of novel signal elements have great potential to affect receiver behaviour, as female preferences for novel male traits appear to be widespread in animals (Ryan 1998).

2.2.5 Matching signals to altered habitats

Signals are often matched to local environmental conditions (Endler 1992). Changes to the signalling environment (visual, olfactory, or acoustic) alter the efficacy of signals, thereby inducing changes to signal expression. For example, increased water turbidity not only affects behaviour and the transmission of visual signals, but also their expression. In palmate newts, water turbidity decreases the size of male secondary sexual traits, an effect that is not attributable to reduced foraging efficiency in turbid water (Secondi et al. 2007). One potential explanation for reduced investment in visual signals in turbid waters is that under conditions in which visual signal transmission is poor, males reallocate resources towards other activities such as mate searching or to other types of signals (e.g. olfactory). As discussed below, this can be accompanied by increased attention by receivers to more readily detectable cues (e.g. Heuschele et al. 2009).

As is the case for water turbidity, many human environmental disturbances primarily affect signal transmission, with changes to investment into signal expression being a secondary response. For example, anthropogenic noise pollution and urbanization drastically change acoustic signal transmission, which, in turn, alters signal expression (reviewed in Laiolo 2010; Slabbekoorn et al. 2010; Warren et al. 2006). As noise pollution tends to be both loud and low pitched, animals that signal in the presence of anthropogenic noise tend to increase amplitude (loudness) and/or increase frequency (pitch), so that they may be heard. Killer whales *Orcinus orca* increase the amplitude of their calls in relation to background noise levels decibel for decibel (Holt et al. 2009). Increases in amplitude are likely to require greater energetic investment, potentially influencing any relationship between the signal and other aspects of an individual's phenotype (i.e. influencing signal content as well as efficacy). As such, changes to signal expression tend to be a secondary consequence of changes to signal transmission, a topic that we will now discuss in greater detail.

2.3 Signal transmission

We define signal transmission effects as those which decrease the signal-to-noise ratio from the time a signal is emitted to the time it is transduced by a receiver. Human activities can alter signal transmission in a number of ways (Fig. 2.1). First, human activities can cause direct masking of animal signals, such as traffic noise masking bird or frog calls, or chemical pollutants interacting with pheromones. Second, they alter properties of the transmission medium, an example being changed light transmission through air or water due to pollution or eutrophication. Third, human activities modify physical structures that interfere with signal transmission. Both the construction of urban landscapes and drastic changes to natural landscapes (e.g. clear-felling, weed invasion) affect the acoustic, visual and chemical signalling environment. For example, urban environments tend to be characterized by large, flat, sound-reflective surfaces, which cause sounds to attenuate more slowly and to degrade due to reverberation. Lastly, human activities can alter levels of interference from other animals, including conspecifics, competitors, and predators, due to human-mediated changes in the population density and distribution of many species. In this section, we briefly review how human activities affect signal transmission for each signalling modality (acoustic, visual, chemical) and the consequences of such changes for animal communication.

2.3.1 Acoustic signals

By far the most attention on the effects of human activities on animal communication has focused on acoustic signals (reviewed in Laiolo 2010). Human-generated noise is widespread and often at levels substantially greater than those encountered in nature (Barber et al. 2010; Warren et al. 2006). Anthropogenic noise in both aquatic and terrestrial environments is characterized not only by high absolute levels, but also by a high degree of spatial and temporal heterogeneity in noise levels, and the prevalence of low frequency sounds (<1 kHz), such as traffic and boat noise (Slabbekoorn et al. 2010; Warren et al. 2006). However, noise pollution also includes higher frequency sounds such as those used to locate and measure objects underwater and to measure ocean temperatures (Slabbekoorn et al. 2010). Crucially, human-generated sounds overlap in frequency with the hearing range of most animals as well as the frequencies of the calls of many species (Slabbekoorn et al. 2010), including low frequency specialists such as marine mammals (Clark et al. 2009). By masking acoustic signals, anthropogenic noise decreases the active space of individuals, that is, the distance from which a conspecific is able to detect an individual's call. Such a reduction in active space clearly has important implications for animal communication (reviewed in Barber et al. 2010).

In addition to producing noise, humans have altered the acoustic transmission properties of large areas, both through changes to vegetation structure and through urbanization. Natural vegetation structure is correlated with acoustic signal structure (Ryan and Brenowitz 1985), so altered vegetation should have marked effects on communication. Urban landscapes, moreover, are characterized by multiple, large, flat, often parallel surfaces that reflect sound. These have been termed 'urban canyons' because their acoustic properties resemble those of natural canyons (Warren et al. 2006). Such urban canyons create flutter echo, whereby sounds ricochet rapidly between parallel walls, causing slower attenuation (loss of amplitude) and signal degradation due to the multiple reflected sound waves arriving at different times (Warren et al. 2006). Thus, the structure of the urban environment is likely to exacerbate the masking effects of anthropogenic noise on animal signals.

The effects of noise pollution are likely to differ in aquatic and terrestrial environments because the sound transmission properties of air and water are very different (reviewed in Slabbekoorn et al. 2010). Due to the high molecular density of water, sound transmission in water is about five times faster—and therefore wavelengths are about five times longer—than in air. Sound also attenuates less and therefore travels much longer distances in water than in air. By contrast, light attenuates much more rapidly in water than air so many aquatic animals use sound rather than sight for navigation and use acoustic signals for long distance communication. Noise pollution may therefore affect different aspects of animal behaviour and lead to different responses in aquatic versus terrestrial environments.

Animals can respond to noise pollution in four main ways: (1) by changes to their spatial distribution or density to avoid localized areas with high noise levels (Bayne et al. 2008); (2) by changing the temporal distribution of calling behaviour (Fuller et al. 2007); (3) through an absolute reduction (or increase) in total calling effort (Sun and Narins 2005); or (4) by changing the structure of their calls. Changes to call structure include increased amplitude (e.g. Holt et al. 2009), changes to pitch (e.g. Parris et al. 2009; Verzijden et al. 2010), increased redundancy of call components (e.g. Brumm and Slater 2006) and use of narrower band widths (pure tones, see Slabbekoorn et al. 2002).

The changes exhibited by a species will depend on numerous factors, including the initial structure of the call. For example, Parris and Schneider (2009) showed that a bird species with a lower frequency call increased its call frequency in response to traffic noise whereas a species with a higher frequency call did not. Changes to call structure can have important implications for mate choice when there is a trade-off between signal efficacy and content. For example, in many species, frequency is negatively correlated with body size and larger, lower-frequency males are more attractive (Ryan and Keddy-Hector 1992). Larger individuals produce lower frequency sounds, yet high-pitched sounds are more audible in noisy environments. Thus, individuals face a conflict between attractiveness and audibility. Hu and Cardoso (2009) further suggested that bird species with naturally higher-frequency signals should fare better in urban habitats.

To date, the great majority of evidence for an effect of anthropogenic noise on animal communication derives from studies of birds (reviewed in Barber et al. 2010; Laiolo 2010). However, an increasing number of studies show similar patterns in amphibians (e.g. Cunnington and Fahrig 2010; Parris et al. 2009; Sun and Narins 2005). There is a growing awareness of the effects of anthropogenic noise on communication in aquatic environments (Clark et al. 2009; Slabbekoorn et al. 2010). For example, ship noise decreases the ability of toadfish *Halobatrachus didactylus* to detect mate attraction calls (Vasconcelos et al. 2007), and several studies have shown that cetacean communication is impacted by human activities (Foote et al. 2004; Miller et al. 2000). Human activities can even result in serious injury or death to echo-locating cetaceans (Jepson et al. 2003). The long range of sound in water suggests that anthropogenic noise could have a broad reach in aquatic environments.

2.3.2 Visual signals

Visual signals can be parsed into spectral, spatial, and temporal components (Rosenthal 2007), each of which can be susceptible to effects from