2. Environmental disturbance and animal communication

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Summary

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 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 (Figure 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.

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 (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 chose 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, industrialisation and urbanisation 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 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 focussed 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 sticklebacks *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 availablitity 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 which 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 signal (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 urbanisation drastically change acoustic signal transmission, which, in turn, alters signal expression (reveiwed 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 aspect 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 which 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. 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 characterised 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 characterised 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 urbanisation. 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 characterised 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 - in water 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 localised 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 (eHolt 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 echolocating 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 disturbance. Transmission of visual signals depends on line-of-sight between the signaller and receiver, on spatiotemporal and spectral differences between signal and background, and on how the medium (air or water) attenuates and scatters light as a function of wavelength and distance. All of these have the potential to be drastically affected by disturbance.

Habitat degradation: changes in occlusion and background.

Many disturbed habitats, from urban areas to cornfields to forest regrowth, contain higher densities of occluding structures. The most basic requirement of visual communication, namely that there be an unoccluded straight-line path between signaller and receiver, is thereby liable to fail. Conversely, disturbance like clear-cutting and coral-reef destruction can increase the line of sight, minimizing signal privacy and therefore rendering conspicuous visual signals more visible to predators.

Visual signals are frequently tuned to maximize contrast with the background. Habitat degradation, such as changes to vegetation structure, can alter the characteristics of the visual background, as can novel structures like buildings, roads, and underwater oil rigs. Novel backgrounds may not only differ in colour and spatial characteristics, but also in the temporal patterns exhibited in wind or current. In anoline lizards, for example, the characteristic 'head bob' display typically contains a high-frequency 'jerky' component that is distinct from the movement of background vegetation (Fleishman, 1986). In two species of *Anolis* lizards, male signallers speed up body movements against a background of moving vegetation (Ord et al., 2007).

In some cases, the structure of complex visual signals may serve to minimise long-distance detection while conveying information at close range. This is notably the case in many tropical reef fishes, where high-contrast, high-spatial frequency patterns merge to closely resemble the background when viewed at a distance (Marshall, 2000). In this case, both functions may be subverted since increased background contrast may be accompanied by reduced transmission efficiency through the medium.

The light environment

With the exception of a handful of organisms that generate their own light, visual signallers rely on modifying the distribution of light available in the environment (Endler, 1978). Before it strikes a receiver, light is filtered through air or water as well as any overhead vegetation. The radiance (light intensity as a function of wavelength) of the light illuminating a signaller therefore varies as a function of vegetation type and vegetation density, and also varies as a function of space and time (e.g. leaves creating patchy cover and moving in the wind). Any alteration to habitat structure will thus change multiple properties of the incident light distribution. Across species of birds (Marchetti, 1993) and fishes (Cummings, 2007), visual signals coevolve with forest canopy structure. Any change in habitat structure should therefore compromise either signal privacy or signal efficacy.

In aquatic organisms, the filtering properties of water present another challenge to signal transmission, both in terms of the quality of light incident on the signaller, and on the way that signals are modified on their way to receivers. Pure water most efficiently transmits the middle (blue-green) wavelengths of the visual spectrum, while filtering out ultraviolet and, most severely, red light. Since phytoplankton absorb middle wavelengths for photosynthesis, eutrophication can flatten the filtering function of water and severely reduce the overall amount of available light. Humic substances, promoted by water runoff and organic decay can further reduce the amount of light available at shorter wavelengths (Fisher et al., 2006).

As is the case with canopy structure, signals coevolve with the transmission medium (Fuller et al., 2005). Changes to the bandwidth of available light can have severe consequences for communication. Two species of cichlid fish in Lake Victoria hybridize because females are unable to distinguish red males from blue males (Seehausen et al., 1997). In sticklebacks, the honesty of male-male agonistic signals is compromised in turbid water (Wong et al., 2007).

Although most work has focused on changes to the spectral environment, spatiotemporal cues are generally more salient to receivers (Rosenthal, 2007). These can also be affected by degradation. Overall light availability affects the detectability of fine spatial patterns. Many animals express spots, stripes, and complex textures which might not be discriminable in turbid or low-light habitats. ‘Veiling light’ scattered by particles between the signal and the receiver can also interfere with signal detection, as well as disrupt the polarization signals used by many invertebrates (Shashar et al., 2004).

2.3.3 Chemical signals

To our knowledge, there are no studies demonstrating effects of airborne pollutants on chemosignal transmission in terrestrial organisms; however, the interaction between volatile hydrocarbons and atmospheric emissions is well known in pollution chemistry (Zhang et al., 2007). It is not unreasonable to speculate, therefore, that the active space of windborne insect pheromones might be reduced in polluted environments.

By contrast, numerous behavioural studies suggest that pheromonal communication can be compromised by chemical changes to the aquatic environment. In the water, chemical signals have the potential to interact with a host of dissolved and suspended substances. As will be discussed below, these substances can also affect receiver perception. These two effects are difficult to disentangle in studies of chemical communication. In visual and acoustic studies, physical measures of signal degradation (e.g. Nemeth and Brumm, 2010; Seehausen et al., 1997) can decouple transmission effects from changes to receivers. Most studies of chemical signalling, however, rely on behavioural assays, making it difficult to disentangle effects on transmission and on reception. We briefly discuss case studies of chemical interference with aquatic communication, and then return to effects on receivers in the next section. **Box 1** details the best-understood of these cases, the effects of pH on alarm signalling in ostariophysan fishes.

Human impacts can markedly increase the salinity of freshwater and brackish environments (Beeton, 2002). Salt concentrations can affect sensory responses to odorant cues (Velez et al., 2009) and salts could interact with the structure of chemosignals as well. In the Pacific blue-eye fish *Pseudomugil signifer*, response to chemical shoaling cues is reduced by about 20% in saltwater relative to freshwater (Herbert-Read et al., 2010). This basic change in water chemistry can therefore have important impacts on communication.

Humans can also influence the concentration of dissolved organic chemicals in natural bodies of water. Humic acids (HA) are a ubiquitous by-product of organic decay in freshwaters (but HA concentrations can be substantially increased by processes such as eutrophication (Thomas, 1997). HA levels are also higher in disturbed environments associated with agricultural manure and other organic wastes (Kappler and Haderlein, 2003).

Elevated levels of HA in aquatic habitats are of particular interest due to their apparent effect in impairing the recognition of conspecific sexual pheromones (Fisher et al., 2006; Hubbard et al., 2002). Mesquita et al. (2003) found that HA tend to dissolve relatively water-insoluble organic substances such as steroidal pheromones, reducing their biological availability to organisms that normally detect these chemicals as part of their communication. Small proteins can also be encapsulated by HA (Zang et al., 2000). Hubbard et al. (2002) proposed that the steroid portion of pheromones adsorbs onto the surface of HA microvesicles that form in water, rendering the pheromone effectively unavailable for olfactory detection. HA can also bind to odorant receptors, as discussed below.

In the swordtail fish *Xiphophorus birchmanni* females lose their preference for conspecific males over heterospecific males in water with elevated levels of HA (Fisher et al., 2006). This impairment of chemical communication may have major implications for the evolutionary fate of many such species because of the potential for interspecific hybridization. Similarly, zebrafish *Danio rerio* failed to distinguish conspecifics from goldfish *Carassius auratus* in HA-treated water (Fabian et al., 2007).

[BOX START]
pH and chemical communication in teleost fishes

One of the best-studied vertebrate chemosignals is alarm pheromone, or *Schreckstoff.* This substance, identified as hypoxanthine-3-*N*-oxide, is thought to be produced in specialized skin cells by all ostariophysan fishes, which include 64% of extant freshwater fishes (Helfman, 2009). Upon injury, pheromone is released, causing a dramatic antipredator response in nearby fish. Because the signal consists of a single, identified molecule, it is possible to disentangle chemical effects on signals versus receivers; in the section on signal detection, we discuss how environmental impacts on chemoreception can affect perception of alarm pheromone.

Under weakly acidic conditions, the alarm pheromone undergoes a nonreversible covalent change that destroys its capacity to elicit a behavioural response (Brown et al., 2002). Since Brown et al.'s (2002) finding on two cyprinid species, a similar effect of reduced pH on alarm response has been found in multiple fish taxa (Leduc et al., 2004; Olivier et al., 2006). Though outside the realm of communication, learned recognition of predators is also impaired in acidic conditions (Smith et al., 2008; see also Chapter 4).

A widespread anthropogenic cause of acidification is acid rain. Leduc et al. (2009) showed that the responses to alarm pheromone of juvenile Atlantic salmon *Salmo salar* were impaired in small nursery streams following rainfall, in contrast to those of salmon in streams with higher capacity to neutralise acids. Sublethal changes to water chemistry can therefore have profound ecological impacts via their effects on communication.

Increases in pH, as commonly produced by eutrophication, may also impair chemical communication. In two freshwater snail species, response to predator odour cues is impaired in alkaline water (Turner and Chislock, 2010). By contrast, Heuschele and Candolin (2007) showed that female three-spined sticklebacks increased their sensitivity to pheromone cues in alkaline water. The authors hypothesized that this increased sensitivity might compensate for the reduced salience of visual cues in eutrophic waters.
[BOX END]

As will be discussed below, chemical disturbance can also have dramatic effects on receivers. With alarm pheromone as a noteworthy exception, very few chemosignals have been characterized for aquatic creatures, which as discussed at the beginning of this section are likely to suffer the greatest impact from disturbance of the chemosignalling environment. The interaction between aquatic pheromones and the aquatic environment is an open area for research.

2.4 Signal detection

Receiver response to a signal involves multiple steps. First, structures in the sensory periphery must transduce properties of the external environment (photons, pressure changes, volatile molecules) into neurochemical signals. These stimuli must be detected above background noise, and they must be perceived appropriately in order to produce a functional behavioural response. Each of these steps, from peripheral transduction to receiver behaviour, is susceptible to interference from anthropogenic effects.

Environmental disturbance can sometimes have a disabling impact on signal detection. Sensory noise can make detection difficult; this is discussed in detail in the section on signal transmission. In numerous forms, however, noise can have more lingering effects on sensation. Exposure to ambient acoustic noise during ontogeny retards development of the auditory cortex in rats (Chang and Merzenich, 2003). The spectral quality of the light environment determines the relative abundance of different classes of cone photoreceptors; fish raised in monochromatic light are more sensitive to the wavelengths they have been exposed to during ontogeny (Fuller et al., 2005).

Since olfaction requires direct interactions between environmental chemicals and biological tissues, chemoreception appears to be particularly susceptible to disruption from environmental sources (reviewed in Lurling and Scheffer, 2007). Exposure to low concentrations of cadmium impaired the alarm response of juvenile rainbow trout *Oncorhynchus mykiss* (Scott and Sloman, 2004), and exposure to copper caused a reduction in the density of olfactory receptor cells and a loss of the alarm response in Colorado pikeminnows *Ptychocheilus lucius*; the authors argued that environmental concentrations of copper could occasionally cause such damage (Beyers and Farmer, 2001). This damage could have long-lasting consequences: fathead minnows *Pimephales promelas*, exposed to copper as embryos failed to respond to alarm pheromone 90 days later (Carreau and Pyle, 2005).

Comparative studies of communication mechanisms have emphasized sensation (but see e.g. Ryan et al., 2009). Very few studies have explicitly examined the effect of disturbance on perception and evaluation. However, there is evidence to show that the constraints imposed by environmental noise increase the difficulty of discriminating among signals; for example discriminating between conspecific and heterospecific signals (e.g. Fisher et al., 2006; Seehausen et al., 1997). Further, changes in the distribution of signals, discussed above, could yield habituation or sensitization to signals; changes in the encounter rate or detectability of particular stimuli can make receivers more or less likely to respond to them. Both habituation and sensitization have been documented in natural communication contexts (e.g. Reichert, 2010) and these low-level learning mechanisms should be susceptible to disturbance-induced changes in signal distributions.

In many cases, responses to signals are learned (see Chapter 4), either by early exposure to signallers (ten Cate et al., 2006) or by modelling the behaviour of other receivers (Dugatkin and Godin, 1992). In either case, responses are dependent on the distribution of other individuals in the population. Changes in the distribution of either signal values, receiver responses, or encounter rates should therefore have substantial impacts on learned responses.

Behavioral responses to signals should also be susceptible to disturbance. For example, female mate choice is heavily dependent on predation risk; females tend to be less choosy in risky environments (Johnson and Basolo, 2003). Introduced predators, habitat alteration, and trophic changes induced by disturbance could all change an individual's perception of risk and, therefore, its response to signals. These may have short- or long-term effects on receiver responses.

2.5 Population-level and evolutionary effects on signals

In this chapter we have focussed on changes to signals at the individual level. However, anthropogenic changes can lead to population-level changes to signal distributions, that is, in the mean and variance of signalling traits. This can occur not only via changes to individual signal expression but also via population level processes such as selective mortality. The most obvious example of this is reduction in the average size of ornaments, such as antlers and horns, in species subjected to trophy hunting (Allendorf and Hard, 2009).

Population level changes in animal signals can potentially result from rapid evolutionary responses to radically altered selective regimes, a topic covered in chapter 16. Alternatively, changes can result simply from major reductions in population size and connectivity, due to massive habitat loss and fragmentation. This can affect phenotypic variation just as it affects neutral genetic variation. For example, inbreeding depression directly affects the expression of acoustic signals in field crickets *Teleogryllus commodus* (Drayton et al., 2007), and small population size causes a reduction in signalling effort in wolf spiders *Hygrolycosa rubrofasciata* (Ahtiainen et al., 2004) and birds (Laiolo and Tella, 2008).

Habitat isolation and loss also affect signal expression indirectly due to both genetic and cultural drift, as in the song dialects of some birds (reviewed in Laiolo, 2010). Cultural drift refers to a process analogous to genetic drift, whereby population reduction and isolation can erode signal diversity and increase differentiation among local song dialects. Cultural drift results from random errors in dialect transmission, but can be accelerated through increases in the rate of learning mistakes and reduced opportunities for learning from models (Laiolo, 2010).

Disturbance can also cause changes in signal distributions that influence signal honesty and reliability and, consequently, selection on those signals. For example, the vastly increased availability of blue objects to bowerbird males should result in reduced variation among males in their ability to acquire blue ornaments. Due to its lower cost, blue bower ornamentation may become an unreliable indicator of male quality, leading to reduced sexual selection on this signal. Proximity to dense concentrations of carotenoids (e.g. orchards, berry farms) might similarly reduce selection for long-wavelength visual ornaments due to increased availability and reduced cost. Changes to signal honesty and reliability can also result from changes to transmission properties of the environment. For example, Wong et al. (2007) showed that in turbid water, visual signals become unreliable predictors of condition in sticklebacks.

At the population level, a widespread driver of signal evolution is reproductive character displacement, whereby signals diverge from those of closely related, sympatric heterospecifics. As pointed out by Servedio (2004), invasive species have the potential to exert selection on native signallers (see Chapter 14). Such signal divergence would serve to minimise gene flow between the introduced and native species. Further, as has been recognized for most of a century (Mayr, 1942), native species are more likely to hybridise in disturbed environments. This may be due to increased opportunities for contact with introduced species or impacts on the way that receivers perceive signals.

Disturbance effects on communication systems can have evolutionary effects that extend far beyond their original impacts. We earlier discussed how humic acids (HA) impair chemical communication in swordtails. HA are found in any natural freshwater body and are considered benign substances; their discharge is entirely unregulated by the US Environmental Protection Agency. Yet, HA have caused irreversible evolutionary changes via their effects on communication. Specifically, by breaking down prezygotic isolating mechanisms between *X. malinche* and *X. birchmanni* (Fisher et al., 2006), HA are responsible for rampant hybridization and introgression between these species. Though very few first-generation hybrids are produced in contemporary populations, later-generation hybrids and backcrosses abound (Culumber et al., 2011), long after disturbance has passed. Via its effects on communication, a non-toxicological disturbance can therefore have irrecoverable evolutionary and ecological consequences.

2.6 Conclusions

Efficient communication is central to the health of animal populations. Given the importance of communication to biodiversity conservation, a more expansive approach to taxa and modalities is in order. Most studies to date have focused on acoustic effects in terrestrial habitats, with a heavy emphasis on birds (reviewed in Laiolo, 2010; Patricelli and Blickley, 2006). Among visual studies, most have centred on spectral changes to the light environment, rather than on how disturbance changes the spatiotemporal aspects of visual signals. Chemical communication in aquatic environments may be one of the most sensitive targets of environmental disturbance, since water chemistry can interact directly with signal transmission, production, and reception.

To our knowledge, there are no published studies that explicitly address anthropogenic effects on communication modalities other than vision, audition, and olfaction. Since vibrational communication depends on the propagation characteristic of specific host plants (Cocroft et al., 2010) and is sensitive to wind conditions (McNett et al., 2010), human-induced alterations of plant communities or habitat structure could have potentially deleterious effects on substrate-borne communication. Mining and other subterranean activities have the potential to disrupt communication in fossorial species (e.g. Nevo et al., 1991). Similarly, transmission of electrical signals is restricted to freshwaters of the rainy tropics; electrocommunication depends on water conductivity, which can change according to the concentration of salts and other substances. The relatively limited environments in which vibrational and electrical communication are possible may be an indication that these modalities are particularly susceptible to disturbance effects.

Finally, there is a dearth of knowledge in general about the mechanisms involved in response to signals beyond low-level properties of sensory systems. Recent studies (e.g. Heuschele and Candolin, 2007) highlight the likely importance of changes in multimodal integration, both in terms of signaller behaviour and the way that receivers process and attend to information. Increased attention to the neural and psychological mechanisms underlying signaller decisions and receiver response is of primary importance both to our basic understanding of how animals communicate, and the applied challenge of understanding how disturbance impacts communication.

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Figure 1. Phases of the signalling process (grey boxes) and major factors affecting each phase (clear boxes) that have been shown to be modified by anthropogenic disturbances.