9

The importance of integrative biology to sexual selection and communication

MICHAEL J. RYAN

9.1 Introduction

I am writing this adjacent to a tropical forest in Panama where I have worked for several decades. I continue to be struck by the number and diversity of organisms here, and how well they function in the world around them. How did all this happen? In this chapter I will focus this general question on the more specific topic of the evolution and mechanisms of sexual communication, and I will draw heavily on my own work and that of my colleagues on one of the inhabitants of this forest.

9.1.1 *A nocturnal serenade*

One of the animals in this forest of which I am most fond is the túngara frog (*Physalaemus* = *Engystomops pustulosus*). Like many animals with lek-like mating systems, male túngara frogs gather at breeding sites where they sexually advertise for females. Their call consists of a long frequency-modulated whine followed by up to seven short bursts of sound called chucks (Figure 9.1A). All males add chucks when they are in choruses and escalate chuck number during vocal competition. Females visit these sites and choose mates. Females prefer calls with chucks, so males that add chucks gain a benefit through sexual selection because they are more likely to mate. Frog-eating bats use the frog's call to locate their anuran prey, and the bats also prefer calls with chucks; thus the males incur a cost through natural selection when adding chucks to their calls. In addition, females are more likely to choose larger males as mates. Thus

Animal Communication Theory: Information and Influence, ed. Ulrich Stegmann. Published by Cambridge University Press.

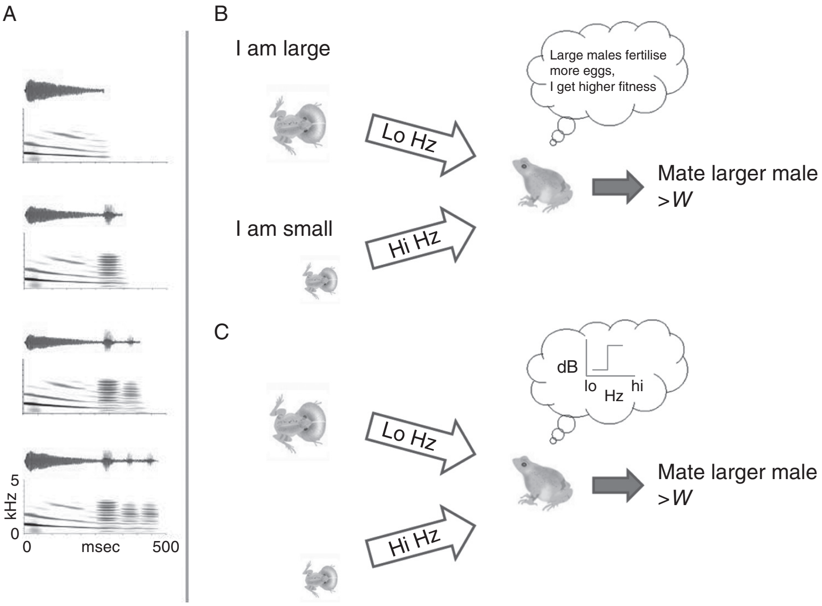

Figure 9.1 A, Waveforms (top of each call) and sonograms (bottom of each call) of mating calls of the túngara frog. From top to bottom a whine followed by 0, 1, 2 and 3 chucks is illustrated. B, C, Two narratives describing sexual selection in túngara frogs. > *W* refers to an increase in fitness.

larger males gain an additional fitness advantage via sexual selection. Larger males fertilise more of a female's eggs than do smaller males. Thus female choice of larger males accrues a fitness advantage to the females due to natural selection. These are the facts (Ryan, 1985, 2010). We can entertain two narratives of the underlying processes (Figure 9.1B, C).

Narrative one: Males *encode* information about their body size in the chuck's frequency; larger males have lower-frequency chucks. *Information* about male body size is transmitted to the female. The females *decode* this information in order to choose males that fertilise more eggs. In the past, selection has favoured the females who *decided* to mate with larger males since these males fertilise more eggs and these females experience greater reproductive success. Of course, for female choice to evolve there must be heritable variation in their mating decisions (Figure 9.1B).

Narrative two: For many animals, the frequency of a vocalisation is *correlated* with the size of the vibrating membrane that produces it. Larger males have larger larynges and thus lower-frequency chucks. In frogs, the *sensory organs* in the inner ear used in hearing are tuned to the frequency characteristics of the call. In túngara frogs, the low-frequency chucks of larger males *better match* the female's tuning than the higher-frequency chucks of smaller males. As larger males fertilise more eggs, selection favouring females to mate with larger males would cause females to evolve auditory tuning that would guide them towards lower-frequency calls. Of course, for female choice to evolve there must be heritable variation in auditory tuning (Figure 9.1C).

It is not unusual for science to adopt different narratives to explain the same phenomenon. In the visual sciences we discuss light as a wave to understand how it travels through the environment but as a particle to describe its interaction with photoreceptors (Bradbury & Vehrencamp, 2011). The first narrative about sexual selection in túngara frogs emphasises how information is encoded and decoded. The second emphasises how the structure and influence of signals are tied to morphology and sensory biology. One might consider these two interpretations as deriving from different levels of analysis: Narrative 1 is the ultimate explanation and Narrative 2 the proximate explanation. They both, however, offer an explanation of the specific mechanisms used in the communication system. One might then consider these two explanations functionally equivalent, that Narrative 1 might be a metaphor for the specific mechanisms outlined in Narrative 2.

I would disagree that these are equally accurate descriptions of the same phenomenon. Consider, for example, the fact that larger males have lower-frequency calls. Narrative 1 posits that males encode information about body size in their calls. In this case, 'encode' does not really refer to something that males do, but instead is a metaphor for a biophysical principle, in the same sense that the amplitude of the sound a rock produces when we drop it on the pavement 'encodes' information about the rock's size.

Narrative 2 specifies the relationship between size and frequency directly, and views it as a simple biophysical phenomenon that is generally applicable and not specific to the problem of communication. The fact that frequency is related to body size does not, of course, preclude its independent evolution.

Of the two narratives, the first might offer the more intuitive and generally appealing explanation, and would probably be more effective in communicating to students the scenario of sexual selection. But as Kennedy (1992) has emphasised, introducing metaphors into evolutionary explanations merely for the sake of convenient communication can be quite successful in capturing the imagination, but it carries the risk of obscuring the real biology of the phenomenon and can unintentionally promote a teleological view of evolution. This seems to be a real danger in studies of animal communication.

In addition to the use of metaphor, another issue in animal communication that requires some attention is the extrapolation from the present to the past, especially the far past. Each of the narratives above suggests how female preferences for chucks and lower-frequency chucks have evolved. The data, however, address the question of current maintenance and not necessarily past evolution. As I argue that sensory biology should be an important component of animal communication studies, so should phylogenetic comparisons. There are several ways to gain insights into the past; given the usual absence of fossils, comparative studies are among the more useful. When applied to the túngara frog system they lead to a not so obvious conclusion.

Anurans have two inner-ear organs that are sensitive to air-borne vibrations (Capranica, 1977; Wilczynski & Ryan, 2010). The amphibian papilla (AP) is more sensitive to lower-frequency sounds, <1500 Hz, and the basilar papilla (BP) is more sensitive to higher-frequency sounds, >1500 Hz. The tuning of the two end organs matches the distribution of spectral energy in the call. In some species only one of the inner-ear organs is recruited for communication, while in others, including túngara frogs, both sensory channels are used (Gerhardt & Schwartz, 2001). A combination of neurophysiological and behavioural studies of túngara frogs show that in the auditory periphery the whine is processed primarily by the AP and the chuck by the BP (Figure 9.1A), and the BP is more sensitive to the lower-frequency chucks of larger males than the higher-frequency chucks of smaller males (Ryan *et al.*, 1990; Wilczynski, Rand & Ryan, 1995). These data, combined with Narrative 2, would suggest that females evolved BP tuning to match the spectral characteristics of the chuck because of the advantage of mating with larger males. Comparative studies allow us to evaluate this hypothesis.

Most close relatives of *P. pustulosus* do not produce complex calls. They all have whines whose dominant frequencies match the tuning of their AP (Wilczynski, Rand & Ryan, 2001). Wilczynski *et al.* (2001) showed that among *P. pustulosus* and seven close relatives there is substantial variation in the tuning of the AP among species. But except for one species, *P. pustulatus*, the tuning of the BPs are almost identical. This suggests that BP tuning is a characteristic of a common ancestor that existed long before the chuck evolved, and there has been little evolution since. These results suggest that the chuck evolved to match the preexisting tuning of the female's BP rather than female tuning evolving to match this call component. Of course, frogs have brains, and we know a considerable amount as to how the signals that stimulate these two end organs are integrated in the túngara frog's central nervous system and interact to result in enhanced stimulation in the frog's main auditory nucleus (Hoke, 2004) and also to stimulate neural networks that are important in decision-making (Hoke, Ryan & Wilczynski, 2007). Some closely related frogs that lack chucks show a preference for their own calls with chucks (Ryan & Rand, 1993) while others do not (Tárano & Ryan, 2002; Ron, 2008). Thus stimulation of the BP seems to play an important part in the evolution of complex calls in the túngara frogs, but there seem to have been concomitant changes in the brain as well.

The details of how this one species of frog hears might seem idiosyncratic if not downright tedious. But the purpose of this chapter is to argue for an integrative approach to studying animal communication, and it is true that the devil is in the detail. In addition to knowledge of current fitness effects, we also need to address a broader understanding of where signals and responses to signals come from, and how the past evolutionary history and the animal's biology in other domains all have an important influence on how animals communicate. Integrative approaches in animal behaviour are becoming quite common (reviewed in Ryan & Wilczynski, 2011), and this has been a most fruitful approach in studies of animal communication (e.g. Gerhardt & Huber, 2002; Greenfield, 2002).

9.2 Sexual selection and aesthetic traits

9.2.1 *Darwinian aesthetics*

We are surrounded by beauty in the animal kingdom. Few can deny how spectacular are the serenades of nightingales, the bountiful colours of coral reef fishes and the flashing of fireflies across an open field. All of these traits have been fashioned by sexual selection. For many of us the assortment of avian plumages that have evolved for sexual signalling as a result of sexual selection is at least as awe-inspiring as the cunning fit of the beaks of Galapagos finches to their feeding ecology which has resulted from natural selection (Figure 9.2). Beauty is in the eyes, ears and nares of the beholder. The fact that we, as humans, find beauty in many of the same sexual traits that evolved because they were attractive to other animals might suggest some generalities in the appreciation of beauty.

The development of Darwin's theory of sexual selection has been well chronicled, especially by Cronin (1991; see also West-Eberhard, 1979). But I think there is something missing in those scenarios. Darwin offered this theory of sexual selection, first in *On the Origin of Species* (1859) and more fully developed in *The Descent of Man and Selection in Relation to Sex* (1871), as an addendum to his theory of natural selection. Natural selection, Darwin thought, was lacking in its ability to explain the evolution of one particular class of traits. These traits shared some commonalities: they were usually sexually dimorphic, often more elaborate in males than females; they were involved in reproduction, either as weapons or sexual signals; and they seemed to be maladaptive relative to survival. These traits were favoured by sexual selection, not because they

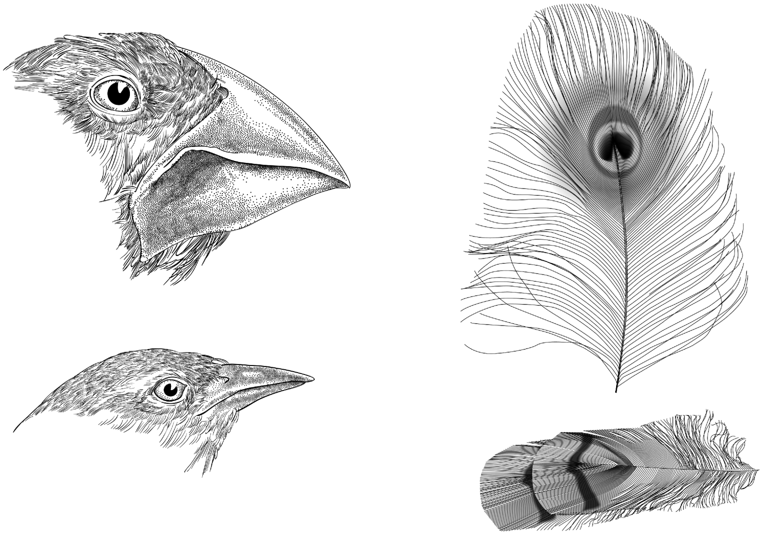

Figure 9.2 The beaks of two species of Galapagos finches that have evolved by natural selection, and two samples of bird feathers that have evolved under sexual selection. Redrawn from Ryan (2001) with permission from *Nature*.

promoted survival but because they promoted mating. Ryan and Keddy-Hector (1992) and Andersson (1994) gave hundreds of examples in which females prefer males with more elaborate traits, such as higher-amplitude calls, greater size, more intense colour, longer tails.

As elaborate sexual signals are more common in males than in females, Darwin phrased his arguments for sexual selection in terms of males competing for female mating partners. This generality seems to hold, although we now know that males and females can fill the opposite roles in different mating systems and that the two sexes can choose and compete with one another simultaneously (Arnqvist & Rowe, 2005; Clutton-Brock, 2007; Gowaty & Hubbell, 2009). Here, I am concerned with sexually selected traits that evolved as communication signals. Thus I will speak more generally of senders and receivers with the understanding that each sex can fill each role and need not be restricted to only one role.

The notion that weapons could evolve under sexual selection was not an issue with Darwin's contemporaries (Cronin, 1991). The problem was in understanding the evolution of the elaborate sexual signals. Darwin stated that females were more attracted to males with elaborate sexual traits. Just as Darwin relied on his analogy between artificial selection and natural selection, he made the same point about sexual selection. Artificial selection had been successful in increasing an animal's beauty to the eyes and ears of the human breeder. When one examines the traits that respond to artificial selection for beauty, they are almost always sexual signals: plumage in pigeons, songs in canaries, colours in guppies. The same response to sexual selection occurs in nature, Darwin argued. Mate choice generates selection on these traits, but why do females have these preferences for extreme and sometimes maladaptive traits in males? Darwin's response was that female animals had an aesthetic sense similar to that of the artificial breeder. Furthermore, Darwin argued that the aesthetic senses were grounded in the animal's sensory biology and these aesthetic senses could be shared widely among some species. Perhaps, then, this is why artificial selection for animals to evolve to become more attractive to humans seems to mimic the process of sexual selection that drives the evolution of traits attractive to that species' receiver.

The statement that females have an aesthetic sense seems like a definition and not an explanation of female preferences, and has been interpreted as Darwin's surrender to this thorny question of the origin of preferences (e.g. Cronin, 1991). I would suggest that perhaps that is not the case, and this is where something has gone missing in previous accounts. In *The Expression of the Emotions in Man and Animals* (1872) Darwin stated:

> When male animals utter sounds in order to please the females, they would naturally employ those which are sweet to the ears of the species; and it appears that the same sounds are often pleasing to widely different animals, owing to the similarity of their nervous systems.

Darwin is arguing that there is selection on senders to employ signals that are inherently attractive given the receivers' sensory, neural and cognitive mechanisms that are already in place. Darwin seemed to think that sexual signals were charming, alluring and seductive, and that they evolved to tickle the receiver's sensibilities. In some ways this echoes Marshall McLuhan's (1964) famous dictum that "the medium is the message". This view does not exclude the possibility that signals could have information relevant to female fitness, but the potency of a signal's interaction with the receiver's sensory biology is one component of the evolutionary process that has received less attention than the emphasis on information encoding and decoding of signals.

A similar point is made by Marler (1998; see also Hartshorne, 1956, 1973):

> The [bird] song functions as affective rather than symbolic symbols, and the variety is generated not to diversify meaning, but rather to maintain the interest of anyone who is listening.

There is an interesting congruence between Darwin's insight and the recent emphasis on the role of the receiver's sensory biology in explaining the diversity of sexual signals (Endler & McLellan, 1988; Ryan, 1990, 1998, 2011; Endler & Basolo, 1998; Endler *et al.* 2005; Grether, 2010). These hypotheses are known as latent preferences (Burley, 1986), sensory traps (West-Eberhard, 1979; Christy, 1995), sensory drive (Endler & McLellan, 1988) and sensory exploitation (Ryan, 1990; Ryan *et al.*, 1990). Endler and Basolo (1998) formalise this jargon, and emphasise that a prediction fundamental to all of these hypotheses is that senders are under selection to evolve sexual signals that coincide with latent or preexisting preferences of receivers. This seems to be exactly what Darwin was asserting.

An animal's sensory biology consists of components which receive, detect and perceive a signal, process and analyse the signal, and then make decisions by marshalling different behaviours in response to different signals. Nervous (peripheral end organs and the brain) and cognitive (analysis of and decisions based on perceived stimuli) systems share many similarities across taxa: these systems habituate; they exhibit heightened response to contrast and greater signal:noise ratio; and they often are more stimulated by signals of greater quantity. It should not be surprising, therefore, that across taxa and sensory modalities we seem to know a sexually selected trait when we see, hear or smell one. By not offering specific adaptive hypotheses as to why females have aesthetic preferences, Darwin might not have been throwing in the towel – he might have assumed he had solved the puzzle.

9.3 The evolution of the unexploited receiver

If senders evolve traits to exploit (*to make productive use of*, Merriam Webster Dictionary) a receiver's preexisting preferences, does it necessarily follow that the receiver incurs a fitness loss when they choose such a mate? Although there are a number of cases in which there is such a cost (Arnqvist & Rowe, 2005), there are some fundamental processes of signal reception that suggest there are inherent benefits as well.

Signal elaboration can increase the potency of any signal, endowing it with a larger active space, a longer active time, greater localisability and enhanced contrast with the background. All of these characteristics of signals should reduce search costs by receivers. There are several costs involved with searching, such as energy, time and predation. There is an energetic cost due to longer paths travelled to the source of the signal. Time is lost, and time is at a premium for external fertilisers, such as frogs, who ovulate at the breeding site and will drop their eggs if they do not find a mate. This explains why female túngara frogs become less selective as the night goes on (Lynch *et al.*, 2005). Another search cost is related to predation risk, and this might be the most important one for most animals. As Bonochea and Ryan (2011) point out, the presence of a predator can cause receivers to become less choosy or even reverse their mating preferences (Evans, Bisazza & Pilastro, 2004; Schwartz & Hendry, 2006), to change thresholds of attractiveness for mating (Demary, Michaelidis & Lewis, 2006; Su & Li, 2006; Vélez & Brockman, 2006) and to reduce the time spent searching for (Karino *et al.*, 2000; Kim, Christy & Choe, 2007) and sampling mates (Karino *et al.*, 2000). By matching a sexual signal to the female's sensory, neural and cognitive biases a male might be doing her a favour, increasing rather than decreasing her fitness, by making it easier and less costly for her to find him.

In cases in which sensory exploitation is suggested, it does not seem that females are behaving optimally, preferring the signal that has the greatest positive impact on their reproductive success. This is where it is crucial to remember two things: reproduction is only one component of fitness; and sensory systems can be subject to selection in numerous domains besides reproduction.

Pollinators make productive use of the pollen and nectar of flowers, but this is to the flower's advantage not its disadvantage. In an extreme example, some orchids exploit male bees that are either so sexually aroused or easily duped that they attempt to mate with the flower, pollinating it in the process. In this case the bee gets no reward of pollen or nectar (Darwin, 1890; Schiestl, 2005), but the cost of missed identification (mating with a flower) is lower than the cost of a missed opportunity (passing up a real, live female). The same calculus might explain how female hosts, such as reed warblers, are exploited by cuckoo parasites: shifting their recognition threshold might result in rejecting some of their own offspring (Kilner, Noble & Davies, 1999). The same explanation applies to model-mimicry systems: passing up a palatable butterfly might be a much better Darwinian decision than taking the risk of eating a poisonous one (Bates, 1862; Joron, 2008).

My point is that to understand why receivers respond as they do to a specific signal, we must understand how the mechanisms that generate this type of response influence the receiver's overall fitness, not just the fitness consequences of making a single mating decision. This is where understanding the neural and cognitive mechanisms underlying receiver responses becomes crucial. We can only examine the fitness effects of the receiver's mate choice when it chooses a mate, but by understanding the mechanisms that generate these responses we gain an appreciation of the more varied fitness effects that it entails. This becomes all the more clear when we consider pleiotropic effects of mechanisms involved in mate choice.

9.3.1 *Pleiotropy and domain specificity*

Central to notions of reliability and information in animal communication is the prediction that receivers should respond to signals only if there is on average a fitness advantage to doing so (e.g. Bradbury & Vehrencamp, 2000; Searcy & Nowicki, 2005). It is important to specify 'on average' because every interaction between a sender and a receiver does not result in an increase in fitness.

There is another concept of 'on average' that applies: the fitness effects of this 'response' also need to include the fitness consequences of all the underlying mechanisms that regulate it across all of its domains. This is a point that is lost on most studies of animal communication. Understanding the potential pleiotropic effects of receiver biases can be important to understanding why receivers respond as they do, and why senders evolve particular signals.

Animals see with their eyes, smell with their nares, hear with their ears and feel with their legs. Those are the sensory end organs that initiate processing of communication signals. It is worth remembering that in almost all cases these modalities did not evolve originally for communication. Once these end organs are stimulated, the processing of signals often continues in parts of the brain more or less dedicated to that modality. In the túngara frog, for example, the VIIIth cranial or auditory nerve communicates between the inner-ear organs and the brain. The neural activity in the brainstem is then transformed into sensory–motor interactions in the diencephalon, followed by motor-related activation in the telencephalon. Hearing the conspecific mating call increases correlations of neural activity between many of these anatomically distant brain divisions (Hoke *et al.*, 2007). The female's response to a sexual signal involves all of these aspects of the sensory system. Evolution of the female's preference for a call occurs somewhere in this circuit (Kimchi, Xu & Dulac, 2007; Hoke, Ryan & Wilczynski, 2008). But these circuits are not solely dedicated to sexual communication. The locomotion motor patterns triggered in the mate choice decision, such as movement away from an undesirable call, are also triggered by predators. The auditory system is exquisitely sensitive to conspecific calls, but it is also sensitive to calls of predatory frogs, rustling sounds made by predator movement (Ryan, Bernal & Rand, 2010; Bonachea & Ryan, 2011) and even the sounds of fire moving through savannas (Grafe, Döbler & Linsenmair, 2002). As with most aspects of an animal's phenotype, sensory systems evolve in response to multiple selection pressures, and the responses to selection are biased by its past evolutionary history. Regardless of why these sensory biases exist, they can have current effects on how receivers respond to signals.

Sexual communication brings the sexes together so they can mate. But sexual reproduction also requires coordination of the participants' physiology, and this is often accomplished by the interaction of mating signals and the animal's internal hormonal milieu. In many of the cases that have been documented, the male is the sender and the female is the receiver. Studies of hormones and behaviour have analysed how reproductive synchronisation between the sexes can be achieved through a series of actions in which the behaviour of one member of the pair influences both the partner's behaviour and its own behaviour. The behavioural interactions of the sexes that bring about reproductive synchrony are well known in a variety of animals. In songbirds, the male's song influences follicular development in the female. In rats, tactile stimulation of the female's flank and tail initiates a mating posture, lordosis, and a cascade of responses that eventually synchronises lordosis with ovulation. In addition, dewlap displays in anolis lizard, calling in green treefrogs, and exogenous hormonal steroids in fishes all influence the physiological or behavioural reproductive state of their conspecific partners (reviewed in Adkins-Regan, 2005; Nelson, 2011; Ryan & Wilczynski, 2011).

Interestingly, in most of these examples the signals of males that stimulate the female's reproductive axis are the same signals that are used by females when they choose a mate. In some cases the signal's influences on reproductive physiology and on mate choice are disassociated in time while in others they are nearly simultaneous. The signals are detected by the same sensory end organs, such as ears or eyes, and are then processed in the brain (Figure 9.3C). After sensory processing, however, the information is fed-forward to either a reproductive physiology axis (e.g. hypothalamus → pituitary → gonads and other endocrine glands) or mate choice axis (thalamus → telencephalon → descending to brainstem and spinal cord motor areas → musculoskeletal system), which then subsequently influences reproductive state or mating behaviour, respectively. On the one extreme, the two domains could be mechanistically dissociated. This would be true if they were stimulated by different signals and relied on different sensory channels and brain regions for processing (Figure 9.3A, B). Our review of the limited data available (Ryan & Wilczynski, 2011; see also Adkins-Regan, 2005; Nelson, 2011) suggests that in many vertebrate systems the same signals are used to stimulate both reproductive state and mating behaviour, and that at least early processing of sexual signals is accomplished by the same sensory channels and the same brain regions in both domains (Figure 9.3C). Thus we expect reproductive physiology and mating behaviours to be mechanistically associated to some degree. The evolution of signals and responses in one domain could influence other functions in other domains.

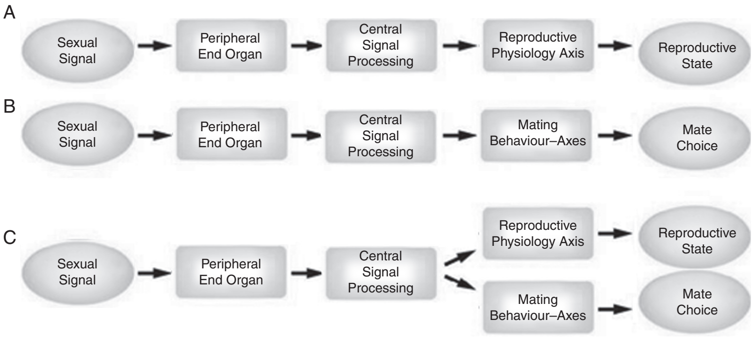

Figure 9.3 A–C, Various ways in which mating signals might influence activation of the reproductive physiology axis and mating behaviour axis.

Just as the need to stimulate the animal's nervous and physiological systems should exert strong selection on signal evolution, ecological selection can also play an important role. Morton (1975; Boncoraglio & Saino, 2007) pioneered the field of evolutionary habitat acoustic by showing how the environment favours the evolution of different acoustic structures, primarily bird song, in different habitats; for example, low frequencies and tones are favoured on the forest floor while high frequencies and high trill rates are more common in open fields (Figure 9.4; Hunter & Krebs, 1979; Wiley, 1991; Slabbekoorn & Smith, 2002; Podos, Huber & Taft, 2004). Senders can also adjust the frequency spectrum of their signals in response to anthropogenic noise (Slabbekoorn & Peet, 2003; Katti & Warren, 2004; Brumm & Slabbekoorn, 2005; Slabbekoorn & den Boer-Visser, 2006). All of these cases show that some primary components of acoustic signals evolve not, or at least not only, because they transmit information but because they enhance the active space of the signal, the area over which the signal can be detected and recognised.

An example of how ecological selection influences both senders and receivers engaged in sexual communication comes from several studies of visual communication in fishes. For example, Cummings (2007) showed that variation in sensitivity of photopigments among species of surf perch in the variable light environment of the Pacific kelp forest evolved in ways that enhance the visual contrast of one of their most common prey. Males, in turn, have evolved signals that match the female's photopigment sensitivity. Similar results have been found in sticklebacks by Boughman (2002) and cichlids by Seehausen, van Alphen & Witte, (1997). In all of these cases the photic environment is thought to influence visual sensitivity, and males, in turn, evolve signals that then match the female's visual sensitivity.

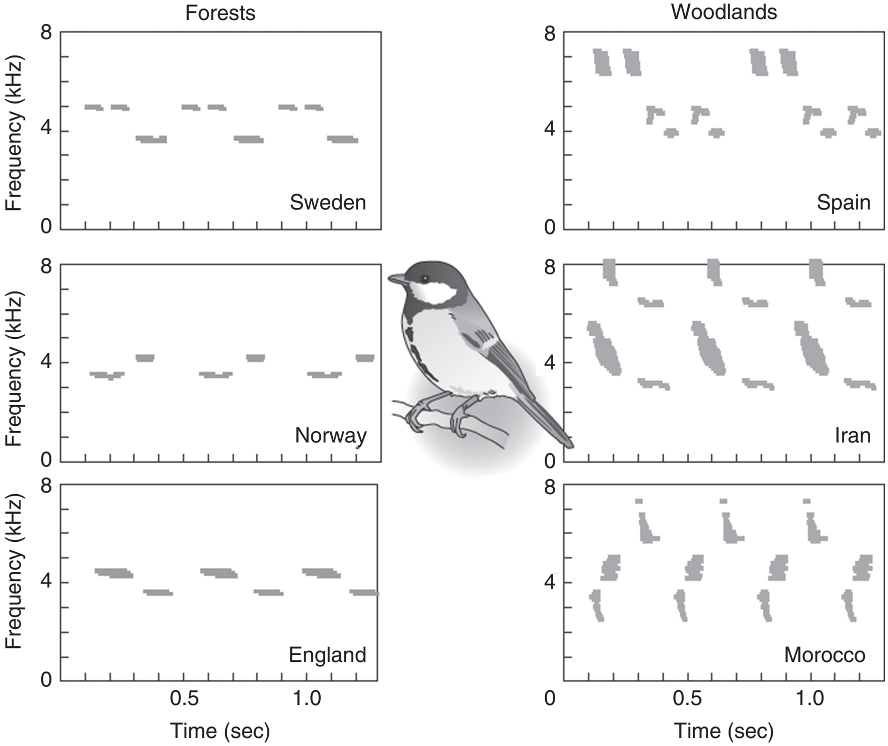

Figure 9.4 Convergence of song structure in great tits within similar habitats. Reprinted from Ryan and Wilczynski (2011) with permission from Cold Spring Harbor Laboratory Press.

A different ecological selection force that influences sexual selection in a fish has been suggested by Rodd *et al.* (2002). Guppies are well known for their extensive orange-pigment pattern variation in nature (Haskins *et al.*, 1961; Endler, 1980) and for female preference for males with more orange. Guppies are attracted to orange fruit in nature. Rodd *et al.* showed that a measure of a female's interest in orange disks, independent of the domains of both foraging and mate choice, was a significant predictor of the strength of her preference for orange coloration in males. The authors concluded that the female's preference for orange evolved in the domain of food preferences, and that males evolved their orange coloration in order to exploit this preference. In this case the evidence for cause and effect is less compelling than in other cases, but this research shows clearly how preferences might be shared across domains. Macias-Garcia and Ramirez (2005) also offer convincing evidence that preferences for pigmentation on the caudal fin of some Goodeid fishes came about through the exploitation of female foraging responses.

Finally, some recent studies show how the details of the animal's cognitive biology can have a strong influence on how sexual communication signals evolve. In our studies of túngara frogs we have shown that adding chucks to the whine of the mating call can influence the call's active time, the time over which the signal is remembered (Akre & Ryan, 2010). Females retained memory for the location of a whine with three chucks for up to 45 seconds, but there was no evidence for memory of a whine with one chuck. As has been suggested with the evolution of warning colours (Guilford & Dawkins, 1991), sexual selection might favour signals that are more likely to be remembered.

A fundamental question in sexual selection asks what counters the evolution of even more elaborate traits. The most important reason is that there are costs associated with the production of elaborate signals, including energetic and predation costs (Andersson, 1994). Cohen (1984) suggested an additional, psychophysical, explanation. Weber's law states that stimulus quantities are discriminated based on their relative and not their absolute differences. Thus a unit increase in a trait, be it call amplitude, tail length, colour intensity or syllable number, is more likely to be discriminated when the overall magnitude of the traits being compared is small, and discrimination is less likely when two traits of greater magnitude have the same absolute difference. For example, when holding weights of 1 kg in each of our two hands we could easily detect an increase of 0.1 kg in one hand, but ascertaining the same absolute difference, 0.1 kg, would be less likely if we were holding 10 kg in each hand. We recently showed that the strength of preference for more versus fewer chucks in calls of túngara frogs follows Weber's law (Figure 9.5; Akre *et al.*, 2011). Females are much more likely, for example, to prefer a whine with two chucks versus a whine with one chuck than they are to show a preference between whines with six versus five chucks. Is this pattern of preference an adaptive response to the manner in which male quality scales to male signals? We were able to reject some predictions of this hypothesis. For example, there was no relationship between male relative condition and the number of chucks he produced. But it was impossible to test all possible adaptive hypotheses. To resolve this issue, we tested frog-eating bats with the same set of calls. These bats use the calls to localise male túngara frogs, one of their common prey items. The frogs and the bats use the same signals but for different reasons, a mate versus a meal; female frogs might want good genes but the bats are only concerned with good protein. As do females, the bats prefer calls with more chucks to fewer chucks. Also, the bat's preference for more versus fewer chucks followed a Weber function almost identical to that of the female túngara frogs (Figure 9.5). The most parsimonious interpretation of these data is that both túngara frogs and the bats that eat them perceive

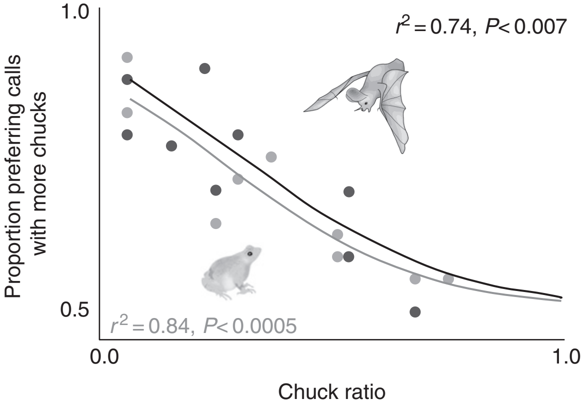

Figure 9.5 Preference for mating calls of túngara frogs that vary in the number of chucks by female frogs and frog-eating bats. The strength of the preference for the call with more chucks is predicted by the ratio in the number of chucks in each of the two stimulus calls being compared by the receiver. Curves are the least-squares fit of the psychometric function (Weber's law). Data are from Akre *et al.* (2011) and used with permission from *Science*.

stimulus quantity in similar ways, and these perceptions of stimulus quantity should influence the dynamics of evolution of complex calls.

This brief summary should make it clear that to understand why signals and receivers evolve one cannot merely focus on how a specific signal influences a specific receiver at a single point in time. As Darwin recognised, survivorship and mating success are two different components of fitness. Sensory systems often function in both of these general domains, and it is not expected that sensory systems can always be optimised for all tasks at hand.

This importance of pleiotropy in animal communication parallels a debate about evolutionary psychology. One of the edifices of evolutionary psychology is massive modularity, which posits that the mind consists of numerous cognitive modules that have evolved to solve different adaptive problems (Cosmides & Tooby, 1992, 1994). An alternative to this extreme domain specificity is the notion that there are domain-general features that influence numerous behaviours involved in different tasks and might be subject to different selection forces. Domain specificity versus domain generality is an empirical question; its resolution probably varies among tasks and taxa, and lies somewhere between the two extremes. Despite the importance that evolutionary psychologists place on massive modularity, Bolhuis *et al.* (2011; see also Bolhuis & Wynne, 2009) suggest that they "... rarely examine whether their hypotheses regarding evolved psychological mechanisms are supported by what is known about how the brain works". Bolhuis *et al.* (2011) go on to conclude that "data from animal experiments is consistent with a general-process account rather than an interpretation involving adaptively specialised cognitive modules". It would be an important contribution to understand to what degree components of receiver systems are general-process versus adaptively specialised.

9.3.2 What do we want to explain?

The goal of studying the evolution of sexual communication should be to understand how it has evolved, not only how the mate choice decision is adaptive to the receiver.

The evolution of sexual signals that take advantage of latent preferences does not exclude the subsequent evolution of preferences to ignore a signal if it on average decreases the receiver's fitness, or to favour even greater elaboration of the signal if it enhances the receiver's fitness (Ryan, 1997). Sensory biases do not prohibit receiver responses from evolving, and I have previously discussed how various forces in selection can act on a receiver (Ryan, 1997). Whether receivers prefer signals that indicate greater resource-holding potential, good genes or just being a conspecific, there are taxon-specific and ecological-specific factors that strongly influence signal evolution and the receivers' responses to them. A fish is not likely to use ultrasonic vocalisations to advertise its genetic quality – even if it could make such sounds, the receiver could not hear them. Even if red might indicate the sender's quality because it contains carotenoids, deep sea fish will not evolve such colours because long wavelengths are filtered out by the environment. If female frogs choose males that make energetically more expensive signals, as Welch, Semlitsch and Gerhardt, (1998) have shown, this can explain why these females attend to pulse duration, but it does not address the broader question of why females are attracted to other components of the call, why males make these types of calls and why frogs call instead of advertising with flashing bioluminescence. The point is that the evolution of communication is a larger question than the fitness consequences of mate choice in a single context.

The strength of selection on a receiver will vary depending on the type of benefits they receive. Benefits are often classified into direct or indirect. Direct benefits include those that have an immediate effect on fecundity. Choosing a mate that holds more resources or is a better parent is one type of direct benefit that could favour the evolution of certain response properties. Reducing search costs is another. When considering direct benefits, it is also important to take into account the fitness effects due to pleiotropy. For example, Cummings (2007) argued that a direct benefit of the mate preference of surf perch for certain colour patterns does not derive from the mating partner but from the foraging advantage that drives the evolution of photopigment sensitivity. The adaptive advantage of this ‘response’, or the underlying physiology that drives it, must be considered over more than one domain. Indirect benefits are those that deliver a genetic advantage to the offspring, and this can be due to passing on ‘good genes’ that enhance survivorship or result in more attractive mates owing to Fisherian runaway selection. Kirkpatrick and Barton (1997) have shown that, in general, selection for responses that result in direct benefits trumps selection for responses that result in indirect benefits.

Summary

The primary point of this chapter is that gaining a deep and thorough understanding of animal communication requires an integration of behaviour, neurobiology and evolution. Quantifying or theorising about the fitness advantages that occur when a receiver responds to a signal is an important component of this understanding, but only one. Only by studying communication as it is embedded in the environment that affects its signal transmission, how it is moulded by the underlying mechanisms that generate its signals and responses, and the details that influence its evolutionary history will we approach Darwin’s notion of the grandeur in this view of life.

References

Adkins-Regan, E. (2005). *Hormones and Animal Social Behavior*. Princeton, NJ: Princeton University Press.

Akre, K. A. & Ryan, M. J. (2010). Complexity increases working memory for mating signals. *Current Biology*, **20**, 502–505.

Akre, K. L., Farris, H. E., Lea, A. M., Page, R. A. & Ryan, M. J. (2011). Signal perception in frogs and bats and the evolution of mating signals. *Science*, **333**, 751–752.

Andersson, M. (1994). *Sexual Selection*. Princeton, NJ: Princeton University Press.

Arnqvist, G. & Rowe, L. (2005). *Sexual Conflict*. Princeton, NJ: Princeton University Press.

Bates, H. W. (1862). Contributions to an insect fauna of the Amazon valley. Lepidoptera: Heliconidae. *Transactions of the Linnean Society of London*, **23**, 495–566.

Bolhuis, J. J. & Wynne, C. D. L. (2009). Can evolution explain how minds work? *Nature*, **458**, 832–833.

Bolhuis, J. J., Brown, G. R., Richardson, R. C. & Laland, K. N. (2011). Darwin in mind: new opportunities for evolutionary psychology. *PLoS Biol*, **9**, e1001109.

Bonachea, L. A. & Ryan, M. J. (2011). Simulated predation risk influences female choice in túngara frogs, *Physalaemus pustulosus*. *Ethology*, **117**, 400–407.

Boncoraglio, G. & Saino, N. (2007). Habitat structure and the evolution of bird song: a meta analysis of the evidence for the acoustic adaptation hypothesis. *Functional Ecology*, **21**, 134–142.

Boughman, J. W. (2002). How sensory drive can promote speciation. *Trends in Ecology and Evolution*, **17**, 571–577.

Bradbury, J. W. & Vehrencamp, S. L. (2011). *Principles of Animal Communication*, 2nd edn. Sunderland, MA: Sinauer Associates, Inc.

Bradbury, J. W. & Vehrencamp, S. L. (2000). Economic models of animal communication. *Animal Behaviour*, **59**, 259–268.

Brumm, H. & Slabbekoorn, H. (2005). Acoustic communication in noise. *Advances in the Study of Behavior*, **35**, 151–209.

Burley, N. (1986). Sexual selection for aesthetic traits in species with biparental care. *American Naturalist*, **127**, 415–445.

Capranica, R. R. (1977). Auditory processing in anurans. *Federation Proceedings*, **37**, 2324–2328.

Christy, J. H. (1995). Mimicry, mate choice, and the sensory trap hypothesis. *American Naturalist*, **146**, 171–181.

Clutton-Brock, T. (2007). Sexual selection in males and females. *Science*, **318**, 1882.

Cohen, J. (1984). Sexual selection and the psychophysics of female choice. *Zeitschrift für Tierpsychologie*, **64**, 1–8.

Cosmides, L. & Tooby, J. (1992). Cognitive adaptations for social exchange. In J. Barkow, L. Cosmides & J. Tooby, eds., *The Adapted Mind: Evolutionary Psychology and the Generation of Culture*. New York: Oxford University Press, pp. 163–228.

Cosmides, L. & Tooby, J. (1994). Origins of domain-specificity: the evolution of functional organization. In L. Hirschfeld & S. Gelman, eds., *Mapping the Mind: Domain-specificity in Cognition and Culture*. New York: Cambridge University Press, pp. 85–116.

Cronin, H. (1991). *The Ant and the Peacock: Altruism and Sexual Selection from Darwin to Today*. Cambridge: Cambridge University Press.

Cummings, M. E. (2007). Sensory trade-offs predict signal divergence in surfperch. *Evolution*, **61**, 530–545.

Darwin, C. (1859). *On the Origin of Species*. London: Murray.

Darwin, C. (1871). *The Descent of Man and Selection in Relation to Sex*. London: Murray.

Darwin, C. (1872). *The Expression of the Emotions in Man and Animals*. London: Murray.

Darwin, C. (1890). *The Various Contrivances by which Orchids are Fertilised by Insects*. London: Murray.

Demary, K., Michaelidis, C. I. & Lewis, S. M. (2006). Fire-fly courtship: behavioral and morphological predictors of male mating success in *Photinus greeni*. *Ethology*, **112**, 485–492.

Endler, J. A. (1980). Natural selection on color patterns in *Poecilia reticulata*. *Evolution*, **31**, 76–91.

Endler, J. A. & Basolo, A. L. (1998). Sensory ecology, receiver biases and sexual selection. *Trends in Ecology and Evolution*, **13**, 415–420.

Endler, J. A. & McLellan, T. (1988). The processes of evolution: towards a newer synthesis. *Annual Review of Ecology and Systematics*, **19**, 395–421.

Endler, J., Westcott, D., Madden, J. & Robson, T. (2005). Animal visual systems and the evolution of color patterns: sensory processing illuminates signal evolution. *Evolution*, **59**, 1795–1818.

Evans, J. P., Bisazza, A. & Pilastro, A. (2004). Female mating preferences for colorful males in a population of guppies subject to high predation. *Journal of Fish Biology*, **65**, 1154–1159.

Gerhardt, H. C. & Huber, F. (2002). *Acoustic Communication in Insects and Anurans*. Chicago, IL: University of Chicago Press.

Gerhardt, H. C. & Schwartz, J. J. (2001). Auditory tunings and frequency preferences in anurans. In M. J. Ryan, ed., *Anuran Communication*. Washington, DC: Smithsonian Institution Press, pp. 73–85.

Gowaty, P. A. & Hubbell, S. P. (2009). Reproductive decisions under ecological constraints: it's about time. *Proceedings of the National Academy of Sciences, USA*, **106**, 10017–10024.

Grafe, T. U., Döbler, S. & Linsenmair, K. E., (2002). Frogs flee from the sound of fire. *Proceedings of the Royal Society of London Series B*, **269**, 999–1003.

Greenfield, M. D. (2002). *Signalers and Receivers, Mechanisms and Evolution of Arthropod Communication*. Oxford: Oxford University Press.

Grether, G. F. (2010). The evolution of mate preferences, sensory biases, and indicator traits. *Advances in the Study of Behavior*, **41**, 35–76.

Guilford, T. & Dawkins, M. (1991). Receiver psychology and the evolution of animal signals. *Animal Behaviour*, **42**, 1–14.

Hartshorne, C. (1956). The monotony-threshold in singing birds. *The Auk*, **73**, 176–192.

Hartshorne, C. (1973). *Born to Sing*. Bloomington, IN: Indiana University Press.

Haskins, C., Haskins, E., McLaughlin, J. & Hewitt, R. (1961). Polymorphism and population structure in *Lebistes reticulatus*, an ecological study. In W. F. Blair, ed., *Vertebrate Speciation*. Austin, TX: University of Texas Press, pp. 320–395.

Hoke, K. L., Burmeister, S. S., Fernald, R. D. *et al.* (2004). Functional mapping of the auditory midbrain during mate call reception. *Journal of Neuroscience*, **24**, 11264–11272.

Hoke, K. L., Ryan, M. J. & Wilczynski, W. (2007). Integration of sensory and motor processing underlying social behaviour in túngara frogs. *Proceedings of the Royal Society of London Series B: Biological Sciences*, **274**, 641–649.

Hoke, K. L., Ryan, M. J. & Wilczynski, W. (2008). Candidate neural locus for sex differences in reproductive decisions. *Biology Letters*, **4**, 518–521.

Hunter, M. L. & Krebs, J. R. (1979). Geographical variation in the song of the great tit (*Parus major*) in relation to ecological factors. *Journal of Animal Ecology*, **48**, 759–785.

Joron, M. (2008). Batesian mimicry: can a leopard change its spots – and get them back? *Current Biology*, **18**, R476–R479.

Karino, K., Kuwamura, T., Nakashima, Y. & Sakai, Y. (2000). Predation risk and the opportunity for mate choice in a coral reef fish. *Journal of Ethology*, **18**, 109–114.

Katti, M. & Warren, P. S. (2004). Tits, noise and urban bioacoustics. *Trends in Ecology and Evolution*, **19**, 109–110.

Kennedy, J. (1992). *The New Anthropomorphism*. Cambridge: Cambridge University Press.

Kilner, R. M., Noble, D. G. & Davies, N. B. (1999). Signals of need in parent–offspring communication and their exploitation by the common cuckoo. *Nature*, **397**, 667–672.

Kim, T. W., Christy, J. H. & Choe, J. C. (2007). A preference for a sexual signal keeps females safe. *PLoS ONE*, **2**, e422.

Kimchi, T., Xu, J. & Dulac, C. (2007). A functional circuit underlying male sexual behaviour in the female mouse brain. *Nature*, **448**, 1009–1014.

Kirkpatrick, M. & Barton, N. (1997). The strength of indirect selection on female mating preferences. *Proceedings of the National Academy of Sciences USA*, **94**, 1282–1286.

Lynch, K. S., Rand, A. S., Ryan, M. J. & Wilczynski, W. (2005). Reproductive state influences female plasticity in mate choice. *Animal Behaviour*, **69**, 689–699.

Macias-Garcia, C. M. & Elvia Ramirez, E. (2005). Evidence that sensory traps can evolve into honest signals. *Nature*, **434**, 501–505.

Marler, P. (1998). Animal communication and human language. *Memoirs of the California Academy of Sciences*, **24**, 1–19.

McLuhan. M. (1964). *Understanding Media: The Extensions of Man*. New York: Mentor.

Morton, E. S. (1975). Ecological sources of selection on avian sounds. *American Naturalist*, **109**, 17–34.

Nelson, R. J. (2011). *An Introduction to Behavioral Endocrinology*. Sunderland, MA: Sinauer Associates.

Podos, J., Huber, S. K. & Taft, B. (2004). Bird song: the interface of evolution and mechanism. *Annual Review of Ecology, Evolution and Systematics*, **35**, 55–87.

Rodd, F. H., Hughes, K. A., Grether, G. F. & Baril, C. T. (2002). A possible non-sexual origin of mate preference: are male guppies mimicking fruit? *Proceedings of the Royal Society of London Series B*, **269**, 475–481.

Ron, S. R. (2008). The evolution of female mate choice for complex calls in túngara frogs. *Animal Behaviour*, **76**, 1783–1794.

Ryan, M. J. (1985). *The Túngara Frog, A Study in Sexual Selection and Communication*. Chicago, IL: University of Chicago Press.

Ryan, M. J. (1990). Sensory systems, sexual selection, and sensory exploitation. *Oxford Surveys in Evolutionary Biology*, **7**, 157–195.

Ryan, M. J. (1997). Sexual selection and mate choice. In J. R. Krebs & N. B. Davies, eds., *Behavioural Ecology, An Evolutionary Approach*. Oxford: Blackwell, pp. 179–202.

Ryan, M. J. (1998). Receiver biases, sexual selection and the evolution of sex differences. *Science*, **281**, 1999–2003.

Ryan, M. J. (2001). Food, song and speciation. *Nature*, **409**, 139–140.

Ryan, M. J. (2010). The túngara frog: a model for sexual selection and communication. In M. D. Breed & J. Moore, eds., *Encyclopedia of Animal Behavior*. Oxford: Academic Press, pp. 453–461.

Ryan, M. J. (2011). The brain as a source of selection on the social niche: examples from the psychophysics of mate choice in túngara frogs. *Integrative and Comparative Biology*, **51**, 756–770.

Ryan, M. J. & Keddy-Hector, A. (1992). Directional patterns of female mate choice and the role of sensory biases. *American Naturalist*, **139**, S4–S35.

Ryan, M. J. & Rand, A. S. (1993). Sexual selection and signal evolution: the ghost of biases past. *Philosophical Transactions of the Royal Society Series B*, **340**, 187–195.

Ryan, M. J. & Wilczynski, W. (2011). *An Introduction to Animal Behavior: An Integrative Approach*. Cold Springs Harbor, New York: Cold Springs Harbor Laboratory Press.

Ryan, M. J., Bernal, X. E. & Rand, A. S. (2010). Female mate choice and the potential for ornament evolution in the túngara frog *Physalaemus pustulosus*. *Current Zoology*, **56**, 343–357.

Ryan, M. J., Fox, J. H., Wilczynski, W. & Rand, A. S. (1990). Sexual selection for sensory exploitation in the frog *Physalaemus pustulosus*. *Nature*, **343**, 66–67.

Schiestl, F. P. (2005). On the success of a swindle: pollination by deception in orchids. *Naturwissenschaften*, **92**, 255–264.

Schwartz, A. K. & Hendry, A. P. (2006). Sexual selection and the detection of ecological speciation. *Evoutionary Ecology Research*, **8**, 399–413.

Searcy, W. & Nowicki, S. (2005). *The Evolution of Animal Communication: Reliability and Deception in Signaling Systems*. Princeton, NJ: Princeton University Press.

Seehausen, O., van Alphen, J. M. & Witte, F. (1997). Cichlid fish diversity threatened by eutrophication that curbs sexual selection. *Science*, **277**, 1808–1811.

Slabbekoorn, H. & den Boer-Visser, A. (2006). Cities change the songs of birds. *Current Biology*, **16**, 2326–2331.

Slabbekoorn, H. & Peet, M. (2003). Birds sing at a higher pitch in urban noise. *Nature*, **424**, 267.

Slabbekoorn, H. & Smith, T. B. (2002). Habitat dependent song divergence in the little greenbul: an analysis of environmental selection pressures on acoustic signals. *Evolution*, **56**, 1849–1858.

Su, K. F. Y. & Li, D. (2006). Female-biased predation risk and its differential effect on the male and female courtship behavior of jumping spiders. *Animal Behaviour*, **71**, 531–537.

Tárano, Z. & Ryan, M. J. (2002). No preexisting biases for heterospecific call traits in the frog *Physalaemus enesefae*. *Animal Behaviour*, **64**, 599–607.

Vélez, M. J. & Brockman, H. J. (2006). Seasonal variation in female response to male calling song in the field cricket, *Gryllus rubens*. *Ethology* **112**, 1041–1049.

Welch, A. M., Semlitsch, R. D. & Gerhardt, H. C. (1998). Call duration as an indicator of genetic quality in male gray tree frogs. *Science*, **280**, 1928–1930.

West-Eberhard, M. J. (1979). Sexual selection, social competition, and evolution. *Proceedings of the American Philosophical Society*, **123**, 222–234.

Wilczynski, W. & Ryan, M. J. (2010). The behavioral neural science of acoustic processing in anurans. *Current Opinion in Neurobiology*, **20**, 754–763.

Wilczynski, W., Rand, A. S. & Ryan, M. J. (1995). The processing of spectral cues by the call analysis system of the túngara frog, *Physalaemus pustulosus*. *Animal Behaviour*, **49**, 911–929.

Wilczynski, W., Rand, A. S. & Ryan, M. J. (2001). Evolution of calls and auditory tuning in the *Physalaemus pustulosus* species group. *Brain, Behavior and Evolution*, **58**, 137–151.

Wiley, R. H. (1991). Associations of song properties with habitats for territorial oscine birds of eastern North America. *American Naturalist*, **138**, 973–993.

Commentary

Narrative 1 is not just metaphor. It's a shorthand explanation, just like function and adaptation (spelled out, for example, in Millikan, Ch. 5 of this volume). We see no contentious issue here. We, too, endorse integrative studies of animal communication. Ryan's chapter beautifully illustrates the integrative approach, and explains how it followed from avoiding information constructs. However, Botero and de Kort's chapter (Ch. 11) is a beautiful example, too, yet stemmed from an information approach. Informational approaches are certainly problematic, but they don't hold back research.

Andrew G. Horn and Peter McGregor

Response

Regardless of whether Narrative 1 is a metaphor (as it would seem to be according to Kennedy (1992)) or a shorthand explanation, it does not provide the reader with the information about the actual biology that is taking place. For the uninitiated, Narrative 1 can confuse a population-based understanding of selection with a teleological one, it could suggest cognitive abilities in animals that might not exist, and it robs the reader of the grandeur in Darwin's view of life and replaces it with a comic-book version. Why would we want to do this?

Michael J. Ryan