

Learned signals and consistency of delivery: a case against receiver manipulation in animal communication

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11.1 Introduction

It was recently suggested that concepts such as ‘information’ and ‘encoding’ should be dropped from usage because they are not clearly defined when applied to animal communication (Rendall, Owren & Ryan, 2009; Owren, Rendall & Ryan, 2010). We disagree with that assessment and note that the utility of these concepts is firmly based on principles of statistical decision theory, probability monitoring, alternative coding schemes and Bayesian updating (reviewed in Bradbury & Vehrencamp, 2011). Nevertheless, we acknowledge that there remains a valid debate about how often and how much selection should favour the provision of information during animal communication.

One of the arguments used in support of the view that animal signals do not contain information is the observation that some signals trigger reflexive responses that startle receivers, capture their attention and/or elicit direct physiological changes within them (Rendall *et al.*, 2009). For example, the spectral structure of alarm calls in many species appears to be optimally designed to stimulate areas of the brain that regulate arousal and activation. Such design features imply that direct sensory stimulation may be a more parsimonious explanation for why receivers respond to alarm calls than the acquisition of ‘information’ about imminent dangers in the environment (see Rendall *et al.*, 2009). Nevertheless, examples abound of animal signals that are reasonably well

correlated with aspects of the world that are unknown to receivers but important for their fitness (Andersson, 1994; Maynard Smith & Harper, 2003; Searcy & Nowicki, 2005; Bradbury & Vehrencamp, 2011). In these systems, information is said to be ‘encoded’ as a general association between certain stimuli types (i.e. the different signal types or signal intensities) and alternative world states allowing the evolution of adaptive responses that are tailored to specific situations (for explicit theoretical formulations of these ideas see Bradbury & Vehrencamp, 2000; Botero *et al.*, 2010). For example, the tail length of male long-tailed widow-birds (*Euplectes progne*) contains information about individual quality that is useful in mate choice and male–male competition because, on average, individuals with longer tails show a slower decline in condition under intense physical activity (Pryke & Andersson, 2005). Details on the mechanisms that maintain such correlation over time and thereby promote the evolution of ‘honest’ signalling systems can be found elsewhere (e.g. Maynard Smith & Harper, 2003; Searcy & Nowicki, 2005; Bradbury & Vehrencamp, 2011).

Put simply, the current debate on the nature of animal communication appears to be concerned with whether receiver responses are strictly the product of (1) direct sensory stimulation, or (2) the acquisition of new relevant information. However, we think that the two suggested views are not mutually exclusive ‘alternatives’ and that this debate reflects some confusion about proximate and ultimate levels of analysis (*sensu* Tinbergen, 1963). Specifically, proponents of the non-informational view of communication have focused on proximate mechanisms of how signals work, whereas defendants of the informational view have mainly emphasised ultimate causation (see Guilford & Dawkins, 1991, for a review of similar issues). Furthermore, the idea that animal signals are optimally designed to excite perceptual mechanisms in receivers is not incongruent with an informational view of communication. The question is therefore not which view of animal communication is correct, but rather to what extent proximate and ultimate considerations provide a better understanding of signalling systems.

In our opinion, disregarding altogether the possibility of information transfer in animal communication is problematic and potentially short-sighted. Although reflexive attention-stimulation signals are by definition highly effective in eliciting responses, they are also easily exploited by senders and can therefore lead to maladaptive responses in receivers that will eventually promote selection against communication (Seyfarth *et al.*, 2010). We therefore expect such signalling systems to be highly unstable or to persist only when being ‘manipulated’ is somehow advantageous to receivers or when ignoring misleading stimuli is simply too costly. In contrast, signalling systems based on the provision of information are likely to be stable under a broader range of

conditions because they allow receivers a choice and, therefore, a greater chance of benefiting from the exchange (Maynard Smith & Harper, 2003; Searcy & Nowicki, 2005; Bradbury & Vehrencamp, 2011).

To explore these issues, we review in this chapter recently discovered links between song learning ability in oscine birds and various aspects of individual quality that are relevant to potential receivers (Byers, 2007; Botero *et al.*, 2009b; de Kort *et al.*, 2009b). More specifically, we examine the evidence that song consistency, or the ability to produce virtually identical repetitions of any given song component, is a signal that does not conform with the expected demands of reflexive attention-stimulation of receivers. We argue that in this type of communication system, the stimulus that elicits the strongest neurological response (i.e. a deviant song) is precisely what senders should try to avoid in order to be perceived as attractive by females or intimidating by rivals. Thus, selection acts against signal structures that startle or otherwise produce a neurological response in receivers (i.e. less consistent song) not because these stimuli are more costly to produce but because they are associated with less attractive or less intimidating senders. Senders are unable to manipulate receivers in this system because consistency cannot be exaggerated and because their only alternative (i.e. to produce less consistent songs) could lower their own fitness. We conclude that the use of song consistency as a signal cannot be explained without reference to information transfer, and suggest that the basic principles discussed in this chapter may also apply to other signalling systems in which displays require practice or learning.

11.2 Information content of song learning

The acoustic structure of bird songs, like that of many other animal signals, is shaped through sexual selection via mate choice and the competition for mates. Song is a channel of communication in which a variety of parameters can be set, each potentially correlated with different sender attributes and exposed to different pressures of selection. For example, the rate at which songs are produced may be correlated with a sender's condition, whereas the number of song types it sings (i.e. its repertoire size) may correlate with its immunocompetence or resource-holding potential (Vehrencamp, 2000). Playback experiments have repeatedly demonstrated that receivers not only respond to variation in many of these subtle parameters but also that they do so in a way that is consistent with the idea of adaptive information provision. For example, females tend to mate preferentially with males with more elaborate song displays, and rivals tend to avoid them (Collins, 2004). What truly sets bird songs apart from most other sexually selected signals is that their

production, at least in oscines, hummingbirds and parrots, requires learning (Farries, 2001; Beecher & Brenowitz, 2005).

Because learning to sing and storing learned songs in memory bear many similarities with other cognitive processes (Nowicki & Searcy, 2011), it has been suggested that bird songs can provide information on general cognitive ability (Nowicki *et al.*, 2000; Boogert, Giraldeau & Lefebvre, 2008; Botero *et al.*, 2009a; Boogert *et al.*, 2011). Recent experimental studies have provided preliminary, yet not unconditional support for this hypothesis. For example, captive male zebra finches, *Taeniopygia guttata*, with more complex songs show a faster learning curve when mastering a novel foraging task than individuals with simpler songs (Boogert *et al.*, 2008), and wild male song sparrows, *Melospiza melodia*, with larger song repertoires learn more quickly to reach around rather than to peck directly at mealworms presented behind clear Plexiglas (detour-reaching task; see Boogert *et al.*, 2011). These results indicate that by evaluating an individual's song learning abilities, receivers may gain information about the singer's ability to learn in other contexts or to solve certain types of problems. But how general is that information? Should we expect better singers to be generally smarter and song learning to reflect an individual's ability to acquire, store and process information in every other context? Although this question is an active area of research (see Nowicki & Searcy, 2011), the preliminary answer appears to be no. For example, a variety of studies have shown that selection on specific cognitive tasks may promote localised changes in areas of the brain related to the performance of those tasks rather than general cognitive improvements (e.g. Pravosudov & Clayton, 2002; Shettleworth, 2003; Garamszegi & Eens, 2004; Healy, de Kort & Clayton, 2005; Sherry, 2006). In addition, in some species there appears to be no correlation among individual performances in different cognitive tasks (Boogert *et al.*, 2011; Keagy, Savard & Borgia, 2011). These results suggest that cognition, just as song, may be more properly viewed as a multidimensional entity, at least in birds, rather than a single trait, and that different features of song learning may relate to very different cognitive abilities (see Shettleworth, 2010).

One cognitive trait with promising links to the evolution of bird song is the ability to copy or learn complex motor patterns. Motor control areas in the avian brain show remarkable anatomical and topographic similarities with the song control system (Jarvis, 2004; Finlay, Cheung & Darlington, 2005; Feenders *et al.*, 2008). In particular, there are striking parallels between the neural control of feeding and singing, perhaps because both of these activities rely on the movement of some of the same head, beak and tongue muscles (Dubbeldam, 1997). Besides being located in areas immediately adjacent to the song system, more general motor control areas in the bird brain are also organised into anterior and posterior pathways, and there appears to be a similar distinction between

nuclei in charge of movement and nuclei involved in fine-tuning the motor patterns during learning (Feenders *et al.*, 2008). In addition, recent evidence suggests that two important nuclei in the song system (HVC and RA) are active during the learning and sequencing of feeding movements and food-related associative tasks (Tokarev *et al.*, 2011). Taken together, these studies indicate that a singer's ability to learn songs is likely to reflect its ability to learn and reproduce certain other complex motor patterns, especially those involving the head, beak and tongue (see Sakata & Vehrencamp, 2012 for a review). Because such movements are relevant for survival, feeding, fighting and predator avoidance, the information provided by song is therefore likely to have generalised adaptive value in the context of sexual selection.

A relevant distinction at this point is the difference between quantity and quality metrics of song learning. Quantity metrics include the number of different song types an individual can learn (i.e. its repertoire size) and the variety with which these types are presented to receivers (e.g. song versatility; see Derrickson, 1988). Quality metrics, on the other hand, include measures of the ability to sing demanding song types (e.g. song complexity or trill performance; see Podos, 1997), and the ability to copy song models accurately (Nowicki, Peters & Podos, 2002; Holveck *et al.*, 2008). Based on this distinction, we propose that quantity-related metrics of song learning should reflect an individual's ability to process and commit to memory a number of motor patterns, whereas quality-related metrics should more closely indicate its ability to acquire and reproduce these patterns in an accurate and consistent fashion.

The acoustic similarity between renditions of a given song type or syllable type within a song, also known as song consistency (Byers, 2007; Botero *et al.*, 2009b; de Kort *et al.*, 2009b), has recently received an increased amount of attention as a non-subjective measurement of the quality of song learning. A number of studies have shown that song consistency is related to the singer's fitness. In the tropical mockingbird, *Mimus gilvus*, males with greater song consistency have higher reproductive success and enjoy higher dominance ranks (Botero *et al.*, 2009b). Similarly, male black-capped chickadees, *Poecile atricapillus*, with more consistent frequency jumps between the two notes of their fee-bee song tend to achieve higher dominance ranks than less consistent rivals (Christie, Mennill & Ratcliffe, 2004). In the great tit, *Parus major*, older individuals are able to maintain more consistent inter-song intervals than inexperienced males (Lambrechts & Dhondt, 1988; Rivera-Gutierrez, Pinxten & Eens, 2010, 2011). A similar association between age and the ability to produce more consistent repetitions of each song type has been recorded in the banded wren, *Thryophilus pleurostictus* (de Kort *et al.*, 2009b), the tropical mockingbird (Botero *et al.*, 2009b) and the great reed warbler, *Acrocephalus arundinaceus* (Wegrzyn, Leniowski & Osiejuk, 2010). Male zebra finches

from smaller broods also tend to produce more consistent song motifs than those from larger broods (Holveck *et al.*, 2008), highlighting the importance of early-life conditions for the development of song learning (Nowicki, Peters & Podos, 1998).

In addition to the various studies supporting a correlation between male quality and song consistency, several lines of evidence indicate that this aspect of song learning is perceived by receivers and used in sexual selection. In the blue tit, *Parus caeruleus*, females mated to individuals with more consistent inter-song intervals produce larger clutches (Poesel, Foerster & Kempenaers, 2001), and in the chestnut-sided warbler, *Dendroica pensylvanica* (Byers, 2007), and the banded wren, *T. pleurostictus* (Cramer *et al.*, 2011), females prefer extra-pair mates with more consistent songs than their current social partners. Additionally, male receivers in both the banded wren and the great tit respond differentially to playback stimuli that vary only in song consistency (de Kort *et al.*, 2009b; Rivera-Gutierrez *et al.*, 2011).

The observed relationship between age and song consistency (Jones, Ten Cate & Slater, 1996; de Kort *et al.*, 2009b; Rivera-Gutierrez *et al.*, 2010) suggests that the ability to repeat each song type in a consistent fashion may be an acquired trait that improves with practice. This possibility is important because practice cannot be cheated, indicating a potential for song consistency to act as an honest indicator of experience. Although it is not clear what exactly needs to be practised, spectral analysis of the songs of the banded wren may give an indication. In this species, the individual notes in a trill are the units of repetition subject to selection for consistency. These trill notes of the banded wren show a bimodal distribution in amplitude (see Figure 11.1), similar to that observed in the notes of the northern cardinal, *Cardinalis cardinalis*. In the latter species, the temporary reduction in power at the middle of a trill note is associated with a transition from using the left versus the right syrinx to produce the different portions of the frequency sweep (Suthers & Goller, 1997; Suthers, Goller & Pytte, 1999). Young banded wrens often show a disconnection between the higher and lower frequency portions of a trill note, suggesting that they are not yet able to coordinate appropriately the movement of these two sound sources. In addition, both adult and young banded wrens sometimes show a distinct transition between singing narrow and broad bandwidth trills, possibly due to the cessation of sound production with one of the syrinxes (see Figure 11.2). Consistency in reproduction of trill notes is therefore likely to be achieved, at least in some cases, by improving the neuromuscular coordination of the left and right syrinx (see Suthers, 2004).

In conclusion, the current evidence is consistent with the hypotheses that song consistency is associated with multiple aspects of male quality, particularly those related to motor ability, and that receivers make use of this parameter during mate choice and agonistic behaviour. We now turn our

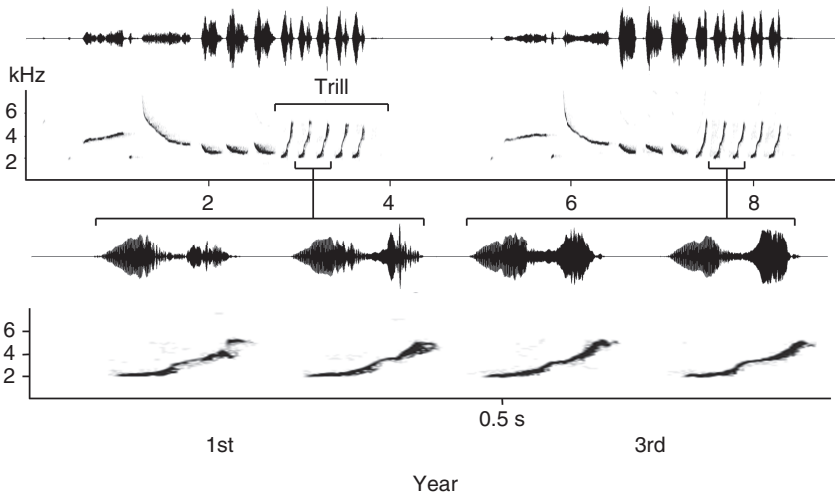


Figure 11.1 A waveform and spectrogram of a song type sung by a banded wren in its first breeding season (left) and the same song type sung by the same male in its third breeding season (top panel). Trill notes are enlarged in the bottom panel. Note in the waveform that each trill note shows two peaks in amplitude. Spectrogram settings: FFT (fast Fourier transform) size: 512 Hz, Hamming window, time resolution = 2.67 ms, frequency resolution = 94 Hz.

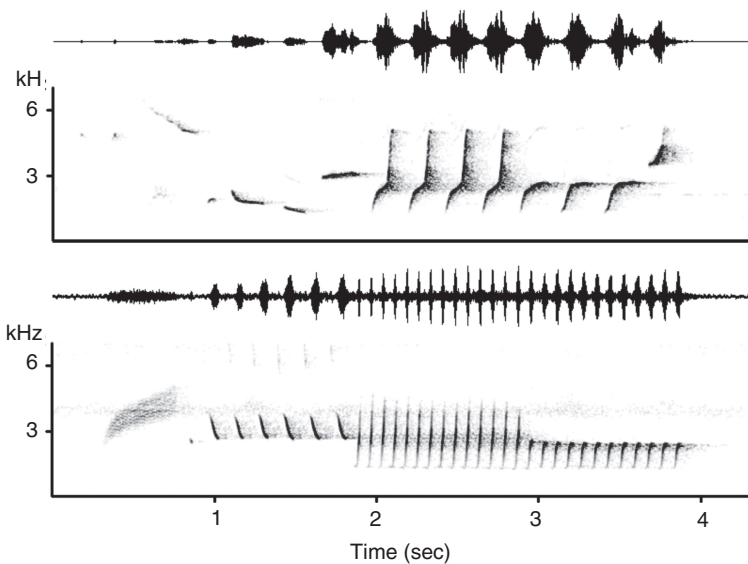


Figure 11.2 Waveforms and spectrograms of two examples of banded wren songs that show a discrete transition between wide and narrow frequency bandwidth use in the trill (latter) part of the song.

attention to how receivers may perceive this feature of song learning and how the potential mechanisms for such assessment may have affected the evolution of this signalling system.

11.3 The perception of learning ability

A possible mechanism to evaluate the quality of song learning is to compare a crystallised song with the model it was derived from.¹ However, this type of assessment requires knowledge of the model used as a reference and does not work for song types that are invented *de novo* by singers (as is the case in catbirds; Kroodsma *et al.*, 1997). As discussed above, a potentially simpler and more generally applicable approach to assessing learning quality is to compare multiple renditions of the same song type or syllable and evaluate a singer's ability to deliver them in a consistent fashion. This procedure requires only that each song type or syllable is repeated multiple times within the sampling period and does not rely on prior experience with a given song type or syllable or a common exposure to a reference model.

But can receivers perceive the subtle differences that are involved in the comparison of highly similar sounds? Auditory neurons in a variety of organisms exhibit responses to deviant stimuli that are presented within a string of similar sounds. This neural response, known as mismatch negativity (MMN) or, in single cells, as stimulus-specific adaptation, is thought to be an adaptive mechanism for the detection of sudden changes in the auditory landscape (Picton, 2011). MMN operates pre-attentively, meaning that it can occur under anaesthesia or when the subject is engaged in other tasks. Nevertheless, MMN responses are intensified when the subject is paying attention to the stimuli (Woldorff *et al.*, 1998; Arnott & Alain, 2002), or when it is familiar with the sounds it has to compare (Näätänen *et al.*, 1997). Although most of this research has been done on human subjects, it has been shown recently that a similar phenomenon occurs in the auditory forebrain of zebra finches (Beckers & Gahr, 2010). In that species, MMN responses can be evoked with either artificial or species-specific sounds (Beckers & Gahr, 2012). It is therefore possible that in the context of sexual selection for song learning, MMN, or a similar neural response, would allow the perception of song consistency by evoking strong neural responses in the auditory forebrain of the receiver whenever it encounters a deviant rendition of a given song or syllable type.

¹ Songs are called 'crystallised' if they have already been learned by the individual and can no longer be changed.

Regardless of the actual neural mechanism involved, a communication system based on the detection of slightly deviant repeats in a train of similar sounds is not conducive to receiver manipulation and is therefore inconsistent with the strictly non-informational view of animal communication (see Rendall *et al.*, 2009; Owen *et al.*, 2010). Specifically, contrary to the suggestion that signals per se should have a structure that is arousing and attention getting, the stimulus that most captures the receivers' attention in this type of communication system (i.e. a deviant song) is precisely what senders should try to avoid in order to appear attractive to females or intimidating to rivals. Moreover, the detection of deviant exemplars in a train of repeated stimuli appears to be independent of the acoustic structure of the song types being repeated because MMN responses can be triggered by very different acoustic stimuli in birds (Beckers & Gahr, 2010, 2012). Furthermore, the fact that MMN responses do not occur after a single presentation of a stimulus (see Sams *et al.*, 1985; Cowan *et al.*, 1993) indicates that what matters in this case is not the acoustic structure of the sound type itself but rather the similarity among repetitions of any given sound.

In a signalling system based on song consistency, selection is likely to favour not only the receiver's ability to perceive subtle differences between similar sounds but also the sender's behaviours that could potentially facilitate this task. Results from auditory testing in the Eurasian starling, *Sturnus vulgaris*, suggest that quick repetition of signals is crucial for the assessment of song consistency. Zokoll, Klump & Langemann (2007, 2008) exposed subjects to a sample stimulus followed by a silent interval and then a test stimulus. The subjects were required to indicate whether sample and test stimuli were the same and were subsequently rewarded if correct, or punished if not. These experiments showed that starlings have an auditory memory in these circumstances of roughly 20 s for spectral parameters and 12 s for temporal parameters, and that memory retention can increase with a greater number of repetitions of sample stimuli. Consistent with these observations, all species that have been evaluated with respect to song consistency tend to repeat syllable or song types in close temporal proximity (a behaviour that is common among many songbirds). Furthermore, most of these species repeat a single syllable type multiple times before switching to another one, either as part of a trill or within a syllable bout. In species exposed to strong selection for repertoire size, such as mockingbirds or wrens, this type of short-term repetition is surprising because such species are expected to maximise vocal versatility and therefore should not repeat any signal at all (see Collins, 2004). Thus, short-term repetitiveness is likely to have arisen from selection for behaviours that facilitate the assessment of song consistency, especially in cases in which quantifying repertoire size is too time-consuming or prohibitively demanding

on the receiver's cognitive abilities (Botero *et al.*, 2008). In addition, consecutive repetition could also be a target of selection by receivers because it can induce exhaustion in the singer and is therefore difficult to cheat (Lambrechts & Dhondt, 1986; but see Brumm *et al.*, 2009). In great tits, song consistency decreases towards the end of a singing bout, and individual quality is related to the number and consistency of consecutive repetitions of a single phrase type (Lambrechts & Dhondt, 1986).

The assessment of learning ability appears to be facilitated through slightly different behaviours in the context of intra-sexual competition. In particular, rival songbirds often engage in counter-singing interactions during which both parties match each other's songs (Krebs, Ashcroft & Vanorsdol, 1981; Whitney & Miller, 1983; Falls, 1985; Stoddard *et al.*, 1992; Shackleton & Ratcliffe, 1994; Beecher *et al.*, 2000; Vehrencamp, 2001; Mennill & Ratcliffe, 2004). By reproducing a common motor programme in close temporal proximity, song matching could facilitate the comparison of rivals' performance levels, motor control and learning abilities (Logue & Forstmeier, 2008). Interestingly, matching may sometimes be restricted to the most demanding elements of a song. For example, male banded wrens sing songs composed of a versatile introduction and a repetitive trill, but during counter-singing, they only match the trilled portion of the song (de Kort *et al.*, 2009a).

11.4 Concluding remarks

There is ample and growing evidence that consistency in singing is a signal of learning ability in several species of songbirds. This metric of learning ability is (a) correlated with different aspects of individual quality such as age, fecundity and social dominance, and (b) correlated with receiver behaviour in both field observations and playback experiments. In addition, circumstantial evidence indicates that the display of song consistency is an evolved signal rather than a cue (see the introduction to this volume) because unlike in cues, senders are not obliged to display consistency in songs. Instead they may choose to sing or not, and to repeat or not each song type in close temporal proximity. The latter is especially apparent in species that facilitate the assessment of consistency via short-term repetition in spite of experiencing concurrent selection for high vocal versatility.

The idiosyncrasies of this communication system are particularly relevant to the current debate about the information content (or lack thereof) of animal signals. First, song consistency relies on properly functioning motor control areas in the brain and appears to be achieved through practice, meaning that it is likely to be an honest indicator of the learning abilities of the singer (an

'index' signal *sensu* Vehrencamp, 2000; Bradbury & Vehrencamp, 2011). Second, this signalling system appears to be based on the perception of signalling states (i.e. deviant renditions of a given song or syllable type) that should be actively avoided by the sender. Given these two features, it is unlikely that senders can exploit receiver sensitivities to manipulate them in any sense. The best a singer can do is to perform at the best of his ability because any deviation from such standard will negatively affect his fitness by rendering him less attractive to females or less intimidating to rivals. Therefore, the hypothesis that animal sounds are designed to elicit a neural response in the receiver regardless of sender correlates (Rendall *et al.*, 2009; Owren *et al.*, 2010) does not appear to hold in this particular case.

The issues described here may also apply more generally to any communication system that relies on ritualisation. In a stimulating essay, Zahavi (1980) pointed out that standardised displays can improve a receiver's ability to compare senders. Furthermore, he pointed out that variation among multiple renditions of a ritualised movement can provide information about the reliability of the signal itself. In other words, an occasional good display may be a matter of luck but a set of consistently good displays can only be achieved by high-quality senders. These ideas closely match the arguments developed above for song consistency and song matching. For example, the visual perception of variability in movement displays is likely to be subject to similar principles to the acoustic perception of consistency because in both cases, receivers must detect deviations from a general pattern (or a standard). Similarly, in both situations receivers benefit from sampling the same behaviour multiple times in short periods of time. Not surprisingly, ritualised movements are also often repeated in close temporal proximity (e.g. Jordao, Curto & Oliveira, 2007).

In conclusion, regardless of the signalling modality employed, we propose that senders should be unable to manipulate receivers whenever repeatability itself is the signal under consideration. Taken together, the arguments we have developed in this chapter suggest that receiver manipulation, one of the basic premises of the non-informational view of animal communication, may not be possible in many visual or acoustic ritualised displays. We therefore advocate the continued use of the concept of information in animal communication and suggest that the issues raised in the non-informational debate are more relevant to the possible origin of signals than to the issue of their evolutionary stability.

Acknowledgements

We would like to express our gratitude to Gabriël Beckers, Jack Bradbury, Sarah Collins, Karolina Kluk-de Kort, William Searcy and Sandra

Vehrencamp for discussion and comments on earlier versions of this chapter and Ulrich Stegmann for inviting us to contribute to this volume and for being an excellent editor.

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