Thesis for the degree of Doctor of Philosophy

Colour Signalling
in Widowbirds and Bishops

Calum Edward Ninnes

UNIVERSITY OF GOTHENBURG

Department of Biological and Environmental Sciences
Faculty of Science

2015

COLOUR SIGNALLING IN WIDOWBIRDS AND BISHOPS

Calum Edward Ninnes

Department of Biological and Environmental Sciences
University of Gothenburg
Box 463, SE-405 30 Gothenburg
SWEDEN
E-mail: calum.ninnes@gmail.com

Cover illustration by Julie Sjögren ©

ABSTRACT

Sexual selection, i.e. differential mating success due to contest competition or mate choice, has produced an amazing diversity of elaborate sexual signals across the animal kingdom, not least the dazzling colours of birds. According to classical 'sender-precursor' models of signal evolution, signals evolve because they convey information beneficial to receivers, such as the senders quality as a prospective mate or strength as an opponent. In contrast, 'receiver-precursor' models emphasize pre-existing receiver biases (e.g. sensory biases or generalization) as the primary drivers of signal evolution. Generally, models of sexually selected signal evolution have primarily been concerned with intersexual (mate choice) rather than intrasexual (agonistic or contest) signals. In particular, there has been almost no application of receiver-precursor models to the design and evolution of agonistic (threat) signals.

This thesis tests agonistic colour signalling in the genus *Euplectes*, 17 species of African widowbirds and bishops, and explores receiver-precursor model explanations for the phylogenetically reconstructed and convergent evolution of red carotenoid-based signals from yellow ancestors. In addition to testing the generality of an agonistic signal function of the carotenoid colour signals, the primary goals were to 1) investigate a pre-existing bias for longer wavelength ('redder') colour hues in yellow-signalling species, 2) test the persistence of a receiver bias in species with highly exaggerated signals, and 3) test signalling theory that suggests agonistic signals must be reinforced by information content for receiver responses to persist.

In a field experiment with the yellow-signalling montane marsh widowbird *E. psammocromius* (**Paper I**), red-manipulated territorial males were more likely to retain their territories, and won more boundary contests against neighbours, compared to control or down-manipulated males. This is the first time that a pre-existing receiver bias has been demonstrated for an agonistic signal. Because *E. psammocromius* is a relatively recently derived species, I then explored the evolutionary age of the receiver bias by testing for it in an ancestrally branching (outgroup) species, the yellow-crowned bishop *E. afer* (**Paper II**). In a captive population, I staged dyadic contests over food between control and red-manipulated males, in which red males secured more time at the feeder than did control males, indicating that the receiver bias (i.e. aversion to red) predated the evolution of red signals in *Euplectes*.

The above experiments suggest strong generalization or 'supernormal stimulus' responses to red in yellow-signalling species, but will this persist in the most exaggerated red species? In a field experiment on the southern red bishop *E. orix* (**Paper III**), I found that males given supernormally red hues were more likely to obtain/retain a territory compared to control-red or down-manipulated males, suggesting that the receiver response remains generalized with respect to hue.

The above results, together with the findings that down-manipulated males fared competitively worse that control males (**Papers I-III**), corroborates the proposed generality of an agonistic signal function on carotenoid colour signals in *Euplectes*.

Lastly, when control *E. afer* males were repeatedly staged in dyadic contests against red-manipulated rivals (**Paper IV**), the initially large treatment effect (time at feeder) for red males quickly decreased over successive trials, suggesting that an innate aversion to the red signal attenuated when the signal was not reinforced by information content.

In summary, I have provided the first evidence that a pre-existing receiver bias has likely driven the evolution and diversification of an agonistic signal, and thus demonstrated the applicability of receiver precursor models for explaining agonistic signal evolution. Additionally, I have corroborated the agonistic signal function of carotenoid colour displays in a further three species distributed across the *Euplectes* phylogeny, strengthening this unique model system for exploring sexual selection and sexual signal evolution. Finally, I found that receiver aversions of supernormal threat signals quickly attenuated, which suggests that the colour signals in *Euplectes* would not have evolved unless they were (and likely still are) reinforced by some (honest) information content; the nature of which remains to be explored.

LIST OF PAPERS
This thesis is based on the following papers, which will be referred to in the text by their Roman numerals.

I. Ninnes, C. E., Andersson, S. 2014. Male receiver bias for red agonistic signalling in a yellow-signalling widowbird: a field experiment. Proceedings of the Royal Society B – Biological Sciences. 281. DOI: 10.1098/rspb.2014.0971

II. Ninnes, C. E., Adrion, M., Edelaar, P., Tella, J. L., Andersson, S. 2015. A receiver bias for red pre-dates the convergent evolution of red color in widowbirds and bishops. Behavioral Ecology. 26: 1212-1218. DOI: 10.1093/beheco/arv068

III. Ninnes, C. E., Webb, S. L., Andersson, S. Are red bishops red enough? On the persistence of a generalized receiver bias in *Euplectes*. Manuscript. Submitted.

IV. Ninnes, C. E., Andersson, S. Calling the bluff? A rapidly declining effect of a manipulated agonistic signal and its implications for signal evolution. Manuscript.

CONTENTS

INTRODUCTION

The incredible diversity of animal form is as spectacular as it is perplexing. Since Darwin and Wallace birthed contemporary biology with the theory of evolution by natural selection (Darwin and Wallace 1858; Darwin 1859), an overarching challenge for biologists has been to explain this staggering diversity. Darwin (1859) also identified, and subsequently expanded on (Darwin 1871), what is now regarded as an important mode of natural selection, namely sexual selection. Now appreciated as having driven the evolution of many of the most elaborate and striking traits of animals, including extravagant colours in male birds (Andersson 1994; Hill 2002), the study of these sexually selected signals is crucial to understanding the diversity of animal traits, and has commanded huge research effort (see Andersson 1994). Why is sexual signal design so diverse (Andersson 1980; Ryan and Rand 1993)? Which models of sexual selection can account for this diversity? This thesis strives to make a contribution to this literature by examining the evolution of colour signal diversity in the genus *Euplectes*. First, however, I will begin with some background as to what signals are, the different evolutionary models that have been posited, and what information sexually selected signals may contain.

What are animal signals?

Maynard Smith and Harper (2003) define an animal signal as "any act or structure which alters the behavior of other organisms, which evolved because of that effect, and which is effective because the receivers response has also evolved". Conventional signals are generally regarded as strategic or arbitrary correlates of quality, or of another parameter about which information is contained (Guilford and Dawkins 1995). However, it has been suggested that the emphasis on information transmission in explaining the function and evolution of animal signals is inappropriate, and more emphasis should be placed on the role of manipulation or 'influence' in signal evolution (Dawkins and Krebs 1978; Owings and Morton 1997; Owings and Morton 1998; Rendall et al. 2009), which better aligns with the potentially divergent interests of signalers and receivers.

Under either framework, the design of animal signals can be deconstructed into two general components; 'efficacy' and 'information content' (or 'strategic design') (Guilford and Dawkins 1991; Guilford and

Dawkins 1993; Andersson 2000), which may be shaped by different selective pressures relating to either detectability or cost dimensions, respectively (Endler 1993; Andersson 2000). As efficacy pertains to the detectability, discriminability, or memorability of the signal (e.g., Buechner et al. 2014), it is influenced by both properties of the surrounding environment and of receiver psychology, which collectively has been referred to as 'sensory drive' (Endler 1992; Endler and Basolo 1998; Endler 2000). Information content pertains to the naturally or sexually selected message of the signal, shaped by costs and benefits to both senders and receivers. The position of the cost-benefit relationship on the continuum between conflict (exploitation) and mutualism will affect the rate and direction of signal evolution. Whilst there is a suite of selective contexts outside of sexual selection that can drive the evolution of plumage signals, such as social signalling, parent-offspring communication, and predator avoidance via e.g. crypsis or warning signalling (Bortolotti et al. 2006), discussion of sexual selection will dominate throughout, as sexually selected signals are the focus of this thesis.

Sexual signalling

Darwin (1871) identified two different (though not always independent; Berglund et al. 1996; Borgia 2006) mechanisms by which sexual selection can drive signal exaggeration, often referred to as intersexual selection (i.e. mate choice), and intrasexual selection (i.e. contest competition). Although these terms are still commonly used, it has been argued that they are not ideal nomenclature, as both types ultimately entail members of one sex (usually males) competing with each other over matings with the other sex, and thus both constitute intra-sexual selection (Andersson and Iwasa 1996). This point is even implicit in Darwin's writings (1871, p. 398), where he says "The sexual struggle is of two kinds; in the one it is between individuals of the same sex, generally the males… whilst in the other, the struggle is likewise between the individuals of the same sex…".

With regard to sexual signals and communication, however, the distinction between intra- and inter-sexual *signals* is more robust, as it refers to the signalling as such, and not the selection acting on senders or receivers. Furthermore, there are role-reversed systems in which males are the choosy sex (Edward and Chapman 2011), and females carry

sexually selected signals (LeBas et al. 2003; LeBas 2006; Clutton-Brock 2009). However, such signals are clearly under investigated in the bird literature (see e.g. Amundsen 2000a; Amundsen 2000b; Amundsen and Pärn 2006). Whilst acknowledging this, the vast majority of avian taxa involve males competing for mating opportunities with females, and therefore this perspective will dominate my discussion here forth.

In birds, intersexual signals have been extensively studied, not least in regards to their diverse and extravagant colouration (Hill 2006), with multiple potential benefits for females to assess male signals (Griffith and Pryke 2006). Receiving less, but still considerable attention has been the role of avian colouration in intrasexual signalling of dominance and aggression (e.g., Peek 1972; Smith 1972; Senar 2006), with the benefits to both senders and receivers of being able to signal and assess competitive ability being intuitive. Establishing signal function is a prerequisite for exploring models of signal evolution, which is the focus of this thesis; the specific nature of the information content behind signals is not, and therefore will not be reviewed here.

Sexual signal evolution
What came first, the chicken or the egg? Essentially the same question can be asked of animal signals; what came first, the signal trait or the receiver response? Whilst a definitive answer has been formulated for the former (Sorensen 1992), a rich array of theories continues to be debated in regards to sexual signals. Models for explaining the evolution of sexual signals often focus on the coevolution of traits and preferences, which is likely often correct in the context of explaining signals in their current observable form. Indeed, Prum (2010) even suggests the Lande-Kirkpatrick model (Lande 1980; Lande 1981; Kirkpatrick 1982) of a preference coevolving with an arbitrary attractive trait (based on Fisherian runaway processes, Fisher 1930) as the appropriate null model for intersexual signal evolution. However, there still must have been either a sender or receiver precursor of the observable signal trait or preference, respectively, to initiate the process of coevolution (Bradbury and Vehrencamp 2011).

Various alternative models for sexual signal coevolution have been proposed which are applicable to both inter- and intra-sexual signals. Indicator models of sexual selection, such as the well tested and supported

handicap (Zahavi 1975; Zahavi 1987), parasite (Hamilton and Zuk 1982), and (subsequently synthesized) immunocompetence handicap (Folstad and Karter 1992) hypotheses, entail the signal containing some 'honest' information content of sender quality, and thus benefiting receivers by allowing assessment of the quality or ability of the sender.

Contrary to the classical (sender-precursor) sexual selection models above, which generally emphasize information content of signals (Endler and Basolo 1998), 'receiver-precursor' or 'perceptual bias' models (Bradbury and Vehrencamp 2011; Ryan and Cummings 2013), which have received less attention but also garnered empirical support, entail a signal evolving to exploit a pre-existing sensory or cognitive bias in the receiver. These models do not require signals to convey any 'honest' information, but rather emphasize selection of signal efficacy.

Although all of these different models are not incompatible, and could operate simultaneously or sequentially (Andersson 1994; Kokko et al. 2002; Garcia and Ramirez 2005), the possibility that receiver biases could not only initiate (Arnqvist 2006), but also exaggerate signals without co-evolutionary processes appears to have been somewhat neglected (but see Jansson and Enquist 2003; Jansson and Enquist 2005). In the case of generalization (see below), a generalized receiver bias could be regarded as an alternative to coevolution as a driver of signal elaboration. This scenario could be envisaged as a receiver initially having a preference for (or an aversion to) the most extreme expression of a trait available in the population, and generalized beyond, thus responding even stronger to 'supernormal' stimuli.

The outcome of this would be selection on the sender trait to become more exaggerated, but the receiver preference would remain unchanged, as long as assessment costs do not increase. Alternatively, the shape and magnitude of a "peak shift" bias (peak responses occurring outside the variation range the receiver is exposed to – see below) could remain the same relative to the signal distribution, but change in position on the dimension as the signal distribution evolves along that dimension. The mechanisms of generalization will be further explained below.

The origin of a receiver bias is a quite distinct consideration. Various possibilities have been theorized, including either the bias being adaptive in another context (e.g. "sensory traps", Endler and Basolo 1998), or being an arbitrary or 'hidden' product of neural networks (Arak and Enquist 1993). The salient point is that receiver biases have been overly

4

considered, at least in ethology, solely in the context of phenomena that *initiate* the process of signal coevolution, and too little concerned with the subsequent signal evolution and especially if and how the bias itself evolves. The impression is rather that sender-receiver coevolution is assumed as a mandatory process driving signal evolution. To this point, it is interesting that the concept of generalization (see below), which has been extensively developed and empirically demonstrated, has not been more thoroughly considered by ethologists for its application to the evolution of sexual signals, despite the under-appreciated significance of receiver psychology being emphasized long ago (Guilford and Dawkins 1991; Guilford and Dawkins 1993).

Receiver-precursor models of signal evolution
The way in which receiver-precursor (pre-existing bias) models have been regarded by ethologists may be exemplified by Bradbury and Vehrencamp (2011): "Sensory biases and responses arise first as a result of natural selection for noncommunicatory functions, and the detection-response system of receivers is subsequently co-opted by senders that evolve matching traits". This may indeed be true in many cases (Ryan 1990; Ryan and Rand 1990; Christy 1995; Ryan 1998; Fuller et al. 2005; Arnqvist 2006), but sensory biases can also arise or exert influence secondarily for existing signals (Ghirlanda and Enquist 2003; see "Generalization" section below). Moreover, Fuller (2009) found little evidence from models that the design of mating preferences should be influenced by adaptive foraging preferences. Whilst authors commonly include implicit or explicit assertions that the sensory biases must have an adaptive origin (e.g. Christy and Backwell 1995; Grether et al. 1999; Grether 2000; Christy et al. 2003; Grether et al. 2005; Kim et al. 2007), others have argued that an adaptive origin for a sensory bias is not requisite, and that 'latent' biases can arise as arbitrary by-products of (even quite simple) nervous systems, as suggested by artificial neural network models (Arak and Enquist 1993; Enquist and Arak 1993; Enquist and Arak 1994), or from other aspects of receiver psychology (Guilford and Dawkins 1991; Guilford and Dawkins 1993; Rowe 1999; Ghirlanda and Enquist 2003; Rowe and Skelhorn 2004; Rowe 2013). The subsequent progression suggested from this starting point is ensuing rounds of coevolution, either through ritualization if there are receiver benefits, antagonistic coevolution (between sensory

exploitation and receiver resistance), or decoupling of the bias and trait and subsequent dissolution of the signal (e.g. Bradbury and Vehrencamp 2011). However, I suggest an alternative scenario has been under-considered.

An arbitrary receiver bias could initially lead to sender benefits through sensory exploitation. However, although receiver biases may initially be arbitrary and beneficial only to the sender, if the trait subsequently acquired enough information content (e.g. production costs from trait exaggeration) that rendered the assessment of it selectively beneficial (or at least neutral) to the receiver, then the trait may continue to evolve along the signal dimension subject to the receiver bias, whilst the receiver bias need not to change. Although this scenario likely requires the signal to have or quickly acquire sufficient information content (so as receivers are not exploited), it does not necessarily require a change in the receiver preference, and thus is not strictly coevolution; the likelihood of receiver preferences remaining static has been a subject of debate (e.g., Basolo and Endler 1995).

Whilst there are examples of 'hidden' sensory biases, in which arbitrary novel traits elicit consistently altered responses (e.g. Johnson et al. 1993; Burley and Symanski 1998), these provide only weak evidence for the importance of receiver biases driving signal evolution if the traits have not evolved in the taxa or their relatives (Arnqvist 2006). More convincing hypotheses of signal evolution via pre-existing receiver biases must be derived from trait reconstructions based on phylogenies; the prediction being that outgroup taxa (lineages diverged before the appearance of the signal trait) display the receiver bias without the trait, but that terminal taxa display both. Such hypotheses can be hard to test (Shaw 1995; Martins 2000), namely due to the work of developing both a robust phylogeny and ancestral character state reconstruction. Examples include tungara frogs (Ryan et al. 1990; Ryan and Rand 1993), and swordtails of *Xiphophorus* fish (Basolo 1990; Basolo 1995a; Basolo 1995b; Basolo 1996); the latter sensory bias may be for overall length (Rosenthal and Evans 1998), but has selected for the trait nonetheless.

The genus *Euplectes* now represents a system in which these criteria have been met, providing the opportunity to investigate the potential role of pre-existing receiver biases in driving signal evolution. As generalization is an important, but perhaps under appreciated phenomenon that explores alternative (to the sensory exploitation of

adaptive preferences) and more mechanistic explanations of responses to exaggerated stimuli, it will be discussed further below.

Generalization

If a receiver response is triggered by a specific stimulus, similar stimuli will also often elicit a response. Whilst more modified stimuli will usually be less effective at doing so, they are sometimes even more effective than familiar stimuli. The latter underpins the concept of 'generalization' (Ghirlanda and Enquist 2003), and has been termed either 'supernormal stimulation' in ethology (Tinbergen 1951), 'peak shift' in psychology (Mackintosh 1974), or recently often 'response bias' (Enquist and Arak 1998), 'receiver bias' (Jansson and Enquist 2003), or 'perceptual bias' (Ryan and Cummings 2013). Whilst ethologists have emphasized adaptive questions about receiver biases and their origins (see previous section), generalization studies typically explore the phenomenon from a more mechanistic perspective.

Studies of generalization examine receiver responses along multiple positions of a stimulus dimension, describing the shape of the response gradient. The term "peak shift" comes from studies in experimental psychology in which animals are conditioned to a positive and a negative stimulus along a given dimension, and showed subsequent peak responses for stimuli more extreme than the positive stimulus (in the direction away from the negative stimulus), and vice versa (Stevenson 1966; Wills and Mackintosh 1998). For these peaked response gradients, responses decrease again as stimuli move ever further away from the positive stimulus on which the animal was trained (Hanson 1959). The distance of the response peak (to exaggerated stimuli) from the initial positive stimulus is typically related to the distance between the initial positive and negative training stimuli; the closer they are, the further away the peak responding is (or the larger the 'peak shift' is) (e.g., Ohinata 1979; Cheng et al. 1997; see Ghirlanda and Enquist 2003). Alternatively, 'monotonic' (or 'open-ended') response gradients have also been observed, in which response magnitude continues to increase as the stimuli move further along the dimension (e.g., Huff et al. 1975; Baerends et al. 1982; Ghirlanda 2002).

Stimulus dimensions can be classified as 'rearrangement' or 'intensity' dimensions. For example, variation in monochromatic light

wavelengths (a stimuli dimension used in many studies; see Ghirlanda and Enquist 2003) can be classified as a rearrangement dimension, that is, in many species total receptor activation is approximately constant over considerable wavelength ranges (Ghirlanda and Enquist 2003); however, differences in receptor cone sensitivities could add an intensity component for complex light. Conversely, sound amplitude of a given frequency is an example of an intensity dimension. Size dimensions are a trickier case, which may often contain changes in both arrangement and intensity, though generalization responses to size dimensions tend to be similar to those for intensity dimensions (Ghirlanda and Enquist 2003).

Although the study of learned responses has dominated in generalization literature from experimental psychology, as is the tradition of that field, it is important to point out that both genetically inherited and individually learned responses generalize to novel stimuli (Ghirlanda and Enquist 2003). Ethologists have tended to separate the study of innate and learned responses, and assigned them the separate terms 'supernormal stimulation', and 'peak shift'. Furthermore, it has been claimed that innate behaviours result in monotonic generalization gradients, while learned behaviours do not (Baerends and Kruijt 1973; Hogan et al. 1975; Lorenz 1981). However, a review of the literature does not support this distinction (Ghirlanda and Enquist 2003), and moreover, most responses (like behaviours in general) are likely produced through both innate and learned components.

The literature on generalization just discussed is relevant to the study of sexual signals in *Euplectes,* within which the phenomenon has already been demonstrated for one signal, the elongated tails. In four widowbird species, females prefer males with longer tails (Andersson 1982; Andersson 1992; Pryke and Andersson 2002; Pryke and Andersson 2005), which in two experimental studies included supernormally long tails (Andersson 1982; Pryke and Andersson 2002), indicating a receiver bias and potential generalization gradient for a tail length signal. Secondly, males from two species of widowbirds show increased aversion to congeners with both naturally and experimentally (though within the natural variation) larger or longer wavelength colour signals (Pryke et al. 2001; Pryke et al. 2002; Pryke and Andersson 2003a; Pryke and Andersson 2003c), and since light wavelength dimensions are common examples of generalization in other studies, changes in colour signal

wavelength in *Euplectes* is a prime candidate to display receiver biases for supernormal stimuli.

Lastly, a problem that has already been implicitly indicated above, may exist around terminology and the conceptualization of terms. Novelty (an often used term) implies a completely unique trait, yet it is often subjective whether to consider various traits as discretely different (e.g. yellow vs red), or as two traits at different positions within the variation of a continuous variable (e.g. shorter vs longer wavelength colour hue); a distinction between identifying an objective stimulus gradient, or a more subjective classification of "similarity" (Ghirlanda 2002). The difference in this classification has important ramifications for thinking regarding receiver psychology. For example, a "receiver bias" for a "supernormal stimulus" may not seem so arbitrary or obscure if receiver generalization is occurring. Conversely, an experimental signal that may be deemed 'similar' to a researcher may vary in various other dimensions important to the animal, which could explain differences in responses, or lack thereof. If receivers discriminate sender traits directionally based on variation within a stimulus dimension, like light wavelength or sound intensity, and that receiver generalization gradient peaks outside of the natural range of variation, it is perhaps not so bizarre to find preferences for "novel" stimuli, even for complex (multi-dimensional) traits like colours, or to not find them due to confounding effects of chroma or brightness dimensions, for example. In the end, this comes down to the validity of the models of the "object spaces" (Ghirlanda 2002).

Signal honesty and intrasexual signals
Whilst both inter- and intra-sexual signals can function to signal (or be "indicies" of; Maynard Smith and Harper 2003) individual quality (Andersson 1994; Berglund et al. 1996), mate choice signals do not necessarily need to be condition dependent (e.g., runaway processes, see above). Agonistic signals, on the other hand, should be expected to contain honest information content of condition or fighting ability, either directly via the cost to produce or to bear, or via socially mediated costs that make cheating unprofitable (e.g. 'badges of status', Pärt and Qvarnström 1997; Senar and Camerino 1998); receivers should otherwise evolve resistance to exploitative signals (Seyfarth et al. 2010). For avian plumage colour signals, honest information about fighting ability is the most common

strategic content (Senar 2006), and plumage signalling of both status and fighting ability has been shown to be ubiquitous across multiple species with different plumage types (Santos et al. 2011). Additionally, despite plumage signals being semi-static (reflecting condition at time of production and not subsequently changing), they have been shown to reflect current condition (e.g. red-winged blackbirds, Merrill et al. 2015). Therefore, despite little research into the honesty-regulating mechanisms of agonistic signals in *Euplectes* (or other taxa), it is reasonable to assume that some such mechanisms are present.

Euplectes: widowbirds and bishops

The 17 species of African widowbirds and bishops in the genus *Euplectes* are small (~13-45 g) passerine birds in the weaver subfamily Ploceinae (Sibley and Ahlquist 1990) or alternatively family Ploceidae (Fry and Keith 2004). The genus seems to have radiated from gregarious seed-eaters at least as recently as within the Pleistocene (Crook 1964; Craig 1980), and similarities in general ecology and behaviour across species (Emlen 1957; Craig 1980), and hybridization in captivity (Gray 1958; Colahan and Craig 1981), suggest recent speciation. They are distributed across sub-Saharan Africa in habitat varying from reed beds to moist open grassland and savanna (Hall and Moreau 1970; Fry and Keith 2004), and primarily feed on grass seeds, but opportunistically also on nectar and insects (Fry and Keith 2004; Craig 2014). The entire genus is polygynous, and with the exception of the lekking Jackson's widowbird (E. jacksoni; (Andersson 1989)), males practice resource-defense polygyny with varying degrees of nest building but no incubation or offspring provisioning (Craig 1980). All species show dramatic sexual and seasonal dimorphism. Females and nonbreeding males are sparrow brown across all species. At the onset of the breeding season, adult males moult into jet-black nuptial body plumage, with contrasting yellow to red carotenoid pigmented, or in 3 of >33 subspecies (Prager et al. 2008) white or melanin-brown, plumage patches which vary greatly in extent and location. During this moult, widowbird, but not bishop, males replace their rectrices, growing black tails that are elongated to a variable extent across species (7-50 cm) (Andersson and Andersson 1994).

The diverse variation in sexual signal design of *Euplectes* has inspired classic studies on mating systems and sexual selection (Lack

1935; Emlen 1957; Crook 1964; Lack 1968; Andersson 1982). Elongated nuptial tails function as female choice signals in four widowbird species (Andersson 1982; Andersson 1992; Pryke and Andersson 2002; Pryke and Andersson 2005), and female discrimination of tail length was also detected in the short-tailed red bishop *E. orix* (Pryke and Andersson 2008). Conversely, no indications of female choice for tail length were found in another widowbird species (*E. macrourus*), and it was instead suggested to have an agonistic function (Savalli 1994a; Savalli 1994c). Based on studies in two widowbird species (Pryke et al. 2001; Pryke et al. 2002; Pryke and Andersson 2003a; Pryke and Andersson 2003c), red coloured plumage patches were shown to function as agonistic signals, however mixed evidence was found for agonistic function of colour signals in red bishops (Edler and Friedl 2010b). The function of colour signals in yellow *Euplectes* species remains untested, except that size of yellow epaulets did not correlate with female settlement in *E. macrourus* (Savalli 1994a).

A robust subspecies-level phylogeny (Prager et al. 2008) and ancestral character state reconstruction of tail elongation (Prager and Andersson 2009) and both discrete and continuous colour evolution (Prager and Andersson 2010) have been assembled for *Euplectes*; the latter suggesting several independent gains of red colouration from ancestral yellow. These studies provide a rare foundation and context enabling further investigation of phenomena that may be influencing signal evolution in *Euplectes*, such as generalized receiver biases. Interestingly, the convergent evolution of red colouration in *Euplectes* parallels findings from another system in which phylogenetic and ancestral character state reconstructions have been done, namely the New World blackbirds (Friedman et al. 2011), further motivating investigation for receiver biases by suggesting they may be widespread, at least among avian clades. This thesis will focus on three *Euplectes* species which represent signal types or lineages with unclear or untested colour signal functions, and which are the most interesting for exploring putative receiver biases: montane marsh widowbird (*E. psammocromius*), yellow-crowned bishop (*E. afer afer*), and southern red bishop (*E. orix orix*). Further details on these species are provided in the methods section, and their position in the phylogeny is shown in Figure 1.
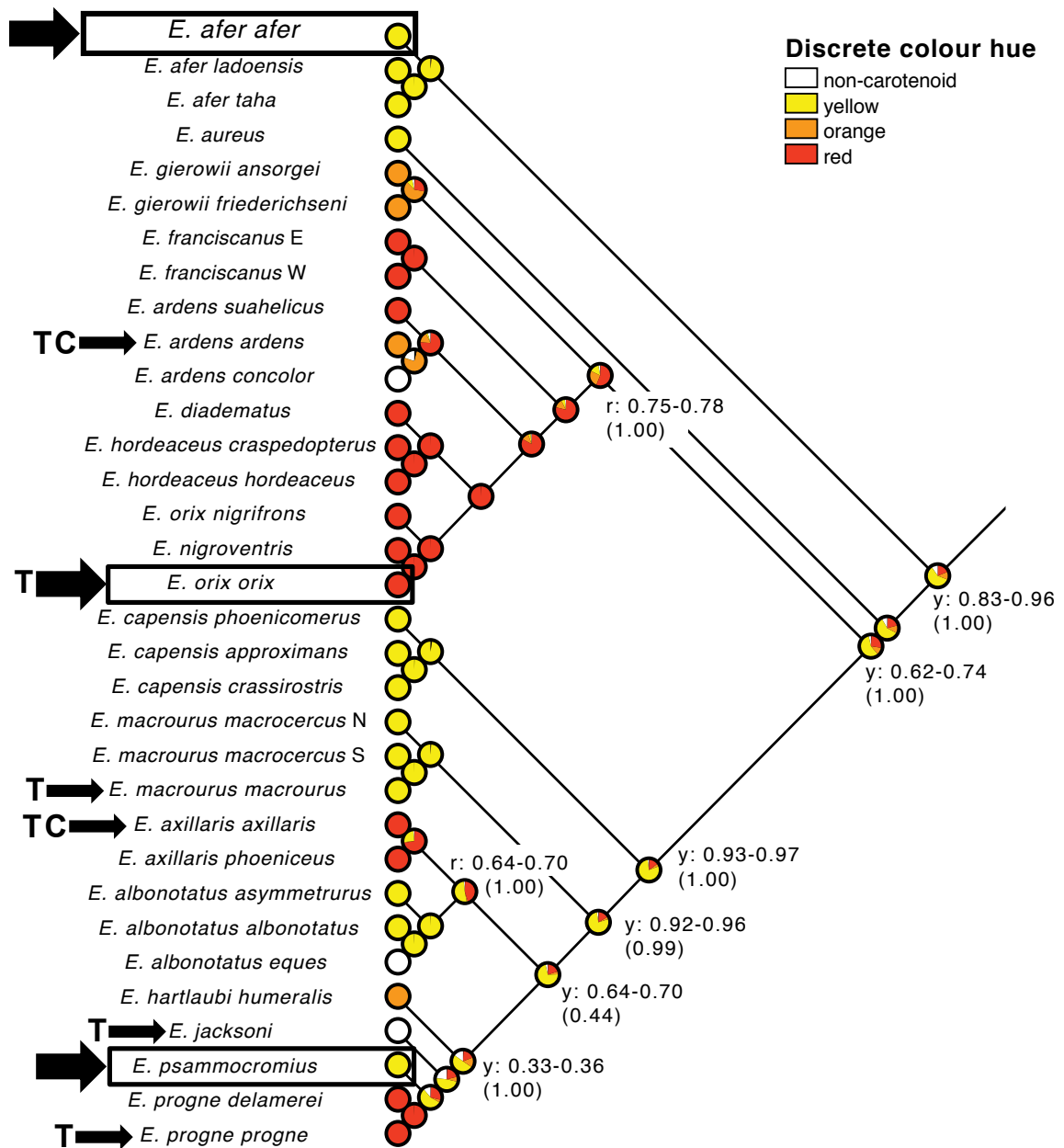
Figure 1: Phylogeny for *Euplectes* showing discrete character state reconstructions, adapted from Prager and Andersson (2010). Species studied in this thesis are indicated by black boxes and wide arrows. Thin arrows indicate species in which sexual selection of either tail length (T) or colour (C) has been previously investigated.

AIMS OF THESIS

1. To test the generality of an agonistic signalling function of carotenoid colour plumage in contexts that remain untested in *Euplectes*. Specifically, I experimentally test if plumage colour displays affect male contest competition in two yellow-coloured species (**Papers I & II**), and in a red bishop species in which a previous study produced mixed results (**Paper III**).

2. To test for a pre-existing receiver bias for redder (longer wavelength) colour hues in *Euplectes*. In particular, I examine the effect of experimental reddening on male contest competition in a yellow species with red-pigmented sister taxa (**Paper I**), and in one that constitutes an outgroup to the rest of the genus (**Paper II**), respectively.

3. To examine whether a receiver bias for longer wavelength colour hues remains observable in the *Euplectes* species with the most exaggerated red colouration (**Paper III**).

4. To test status signalling theory regarding attenuation of receiver responses with increased exposure to a signal lacking information content (**Paper IV**).

METHODS

In this section, the intention is not to repeat all of the methodological details that are contained within the papers. Instead, I provide a summarized version with additional details that typically do not make it in to final manuscripts.

Study species

The following are more specific descriptions and details for the species studied in this thesis.

*Montane marsh widowbird, E. psammocromius (**Paper I**)*

The montane marsh widowbird is one the least studied *Euplectes* species, mainly due to a very restricted distribution to areas that are not easily accessible; grasslands of the Southern highlands of Tanzania, and the Nyika plateau of Malawi. They are one of the larger *Euplectes* species, with adult breeding males weighing on average 40.5 g (range 34-45.5 g), and with an average tarsus length of 32.1 mm (range 30.2-33.4 mm). Breeding males have a nuptial plumage typical of widowbirds, with all feathers being jet-black except for the lesser and medium wing coverts, which in this species are yellow and 'buff', respectively; this species is also sometimes called the 'buff-shouldered widowbird'. Breeding males have highly elongated and graduated tails, with an average tail length of 281 mm (range 237-325 mm). Like all widowbirds and bishops, they roost communally in reed-vegetated marshes, in this case in the streams along the valley bottoms. In the shorter grass on the valley slopes, males defend territories to which they attempt to attract females to nest. The preferred habitat for territories appears to be the water-laden, tussocky grassland on the lower slopes, presumably because this is the preferred nesting grass for the females (pers. obs.).

Territorial males exhibit a range of sexual behaviours (pers. obs.), the most common of which are: 1) Display flights in which they slowly fly short distances within their territories with their tail plumes fanned horizontally, presumably an advertisement to females. 2) Chasing any intruding males until they have vacated the territory. 3) Territorial boundary contests with neighbours, which involves posturing with rapid

wing flicks with the yellow (and buff) epaulets exposed (see **Paper I** methods). 4) A behaviour I have named "upright cricket call" depicts a perched male that adopts a straight upright posture, erects the feathers around the head and neck region, and scans his head from side to side while vocalizing rapidly (a sound akin to a cricket), sometimes culminating with wings extended and colour epaulets exposed; it is yet unclear who the target receivers are. 5) In the event that a female or females investigates and allows a male to approach, the male typically performs a 'courtship dance'. This is a highly stereotyped behaviour, in which the male perches within ~30 cm of the female, with head, neck, and epaulet plumes erected, bobs and weaves his head from side to side with a raspy vocalization, and gradually (almost hypnotically) edges closer to the female. Females often fly away during this display, but when a female remains and allows a full approach, both birds typically disappear into the long grass (presumably for copulation, but impossible to see). Although not all these behaviours are presented in this thesis, they suggest a large scope for future behavioural studies in this species, and that both the striking tail and plumage signals are likely coupled with various specific display behaviours, potentially also including vocalizations.

*Yellow-crowned bishop, Euplectes afer afer (**Papers II & IV**)*

There are three subspecies of yellow-crowned bishops (Prager et al. 2008), which have different geographic distributions, but together span most regions of sub-Saharan Africa, except the central lowland rainforests and the deserts in the southwest (Fry and Keith 2004). In addition, invasive populations have established in parts of North and Central America, Japan, and Southern Europe; the birds used in this thesis were

caught from an invasive population in Southern Spain. Male *E. afer* are small (15.5–19.2g; **Paper II**), with nuptial plumage showing the forehead, crown, nape, back and rump bright yellow from dietary carotenoid pigments (Prager et al. 2009), and the remaining body feathers jet-black. However, unlike widowbirds, they retain their brown primaries and retrices from their non-breeding plumage. Males vigorously defend breeding territories in shrub/grassland vegetation, from which they typically display with their yellow crown feathers erected, attempting to repel rival males and attract females to nest (Craig 1980). There are no previous studies of *E. afer* in the context of sexual selection.

*Southern red bishop, Euplectes orix orix (**Paper III**)*

These small-medium sized bishops (males are 24-30 g; **Paper III**) live in flocks in open grassland and cultivations in eastern and southern Africa. Males' nuptial plumage shows a black forecrown, face, and belly, and a bright orange-red hindcrown, nape, breast and rump (wings and tail remain brown). They breed near water, preferentially in reeds (*Phragmites sp.*) or bulrushes (*Typha*) lining dams or rivers, where males compete to establish small territories that are aggressively defended against intruders by 'supplant chases' and 'threatening matches' at the territory boundaries (Craig 1980). In the latter, the males silently hop and posture before each other, with the bill pointed at the opponent, and the red neck, crown and throat plumage raised to form a striking scarlet-red collar surrounding the black face and bill. They are one of the more well-studied *Euplectes* species, with several studies examining their breeding biology. Male reproductive success is predicted by the number of nests a male builds in his territory, which is related to territory tenure (Friedl and

Klump 1999), but not directly to the colour signal (Edler and Friedl 2011). A female preference for longer tails has been found, even though *E. orix* has a short tail that is not nuptially moulted (Pryke and Andersson 2008). Age has been found to correlate with some plumage characteristics (Edler and Friedl 2012), and age to correlated with dominance, and colour hue, although differently so in different experiments (Edler and Friedl 2010b) . Plumage characteristics were also found to be related to indices of health (Edler and Friedl 2010a).

Study areas and general field methods

The study site for **Paper I** was in the Mtitu valley, in the Southern highlands of Tanzania. This was a remote location, which was accessed first by a ~2.5 hour drive from Iringa on unsealed roads, then a subsequent ~30min drive over grass, through a small settlement and down into the valley, where a camp would be set up. As there were no facilities on site, we would conduct field trips of two weeks duration, interspersed by overnight returns to Iringa to re-supply. During field trips, catching (using mist nets) at the roost site would be conducted on every morning that weather conditions permitted, with males brought back to camp (~100 m away) to collect morphometric and colorimetric measurements of the population. Following this, we attempted to catch territorial males at their territories by using spring-loaded snap-traps with a model intruder placed atop of it. Latency to physical attack of the model (and thus capture) was variable, with typical capture rates being one-two males per day. Usually males would first attempt threat displays, progressing to lunges before physical attack; a minority of males never escalated to physically attacking the model, to which capture attempts were abandoned after two days. Captured males were immediately taken to camp where morphometric and colorimetric measurements were taken, and manipulations applied. A small generator was used to power the computer, spectrometer, and light source.

The study site for **Papers II & IV** were outdoor aviaries located a ~20 min drive outside of Sanlucar la Mayor (west of Sevilla), Spain, and was easily accessible. There were full facilities on site. Figure 2 shows the aviary facilities.

Figure 2: Three-tiered aviary set up. The dotted box shows one experimental cage, with arrows indicating where dividers can be placed.

The study sites for **Paper III** were located on the Western outskirts of Port Elizabeth, South Africa, and were easily accessible. As there were no facilities on site, a car battery was used to power the spectrometer and light source, and was recharged every night. Because these breeding sites were also roosting sites, mist nets could be erected at dawn and catching would proceed all day (as weather allowed), although was usually most productive just after dawn when most birds left to feed and the nets were least visible. Catching rates would vary depending on conditions, with between 0-19 *E. orix* males being caught and processed per day. Males were processed on site as they were caught, with morphometric and colorimetric measurements recorded, and manipulations applied. After an adequate sample size was achieved, and before the breeding season progressed too far, catching was stopped and 15 days allowed to pass before surveys began.

Aviary experiments

Full details of the aviary experiments are provided in **Paper II**. However, an additional illustration is provided below (Figure 3) to help conceptualize the experimental setup. Briefly, each of two males (one control and one red-manipulated) was placed in either end of a three-chambered cage on the evening prior to trials commencing; the side that each treatment was on alternated across trials. Each male was provided with water, but not food, to ensure motivation to feed during dyadic contests the subsequent morning. The opaque dividers were removed at least 10 mins before the trial began, to allow males visual contact with each other and the feeder. The transparent (wire) dividers were then removed, and the ensuing 10 min dyadic contest was video recorded for subsequent analysis.
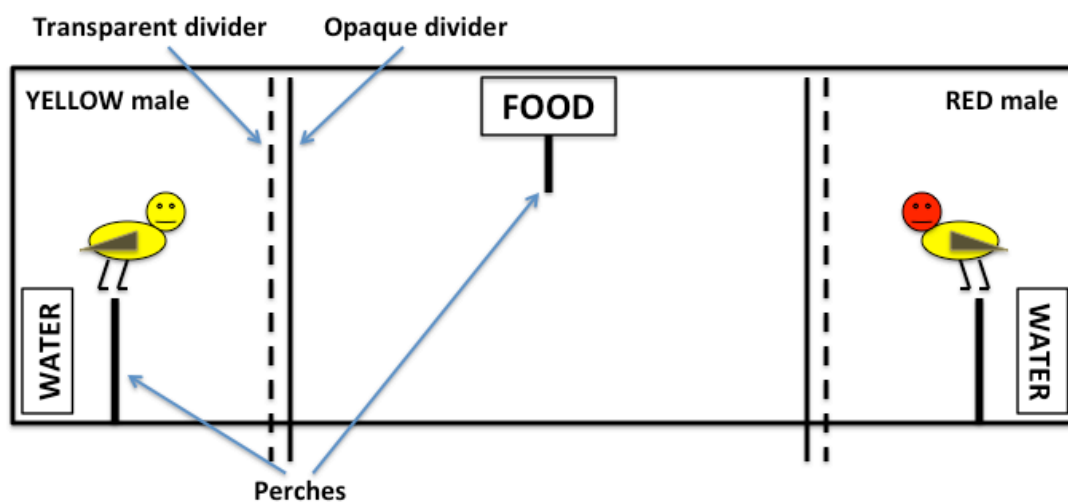

Figure 3: Illustration showing the aviary setup of dyadic contests.

Colour manipulations

Manipulations were done using Copic art markers (Too Marker Products, Tokyo, Japan). Before each experiment, a range of different marker colours were tested on specimens at the University of Gothenburg, and spectral reflectance of the test manipulations was assessed to guide selection of the marker type that best achieved the desired spectral reflectance. The final markers used were the following: For *E. psammocromius* (**Paper I**), R08 was used for the red treatments as it closely matched the reflectance of the red patch in the sister species *E. progne*, Y13 (yellow) was used for control

treatments as it was a 'lighter' yellow that did not significantly alter natural reflectance, yet had the same physical effect on the plumage (see below), and black100 was used to remove the signal.

For *E. afer* (**Papers II & IV**), R29 was used for red treatments as it produced spectra similar to red bishop species, Y13 was used for yellow (as above) and, in preliminary trials, G02 (green) was used to reduce the hue (λ_{R50}) without removing the signal. For *E. orix* (**Paper III**), R27 was used for red treatments as it produced the largest increase in hue (λ_{R50}) while retaining an identical spectral shape to the natural colouration, Y17 was used for controls as it did not significantly alter spectral reflectance, G02 was used to reduce the signal (all colorimetrics) while leaving patch shape distinguishable from adjacent black feathers, and black100 was used to remove the signal (the latter in a supplementary experiment). Although other studies using these markers have often used the colourless blender (Copic code 0) for control treatments, I found that coloured markers had a physical effect on plumage that was not produced by the colourless marker, and thus wanted to exclude this potentially confounding effect.

Application of the treatment involved slowly moving the marker across the relevant plumage patch, allowing time for the feathers to become saturated by the ink. For larger feathers (lesser wing coverts of *E. psammocromius* and collar feathers on *E. orix*), ink was also applied from the underside of the feathers to ensure full coverage. Figures 4 and 5 show examples of the manipulations for *E. psammocromius* (**Paper I**) and *E. afer* (**Paper II**), respectively.

Reflectance spectrometry

Throughout this thesis, methods of reflectance spectrometry used to derive the objective colorimetric measurements followed the protocols of Andersson and Prager (2006), and are described in the methods sections of each paper. However, since 'hue' (λ_{R50}) is such a central parameter in this thesis as well as previous research on *Euplectes*, an additional illustration is provided below (Figure 6). The hue or 'spectral position' measurement, λ_{R50}, is the wavelength (x-axis) at which the reflectance (y-axis) is halfway between its minimum and maximum.
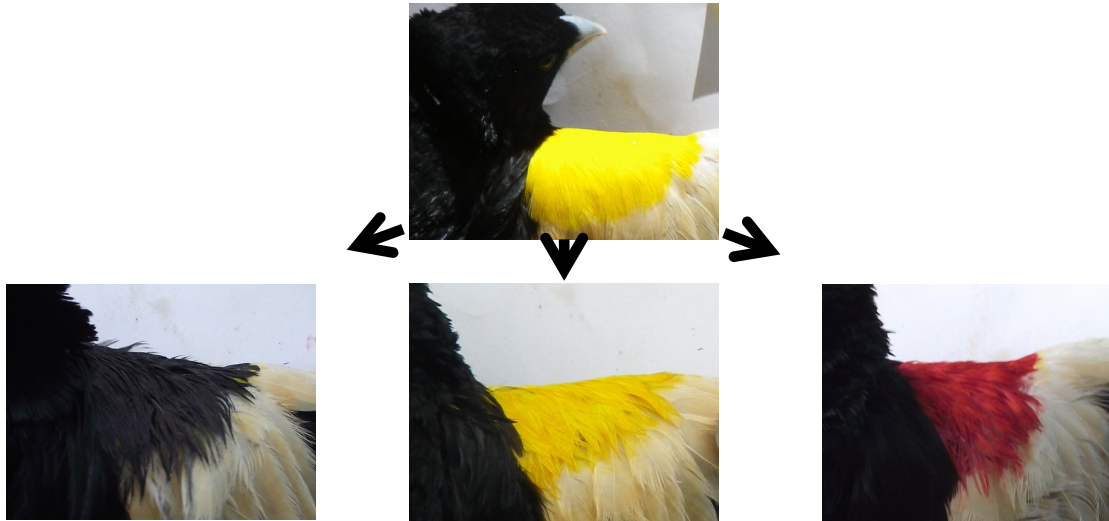
Figure 4: examples of the three colour manipulations used on *E. psammocromius* (**Paper I**). The top picture is a pre-manipulated male, and the bottom pictures are (from left to right) black, control, and red manipulations.

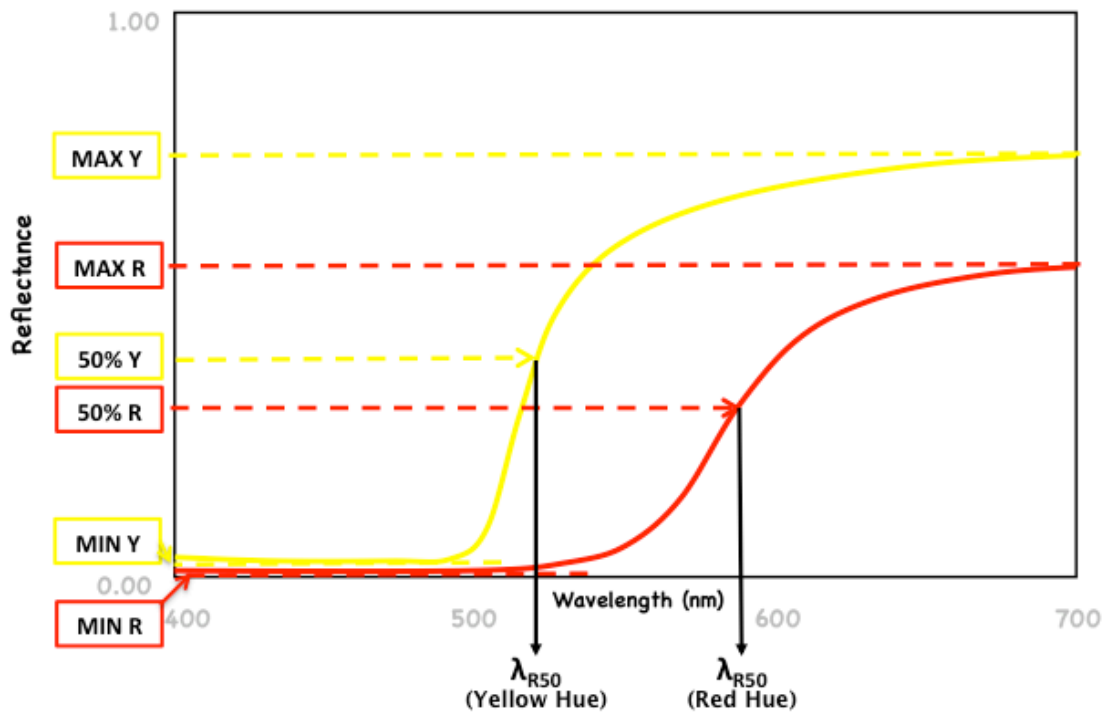Figure 5: An example of an *E. afer* male receiving a red manipulation

Figure 6: Two example reflectance curves (from yellow and red *Euplectes* plumage, respectively) illustrating the hue metric (λ_{R50}); the wavelength (on x-axis) at which reflectance (y-axis) is halfway between its minimum and maximum.

SUMMARY OF MAIN RESULTS

Paper I

Following manipulation, significant differences were found between treatments for territory retention by *E. psammocromius* males ($P < 0.02$), with 100% of red treatment males, 78% of control males, and 67% of black treatment males retaining their territories (Figure 7). Highly significant differences were found between treatments in the outcomes of boundary contests ($P = 0.001$; Figure 8). The mean percentage of wins across individuals within each treatment was: red 95.8%, control 43.4% and black 12.5%.
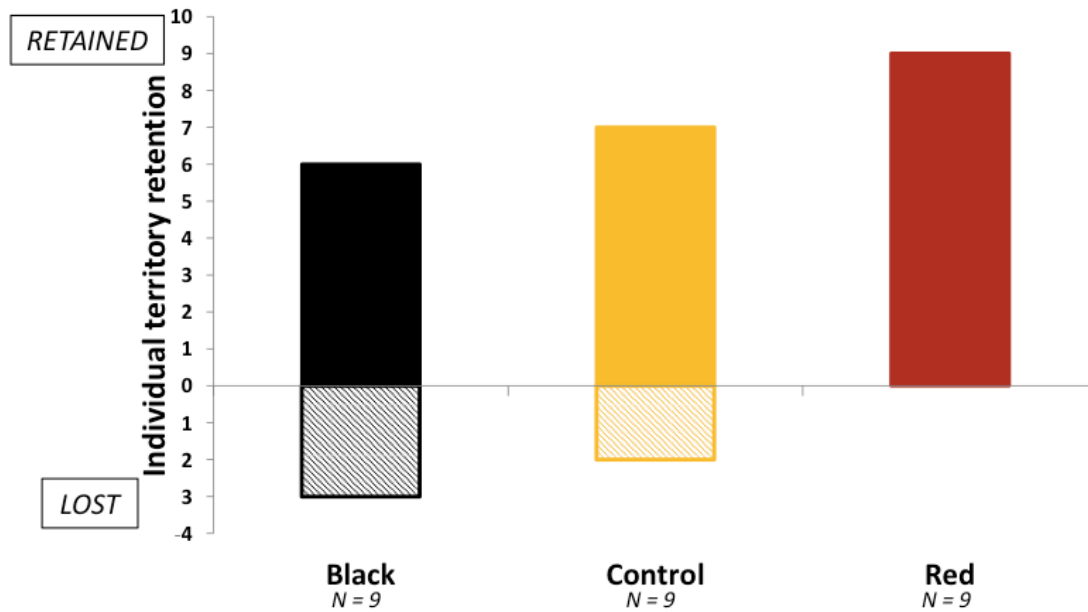
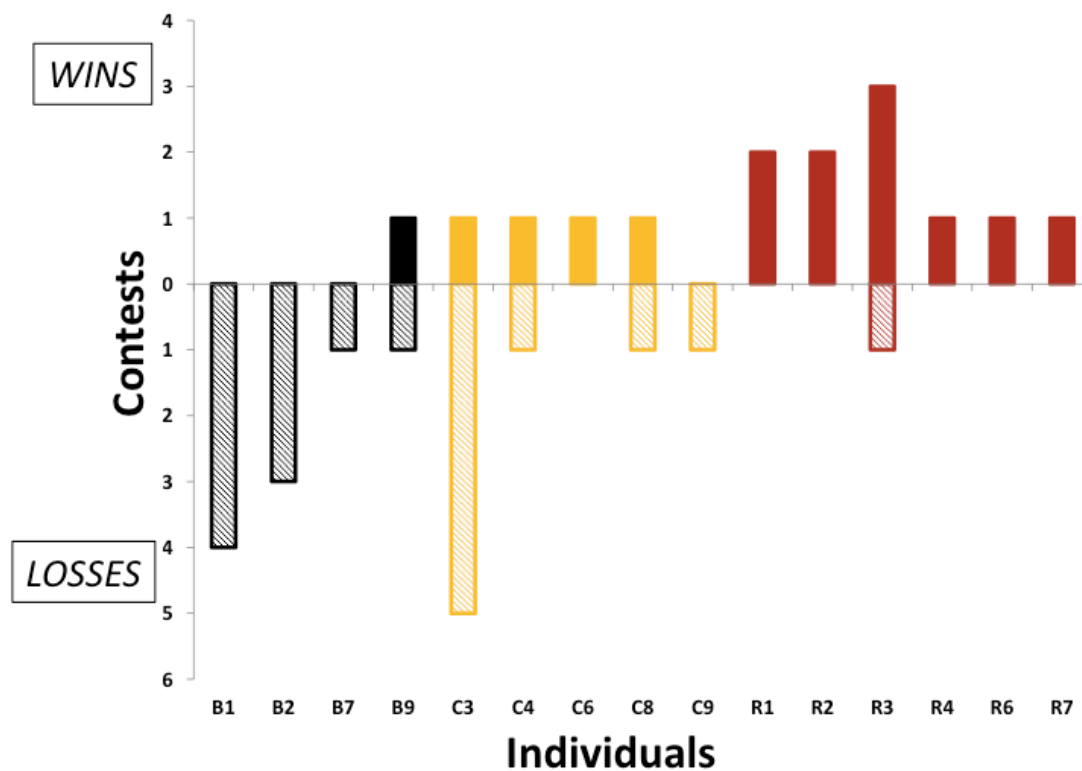Figure 7: Territory retention across treatments. (Reprint from **Paper I**).

Figure 8: Results of boundary contests for individuals from the three treatments ("B" = black, "C" = control, "R" = red). An LSD test revealed that males from the red treatment won significantly more contests than males from control ($P =$ 0.006) or black ($P < 0.001$) treatments, and control males won contests more often than black treatments ($P < 0.02$). (Reprint from **Paper I**).

23

Paper II

Colour treatment was a significant predictor of "seconds at feeder" (P = 0.005), with red-manipulated birds accessing the feeder for 304±51 s compared with 198±48 s for control birds (Figure 9). No other morphometric covariates approached significance (P = 0.31–0.93). There was no significant difference (P = 0.16) in the number of supplants performed by red-manipulated males (2.82; [1.50–5.32]) compared with control males (1.48; [0.79–2.80]; Figure 9). As above, all potential covariates were non-significant (P = 0.30–0.81).
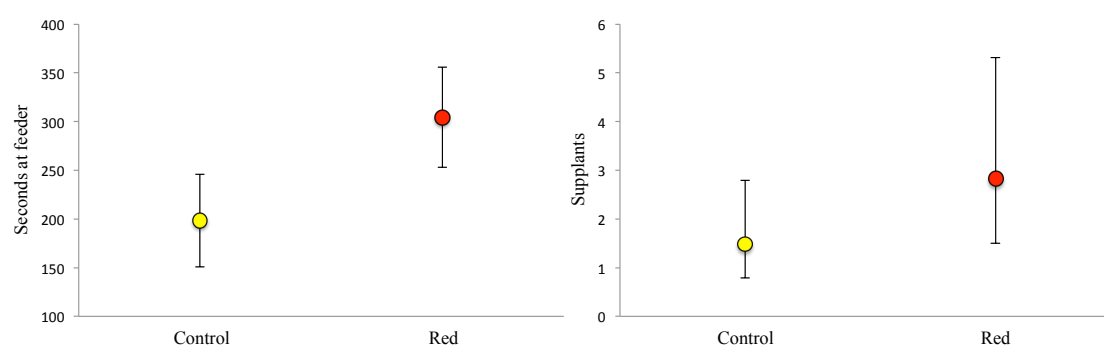

Figure 9: Estimated marginal means (± 95% CI) of seconds spent at the feeder, and of number of supplants, for control birds (yellow, left circles) and red manipulated males (red, right circles). (reprint from **Paper II**).

Paper III

There were significant differences between treatments in the proportion of male *E. o. orix* subsequently seen possessing a territory (P < 0.01); 76.2% of super-red males were recorded as territory owners at the end of the experiment, compared to 45% of control-red males, and 23.8% of green males (Figure 10). No morphometric or pre-manipulation colorimetric covariates approached statistical significance. In a supplementary experiment using only red (N = 9) and black (N = 9) manipulations, three red males, but no black males, were subsequently seen possessing territories.
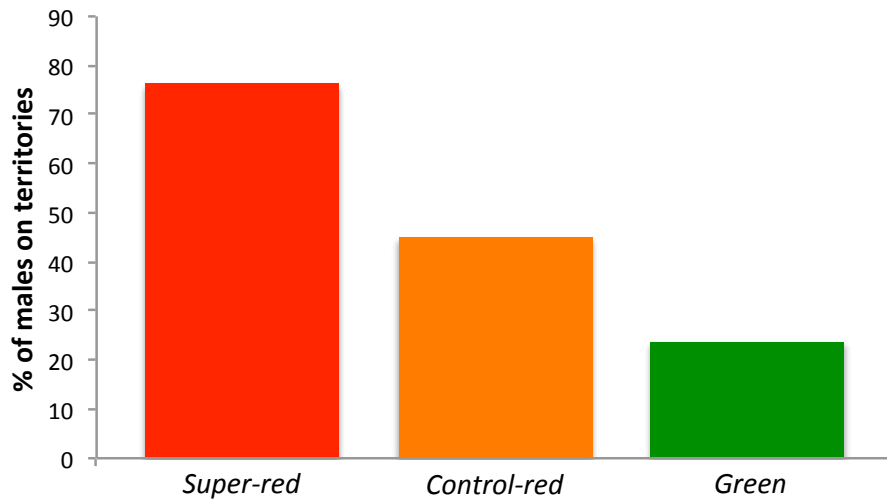
Figure 10: Percentage of males from each treatment of the main experiment (N=21 each) that subsequently possessed a territory.

Paper IV

During repeated dyadic contests between pairs of control-yellow and red-manipulated *E. a. afer* males, red males secured significantly more time at the feeder in the first trials compared to trials three-eight ($P = 0.029$; Figure 11). Differences between opponents in morphometrics or pre-manipulation hue did not approach statistical significance as covariates.
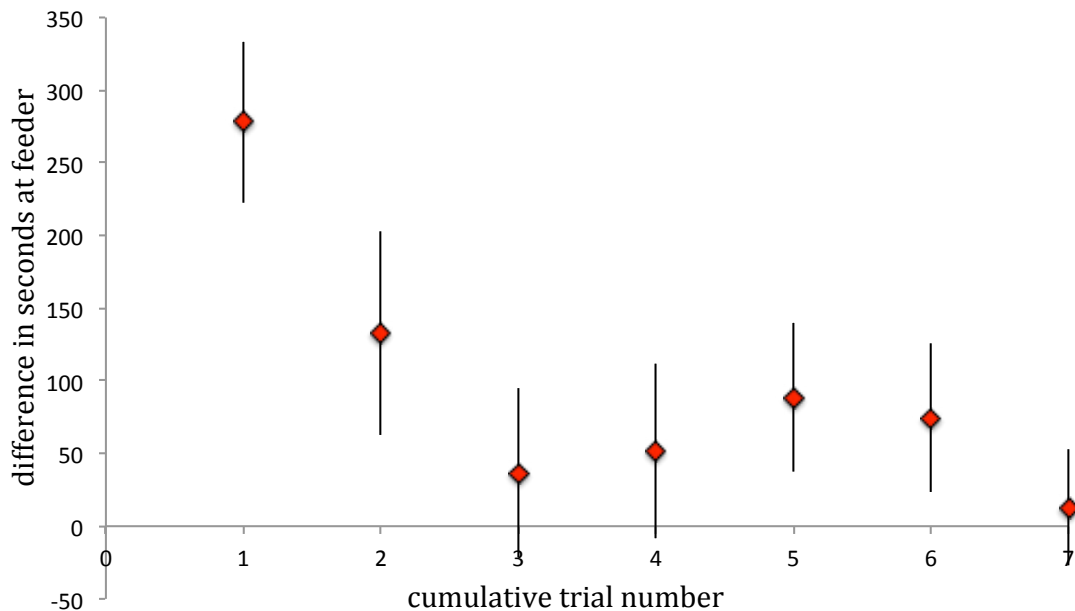

Figure 11: Mean (± 95% CI) difference in time spent at feeder (red male minus control male; i.e., positive values = advantage for the red male) within dyadic contests, plotted against the cumulative number of trials the males had experienced.

SYNTHESIS OF FINDINGS

Agonistic function of colour signals

Based on field and aviary experiments on three carefully selected *Euplectes* species, this thesis presents evidence for a previously suggested, but hitherto insufficiently tested, general agonistic function of carotenoid colour signals in this genus (17 species of widowbirds and bishops). Firstly, in a field experiment on montane marsh widowbirds (**Paper I**), representing the first test of signal function in a yellow-signalling *Euplectes* species, control males won more boundary contests and were more likely to retain their territories compared to down-manipulated males. Secondly, in five dyadic contests (over food) between captive yellow-crowned bishops (**Paper II**), control (yellow) males secured almost twice as much time at the feeder as their down-manipulated opponents, and also tended to more successfully supplant their rivals, although this difference was not statistically significant due to the small sample size. Lastly, in a field experiment with southern red bishops, control males were more likely to subsequently possess a territory than down-manipulated males (**Paper III**). These results, together with the main findings (below) that greatly 'up-manipulated' (supernormal) colour signals positively affected male contest competition in all experiments, strongly support a universal agonistic signalling function of both yellow and red carotenoid coloured plumage in the widowbirds and bishops.

These findings corroborate and extend previous research in *Euplectes*, and provide a unique foundation for further exploration of selection and evolution of sexually selected colour signals, in particular the details of receiver cognition and responses which can be quicker and more accurately tested in contest as opposed to mate choice situations. As regards the latter, however, it should be noted that this thesis does not address whether these colour signals also have other (e.g. mate choice) functions, which especially in bishops is an interesting possibility considering that they lack the elongated tails that are subject to female choice in their close relatives. However, previous studies on southern red bishops suggested that females selected males based on the number of nests they had constructed (Friedl and Klump 1999), which could be a consequence of superior competitive ability, that is to be able to successfully defend a territory AND invest heavily in nest building.

Receiver bias for longer wavelength 'supernormal' hues

Intersexual signals have traditionally received more attention than intrasexual signals in the study of sexual selection. This is most obvious in the case of receiver-precursor ('sensory bias') models of signal evolution, for which their application to intrasexual signals has been almost completely ignored (but see Stephenson and Ramírez-Bautista 2012). The genus *Euplectes*, where an ancestral character state reconstruction (Prager and Andersson 2010) suggests directional and convergent evolution of red from ancestral yellow agonistic colour signals, presents an ideal context in which to test receiver-precursor models of agonistic signal evolution. In a field experiment with montane marsh widowbirds (**Paper I**), yellow coloured males that were experimentally reddened more successfully retained their territories, and were more likely to win boundary contests with neighbouring males, compared to control yellow males. This is the first evidence of a pre-existing receiver bias for supernormal stimuli in an agonistic signal.

Because the montane marsh widowbird has relatively recently diverged from red coloured sister species, the evolutionary age of the putative pre-existing receiver bias was traced in the most ancestral (outgroup) lineage of the genus, represented by the yellow-crowned bishop (**Paper II**). Red-manipulated males outcompeted yellow control males for access to a feeder, suggesting that the receiver bias likely predates the radiation of the genus. Taken together with other findings that red is commonly associated with agonistic signals in other avian taxa (Senar 2006; Pryke 2009; Santos et al. 2011), a perceptual bias for (i.e. aversion of) red in male-male contest signals could be more generally widespread in birds.

The next question to address was to investigate what selection pressure on colour hue remains in species that have evolved red signals. Have red-signalling species 'caught-up' to a pre-existing receiver bias for 'red', or is a generalized preference still selecting for longer wavelength hues? In a further experiment, we tested whether a receiver bias for longer wavelength hues was present in a species that has evolved its signal far along the hue dimension, and displays red plumage (**Paper III**). Southern red bishop males that had their hue experimentally increased (outside the natural range of variation) were more likely to be in possession of a breeding territory than either control or down-manipulated males. This could indicate one of several scenarios: 1) a pre-existing receiver bias has,

since its origin, selected for (and still selects for) colour hues that are supernormal to the longest wavelength hues of extant species; 2) innate and/or learned generalization ('peak-shift') produces increased responding for stimuli (hues) that are supernormal to whatever the current signal (hue) distribution is for the population; or 3) some combination of the above.

In relation to the above, however, it is interesting that yellow-signalling *Euplectes* displayed increased responding to red signals, which represents a large shift on the hue dimension. This suggests: 1) a very (unusually) large generalization (peak shift) gradient, 2) a monotonic gradient, which would be uncharacteristic for this type of stimulus dimension (Ghirlanda and Enquist 2003), or 3) that another correlated dimension of colour is an additional or even principal component of the stimulus; the lack of effect of brightness and chroma metrics on receiver responses, however, argue against this.

What happens when signals have no content?

Though there has been disagreement over the relevance of both manipulation-based and information-based perspectives on the evolution of animal signals (Rendall et al. 2009; Seyfarth et al. 2010), the trivializing of either seems unhelpful, as both approaches should be seen as complimentary in evaluating both the design and maintenance of signals, respectively. While receiver biases can help explain the design of signals, theory suggests that an agonistic signal must have or acquire some information content of benefit for the receiver to assess, otherwise the receiver will evolve resistance to responding, and the signal will disappear (Seyfarth et al. 2010). This is supported by studies showing that generalization gradients change (Pierrel and Sherman 1960) and biases tend to recede with increasing test phase length (Crawford et al. 1980; Cheng et al. 1997), which may be the effect of the subjects learning that the test stimuli are not reinforced (Ghirlanda 2002; Ghirlanda and Enquist 2003). This thesis tested the importance of information content in *Euplectes* colour signal evolution by investigating whether the receiver bias for experimentally exaggerated redder colour signals in yellow-crowned bishops changed over successive trials in which control males were encouraged to challenge experimental dominants in dyadic contests over food (**Paper IV**). Effects were found to be significantly larger in initial

trials, and quickly decreased with receiver experience over successive trials. This suggests that variation in colour signal hue is likely linked to information about competitive ability in natural populations, as would be expected of an agonistic signal. Further research is needed to reveal the specific mechanisms on signal honesty.

CONCLUSIONS AND FUTURE PERSPECTIVES

The findings of this thesis corroborate the agonistic signal function of colour plumage previously demonstrated in two widowbird species in a further three *Euplectes* species, including the first evidence for an agonistic signal function of yellow colour signals. This work builds of the mounting body of research on *Euplectes* that is making it a unique study system for investigating the evolution of sexual signals. It would be interesting for future research to test the agonistic effects of variations in colour hue within the natural range of variation, especially in yellow species, which display relatively low variation. Furthermore, testing for a role of colour signals in female choice in the bishop clade would be interesting. Berglund et al. (1996) suggest that signals may often first evolve as 'armaments' (for male-male competition), and that the necessitated honesty of these signals may be co-opted as 'ornaments' (for female choice). It is possible that this has occurred in the bishop clade, and therefore could explain the absence of elongated tails. Alternatively, previous studies have indicated that females may select males based on nesting habitat and resources provided, which in turn may be (at least partially) a product of competitive ability (Friedl and Klump 1999; Friedl and Klump 2000).

This thesis reveals, for the first time, a pre-existing receiver bias for an agonistic signal, demonstrating the applicability of receiver-precursor models in explaining the evolution of intrasexual signal design. However, showing a receiver bias for a supernormal stimulus at only one location on the signal dimension does not provide much detail on the shape of the generalization (responding) curve. To this end, tests using stimuli at multiple positions along the signal dimension would be interesting, especially to see where responding decreases again. Additionally, whilst indications from *Euplectes* and other taxa (e.g., Grether et al. 2015; Sefc et al. 2015) indicate red as a very general aversive or threatening stimulus (including in humans, Attrill et al. 2008), possibly because it elicits attentional biases (Buechner et al. 2014), dissecting the importance of

innate biases versus a (perhaps additional) learned generalization remains a challenge. A combination of the manipulative and informational approaches may best help understand the origin and evolution of signal design. Furthermore, it is apparent from **Paper IV** that responses to artificially applied redder signals quickly attenuate, suggesting the signals must be reinforced with information for them to be maintained. However, whether redder signals themselves are costlier to produce or carry, or whether they function by increasing efficacy of another informational cue remains to be determined.

ACKNOWLEDGEMENTS

experiments in Spain, and subsequently back in Gothenburg – always with great enthusiasm!

Many thanks to Stacey Webb, and husband Steve, for hosting me in their house in South Africa, and to Stacey for helping with permits and permissions, and helping with fieldwork despite not feeling great.

Shout-out to all my fellow PhD students, past and present, which have provided a stimulating environment both academically and socially (as long as I didn't win poker too often ;), and have made for some happy memories! Thanks to Willow Lindsay, who has been someone with mutual interests, provided helpful feedback on manuscripts, as well as friendship, and whom I wish had arrived sooner.

Big thanks to the absolutely wonderful administrative staff, especially Ann-Sofie, Lena, Lilioth, and Bernth, who have always been helpful and happy to explain things to the dumb kiwi who hasn't mastered Swedish.

Much thanks to my awesome family, who have always been supportive of me in whatever I chose to do (whilst also wondering why I moved as far away from them as was possible – it wasn't intentional!) – much love!

Lastly but in no way leastly, lots of thanks and love to my loving partner Julie, who provides me with nothing but support, patience, happiness, love, and yes even help in the field! Also thanks and love to my Swedish family, the Sjögrens (& Jimenez/Lindblad), for welcoming me into their family.

CITED LITERATURE

Amundsen T (2000a) Female ornaments: genetically correlated or sexually
    selected. In: Epsmark Y, Amundsen T, Rosenqvist G (eds) Animal
    signals: Signalling and signal design in animal communication. Tapir
    Academic Press, Trondheim, Norway, pp 133-154

Amundsen T (2000b) Why are female birds ornamented? Trends in
    Ecology & Evolution 15:149-155

Amundsen T, Pärn H (2006) Female coloration: review of functional and
    nonfunctional hypotheses. In: Hill GE, McGraw KJ (eds) Bird
    coloration, pp 280-345

Andersson M (1980) Why are there so many threat displays? Journal of
    Theoretical Biology 86:773-781

Andersson M (1982) Female choice selects for extreme tail length in a
    widowbird. Nature 299:818-820

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

Andersson M, Iwasa Y (1996) Sexual selection. Trends in Ecology &
    Evolution 11:53-58

Andersson S (1989) Sexual selection and cues for female choice in leks of
    Jacksons widowbird Euplectes jacksoni. Behavioral Ecology and
    Sociobiology 25:403-410

Andersson S (1992) Female preference for long tails in lekking Jacksons
    widowbirds - experimental-evidence. Animal Behaviour 43:379-388

Andersson S (2000) Efficacy and content in avian colour signals. In:
    Epsmark Y, Amundsen T, Rosenqvist G (eds) Animal signals:
    signalling and signal design in animal communication. Tapir
    Academic Press, Trondheim, Norway, pp 47-60

Andersson S, Andersson M (1994) Tail Ornamentation, Size Dimorphism
    and Wing Length in the Genus Euplectes (Ploceinae). Auk 111:80-86

Andersson S, Prager M (2006) Quantifying Colors. In: Hill GE, McGraw KJ
    (eds) Bird Coloration. Harvard University Press, Cambridge (MA),
    pp 41-89

Arak A, Enquist M (1993) Hidden preferences and the evolution of signals.
    Philosophical Transactions of the Royal Society of London. Series B:
    Biological Sciences 340:207-213

Arnqvist G (2006) Sensory exploitation and sexual conflict. Philosophical
    Transactions of the Royal Society B: Biological Sciences 361:375-
    386

Attrill MJ, Gresty KA, Hill RA, Barton RA (2008) Red shirt colour is
    associated with long-term team success in English football. Journal
    of Sports Sciences 26:577-582

Baerends G, Kruijt J (1973) Stimulus selection. In: Hinde RA, Stevenson-
    Hinde J (eds) Constraints on learning. Academic Press, New York, pp
    23-50

Baerends GP, Drent RH, Hogan-Warburg AJ, Blokzijl GJ, Molen AGvd, Vos OCd, Baarda HJ, Mudde MJ, Kruijt JP, Vodegel R (1982) The herring gull and its egg: part II. The responsiveness to egg-features. Behaviour 82:I-416

Basolo AL (1990) Female preference predates the evolution of the sword in swordtail fish. Science 250:808-810

Basolo AL (1995a) A further examination of a pre-existing bias favouring a sword in the genus *Xiphophorus*. Animal Behaviour 50:365-375

Basolo AL (1995b) Phylogenetic evidence for the role of a pre-existing bias in sexual selection. Proceedings of the Royal Society of London. Series B: Biological Sciences 259:307-311

Basolo AL (1996) The phylogenetic distribution of a female preference. Systematic Biology 45:290-307

Basolo AL, Endler JA (1995) Sensory biases and the evolution of sensory systems. Trends in Ecology and Evolution 10:489-489

Berglund A, Bisazza A, Pilastro A (1996) Armaments and ornaments: an evolutionary explanation of traits of dual utility. Biological Journal of the Linnean Society 58:385-399

Borgia G (2006) Preexisting male traits are important in the evolution of elaborated male sexual display. Advances in the Study of Behavior 36:249-303

Bortolotti GR, Hill G, McGraw K (2006) Natural selection and coloration: protection, concealment, advertisement, or deception. Bird coloration 2:3-35

Bradbury JW, Vehrencamp SL (2011) Principles of animal communication, 2nd edn. Sinauer Associates, Sunderland (MA)

Buechner VL, Maier MA, Lichtenfeld S, Schwarz S (2014) Red - take a closer look. Plos One 9:e108111

Burley NT, Symanski R (1998) "A taste for the beautiful": latent aesthetic mate preferences for white crests in two species of australian grassfinches. The American Naturalist 152:792-802

Cheng K, Spetch ML, Johnston M (1997) Spatial peak shift and generalization in pigeons. Journal of Experimental Psychology: Animal Behavior Processes 23:469-481

Christy JH (1995) Mimicry, mate choice, and the sensory trap hypothesis. The American Naturalist 146:171-181

Christy JH, Backwell PRY (1995) The sensory exploitation hypothesis. Trends in Ecology & Evolution 10:417-417

Christy JH, Baum JK, Backwell PRY (2003) Attractiveness of sand hoods built by courting male fiddler crabs, *Uca musica*: test of a sensory trap hypothesis. Animal Behaviour 66:89-94

Clutton-Brock T (2009) Sexual selection in females. Animal Behaviour 77:3-11

Colahan BD, Craig A (1981) *Euplectes* hybrids. Ostrich 52:58-59

Craig AJFK (1980) Behaviour and evolution in the genus *Euplectes*. Journal
of Ornithology 121:144-161

Craig AJFK (2014) Nectar feeding by weavers (Ploceidae) and their role as
pollinators. Ostrich 85:25-30

Crawford L, Steele K, Malone J (1980) Gradient form and sequential effects
during generalization testing in extinction. Animal Learning &
Behavior 8:245-252

Crook JH (1964) The evolution of social organisation and visual
communication in the weaverbirds (Ploceinae). Behaviour
Supplements 10:1-178

Darwin C (1859) On the origin of species. Murray, London:360

Darwin C (1871) The descent of man, and selection in relation to sex. John
Murray, London

Darwin C, Wallace A (1858) On the tendency of species to form varieties;
and on the perpetuation of varieties and species by natural means of
selection. Journal of the Proceedings of the Linnean Society of
London. Zoology 3:45-62

Dawkins R, Krebs JR (1978) Animals signals: information or manipulation?
In: Krebs JR, Davies NB (eds) Behavioural ecology. Sinauer
Associates, Massachusetts, pp 282-309

Edler AU, Friedl TWP (2010a) Individual quality and carotenoid-based
plumage ornaments in male red bishops (Euplectes orix): plumage
is not all that counts. Biological Journal of the Linnean Society
99:384-397

Edler AU, Friedl TWP (2010b) Plumage colouration, age, testosterone and
dominance in male red bishops (*Euplectes orix*): a laboratory
experiment. Ethology 116:806-820

Edler AU, Friedl TWP (2011) Carotenoid-based plumage colouration in red
bishops (*Euplectes orix*) - signalling presence rather than quality?
Behaviour 148:1377-1397

Edler AU, Friedl TWP (2012) Age-related variation in carotenoid-based
plumage ornaments of male Red Bishops *Euplectes orix*. Journal of
Ornithology 153:413-420

Edward DA, Chapman T (2011) The evolution and significance of male
mate choice. Trends in Ecology & Evolution 26:647-654

Emlen JT, Jr. (1957) Display and mate selection in the whydahs and bishop
birds. Ostrich 28:202-213

Endler JA (1992) Signals, signal conditions, and the direction of evolution.
The American Naturalist 139:S125-S153

Endler JA (1993) Some general comments on the evolution and design of
animal communication systems, vol 340

Endler JA (2000) Evolutionary implications of the interaction between
animal signals and the environment. In: Epsmark Y, Amundsen T,
Rosenqvist G (eds) Animal signals: signalling and signal design in

animal communication. Tapir Academic Press, Trondheim, Norway, pp 11-46

Endler JA, Basolo AL (1998) Sensory ecology, receiver biases and sexual selection. Trends in Ecology & Evolution 13:415-420

Enquist M, Arak A (1993) Selection of exaggerated male traits by female aesthetic senses. Nature 361:446-448

Enquist M, Arak A (1994) Symmetry, beauty and evolution. Nature 372:169-172

Enquist M, Arak A (1998) Neural representation and the evolution of signal form. In: Dukas R (ed) Cognitive ecology. Chicago University Press, Chicago, pp 21-87

Fisher RA (1930) The genetical theory of natural selection: a complete variorum edition. Oxford University Press

Folstad I, Karter AJ (1992) Parasites, bright males, and the immunocompetence handicap. The American Naturalist 139:603-622

Friedl TWP, Klump GM (1999) Determinants of male mating success in the red bishop (Euplectes orix). Behavioral Ecology and Sociobiology 46:387-399

Friedl TWP, Klump GM (2000) Nest and mate choice in the red bishop (Euplectes orix): female settlement rules. Behavioral Ecology 11:378-386

Friedman NR, Kiere LM, Omland KE (2011) Convergent gains of red carotenoid-based coloration in the new world blackbirds. Auk 128:678-687

Fry CH, Keith S (2004) The birds of Africa, Vol. VII. Christopher Helm, London

Fuller RC (2009) A test of the critical assumption of the sensory bias model for the evolution of female mating preference using neural networks. Evolution 63:1697-1711

Fuller RC, Houle D, Travis J (2005) Sensory bias as an explanation for the evolution of mate preferences. The American Naturalist 166:437-446

Garcia CM, Ramirez E (2005) Evidence that sensory traps can evolve into honest signals. Nature 434:501-505

Ghirlanda S (2002) Intensity generalization: Physiology and modelling of a neglected topic. Journal of Theoretical Biology 214:389-404

Ghirlanda S, Enquist M (2003) A century of generalization. Animal Behaviour 66:15-36

Gray AP (1958) Bird Hybrids. A Check - List with Bibliography. Commonwealth Agricultural Bureaux, Farnham Royal, Buckinghamshire

Grether GF (2000) Carotenoid limitation and mate preference evolution: a test of the indicator hypothesis in guppies (*Poecilia reticulata*). Evolution 54:1712-1724

Grether GF, Drury JP, Berlin E, Anderson CN (2015) The Role of Wing
      Coloration in Sex Recognition and Competitor Recognition in
      Rubyspot Damselflies (Hetaerina spp.). Ethology:n/a-n/a

Grether GF, Hudon J, Millie DF (1999) Carotenoid limitation of sexual
      coloration along an environmental gradient in guppies, vol 266

Grether GF, Kolluru GR, Rodd FH, de la Cerda J, Shimazaki K (2005)
      Carotenoid availability affects the development of a colour-based
      mate preference and the sensory bias to which it is genetically
      linked, vol 272

Griffith SC, Pryke SR (2006) Benefits to females of assessing color displays.
      In: Hill GE, McGraw KJ (eds) Bird Coloration. vol. 2: Function and
      evolution. Harvard University Press, Cambridge, USA, pp 233-279

Guilford T, Dawkins MS (1991) Receiver psychology and the evolution of
      animal signals. Animal Behaviour 42:1-14

Guilford T, Dawkins MS (1993) Receiver psychology and the design of
      animal signals. Trends in Neurosciences 16:430-436

Guilford T, Dawkins MS (1995) What are conventional signals? Animal
      Behaviour 49:1689-1695

Hall BP, Moreau RE (1970) An atlas of speciation in African passerine
      birds. Brit. Mus. Nat. Hist., London

Hamilton WD, Zuk M (1982) Heritable true fitness and bright birds: A role
      for parasites? Science 218:384-387

Hanson HM (1959) Effects of discrimination training on stimulus
      generalization. Journal of Experimental Psychology 58:321-334

Hill GE (2002) A red bird in a brown bag; the function and evolution of
      colourful plumage in the house finch. Oxford University Press,
      Oxford

Hill GE (2006) Female mate choice for ornamental colouration. In: Hill GE,
      McGraw KJ (eds) Bird Coloration. Harvard University Press,
      Cambridge, pp 137-200

Hogan JA, Kruijt JP, Frijlink JH (1975) "Supernormality" in a learning
      situation. Zeitschrift für Tierpsychologie 38:212-218

Huff RC, Sherman JE, Cohn M (1975) Some effects of response-
      independent reinforcement on auditory generalization gradients.
      Journal of the Experimental Analysis of Behavior 23:81-86

Jansson L, Enquist M (2003) Receiver bias for colourful signals. Animal
      Behaviour 66:965-971

Jansson L, Enquist M (2005) Testing the receiver bias hypothesis
      empirically with 'virtual evolution'. Animal Behaviour 70:865-875

Johnson K, Rosetta D, Burley DN (1993) Preferences of female American
      goldfinches (Carduelis tristis) for natural and artificial male traits.
      Behavioral Ecology 4:138-143

Kim TW, Christy JH, Choe JC (2007) A preference for a sexual signal keeps
      females safe. PLoS ONE 2:e422

Kirkpatrick M (1982) Sexual selection and the evolution of female choice. Evolution 36:1-12

Kokko H, Brooks R, McNamara JM, Houston AI (2002) The sexual selection continuum, vol 269

Lack D (1968) Ecological adaptations for breeding in birds. Methuen, London

Lack DBA (1935) Territory and polygamy in a bishop-bird, <u>Euplectes hordeacea hordeacea</u> (Linn.). Ibis 5:817-836

Lande R (1980) Sexual dimorphism sexual selection, and adaptation in polygenic characters. Evolution 34:292-305

Lande R (1981) Models of speciation by sexual selection on polygenic traits. Proceedings of the National Academy of Sciences 78:3721-3725

LeBas NR (2006) Female finery is not for males. Trends in Ecology & Evolution 21:170-173

LeBas NR, Hockham LR, Ritchie MG (2003) Nonlinear and correlational sexual selection on 'honest' female ornamentation, vol 270

Lorenz K (1981) The foundations of ethology. Springer-Verlag, New York

Mackintosh NJ (1974) The psychology of animal learning. Academic Press, London

Martins EP (2000) Adaptation and the comparative method. Trends In Ecology & Evolution 15:296-299

Maynard Smith J, Harper D (2003) Animal signals. Oxford University Press

Merrill L, Stewart TE, González-Gómez PL, O'Loghlen AL, Wingfield JC, Ellis VA, Rothstein SI (2015) Epaulet Size and Current Condition in Red-Winged Blackbirds: Examining a Semistatic Signal, Testosterone, Immune Function, and Parasites. Physiological and Biochemical Zoology 88:11-21

Ohinata S (1979) Postdiscrimination shift of the goldfish (*Carassius auratus*) on a visual wavelength continuum. The Annual of Animal Psychology 28:113-122

Owings D, Morton E (1997) The role of information in communication: an assessment/management approach. In: Owings D, Beecher M, Thompson N (eds) Persperctives in Ethology: Vol 12, Communication. Springer-Verlag, New York, pp 359-390

Owings DH, Morton ES (1998) Animal vocal communication: a new approach. Cambridge University Press, Cambridge

Pärt T, Qvarnström A (1997) Badge size in collared flycatchers predicts outcome of male competition over territories. Animal Behaviour 54:893-899

Peek FW (1972) Experimental study of territorial function of vocal and visual display in male red-winged blackbird (*Agelaius phoeniceus*). Animal Behaviour 20:112-118

Pierrel R, Sherman JG (1960) Generalization of auditory intensity following discrimination training. Journal of the experimental analysis of behavior 3:313-322

Prager M, Andersson S (2009) Phylogeny and evolution of sexually selected tail ornamentation in widowbirds and bishops (*Euplectes spp.*). Journal of Evolutionary Biology 22:2068-2076

Prager M, Andersson S (2010) Convergent evolution of red carotenoid coloration in widowbirds and bishops (*Euplectes spp.*). Evolution 64:3609-3619

Prager M, Johansson EIA, Andersson S (2008) A molecular phylogeny of the African widowbirds and bishops, Euplectes spp. (Aves : Passeridae : Ploceinae). Molecular Phylogenetics and Evolution 46:290-302

Prager M, Johansson EIA, Andersson S (2009) Differential ability of carotenoid C4-oxygenation in yellow and red bishop species (*Euplectes spp.*). Comparative Biochemistry and Physiology B-Biochemistry & Molecular Biology 154:373-380

Prum RO (2010) The Lande-Kirkpatrick mechanism is the null model of evolution by intersexual selection: implications for meaning, honesty, and design in intersexual signals. Evolution 64:3085-3100

Pryke SR (2009) Is red an innate or learned signal of aggression and intimidation? Animal Behaviour 78:393-398

Pryke SR, Andersson S (2002) A generalized female bias for long tails in a short-tailed widowbird. Proceedings of the Royal Society of London Series B-Biological Sciences 269:2141-2146

Pryke SR, Andersson S (2003a) Carotenoid-based epaulettes reveal male competitive ability: experiments with resident and floater red-shouldered widowbirds. Animal Behaviour 66:217-224

Pryke SR, Andersson S (2003c) Carotenoid-based status signalling in red-shouldered widowbirds (*Euplectes axillaris*): epaulet size and redness affect captive and territorial competition. Behavioral Ecology and Sociobiology 53:393-401

Pryke SR, Andersson S (2005) Experimental evidence for female choice and energetic costs of male tail elongation in red-collared widowbirds. Biological Journal of the Linnean Society 86:35-43

Pryke SR, Andersson S (2008) Female preferences for long tails constrained by species recognition in short-tailed red bishops. Behavioral Ecology 19:1116-1121

Pryke SR, Andersson S, Lawes MJ, Piper SE (2002) Carotenoid status signaling in captive and wild red-collared widowbirds: independent effects of badge size and color. Behavioral Ecology 13:622-631

Pryke SR, Lawes MJ, Andersson S (2001) Agonistic carotenoid signalling in male red-collared widowbirds: aggression related to the colour signal of both the territory owner and model intruder. Animal Behaviour 62:695-704

Rendall D, Owren MJ, Ryan MJ (2009) What do animal signals mean? Animal Behaviour 78:233-240

Rosenthal GG, Evans CS (1998) Female preference for swords in *Xiphophorus helleri* reflects a bias for large apparent size. Proceedings of the National Academy of Sciences 95:4431-4436

Rowe C (1999) Receiver psychology and the evolution of multicomponent signals. Animal Behaviour 58:921-931

Rowe C (2013) Receiver psychology: a receiver's perspective. Animal Behaviour 85:517-523

Rowe C, Skelhorn J (2004) Avian psychology and communication. Proceedings of the Royal Society of London Series B-Biological Sciences 271:1435-1442

Ryan MJ (1990) Sexual selection, sensory systems, and sensory exploitation. Oxford Surveys in Evolutionary Biology 7:157-195

Ryan MJ (1998) Sexual selection, receiver biases, and the evolution of sex differences. Science 281:1999-2003

Ryan MJ, Cummings ME (2013) Perceptual biases and mate choice. Annual Review of Ecology, Evolution, and Systematics 44:437-459

Ryan MJ, Fox JH, Wilczynski W, Rand AS (1990) Sexual selection for sensory exploitation in the frog *Physalaemus pustulosus*. Nature 343:66-67

Ryan MJ, Rand AS (1990) The sensory basis of sexual selection for complex calls in the tungara frog, *Physalaemus pustulosus* (sexual selection for sensory exploitation). Evolution 44:305-314

Ryan MJ, Rand AS (1993) Sexual selection and signal evolution: the ghost of biases past. Philosophical Transactions of the Royal Society of London. Series B: Biological Sciences 340:187-195

Santos ESA, Scheck D, Nakagawa S (2011) Dominance and plumage traits: meta-analysis and metaregression analysis. Animal Behaviour 82:3-19

Savalli UM (1994a) Mate choice in the yellow-shouldered widowbird - correlates of male attractiveness. Behavioral Ecology and Sociobiology 35:227-234

Savalli UM (1994c) Tail length affects territory ownership in the yellow-shouldered widowbird. Animal Behaviour 48:105-111

Sefc KM, Hermann CM, Steinwender B, Brindl H, Zimmermann H, Mattersdorfer K, Postl L, Makasa L, Sturmbauer C, Koblmüller S (2015) Asymmetric dominance and asymmetric mate choice oppose premating isolation after allopatric divergence. Ecology and Evolution 5:1549-1562

Senar JC (2006) Color displays as intrasexual signals of aggression and dominance. In: Hill GE, McGraw KJ (eds) Bird Coloration. Harvard University Press, Cambridge, pp 87-136

Senar JC, Camerino M (1998) Status signalling and the ability to recognize dominants: an experiment with siskins (*Carduelis spinus*).

        Proceedings of the Royal Society of London Series B-Biological
        Sciences 265:1515-1520

Seyfarth RM, Cheney DL, Bergman T, Fischer J, Zuberbühler K,
        Hammerschmidt K (2010) The central importance of information in
        studies of animal communication. Animal Behaviour 80:3-8

Shaw K (1995) Phylogenetic tests of the sensory exploitation model of
        sexual selection. Trends in Ecology & Evolution 10:117-120

Sibley CG, Ahlquist JE (1990) Phylogeny and classification of birds; a study
        in molecular evolution. Yale University Press, New Haven

Smith DG (1972) Role of epaulets in red-winged blackbird, (*Agelaius
        phoeniceus*) social system. Behaviour 41:251-268

Sorensen RA (1992) The egg came before the chicken. Mind 101:541-542

Stephenson B, Ramírez-Bautista A (2012) Did sexually dimorphic dorsal
        coloration evolve by a pre-existing bias in males in the lizard
        Sceloporus minor? Evolutionary Ecology 26:1277-1291

Stevenson JG (1966) Stimulus generalization: the ordering and spacing of
        test stimuli. Journal of the Experimental Analysis of Behavior 9:457-
        468

Tinbergen N (1951) The study of instinct. Oxford University Press, New
        York

Wills S, Mackintosh NJ (1998) Peak Shift on an Artificial Dimension. The
        Quarterly Journal of Experimental Psychology Section B 51:1-32

Zahavi A (1975) Mate selection - a selection for a handicap. Journal of
        Theoretical Biology 53:205-214

Zahavi A (1987) The theory of signal selection and some of its
        implications. In: International symposium of biological evolution.
        Adriatica Editrice Bari, pp 305-327