Thesis for the degree of Doctor of Philosophy

PHYLOGENY AND SIGNAL DIVERSITY

IN WIDOWBIRDS AND BISHOPS (*Euplectes* spp.)

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"The sight of a feather in a peacock's tail, whenever I gaze at it, makes me sick!"

- Charles Darwin, in a letter to botanist Asa Gray, April 3, 1860

ABSTRACT

Although sexual selection for elaborate signals is well documented in numerous species, the extreme diversity in signal design and expression in many taxa is largely unexplained. This thesis explores phylogenetic, mechanistic and ontogenetic explanations of divergence in two classic condition-dependent signal traits in the African widowbirds and bishops (*Euplectes* spp.); elongated black tails (in widowbirds) and patches of bright yellow or red carotenoid coloration (most prominent in bishops).

A molecular phylogeny of 33 *Euplectes* subspecies (representing all 17 species) was derived using parsimony and Bayesian analyses of mitochondrial and nuclear DNA sequences. A consensus tree, or a sample of the most probable Bayesian trees, was then used in parsimony, likelihood and Bayesian reconstructions of ancestral signal states. Specifically, the discrete presence of a nuptial tail (i.e. prenuptial tail moult), continuous tail length, and discrete as well as continuous reflectance-based measures of carotenoid colour hue were analysed. The proximate basis of interspecific colour variation was investigated using High Performance Liquid Chromatography (HPLC) analyses of feather and plasma pigments in five *Euplectes* species. Finally, the relative importance of nutritional and metabolic constraints behind differential occurrence of C4-keto-carotenoids, and thus red plumage color, in *Euplectes*, was tested by diet manipulation in a yellow and a red bishop species.

Results show monophyly of the genus *Euplectes*, but not of 'widowbirds' or 'bishops'. Most notably, the red-collared widowbird *E. ardens* belongs to a clade of short-tailed bishops and not to the 'true' widowbirds. Extant *Euplectes* furthermore derive from ancestors in which breeding males had short (not prenuptially moulted) tails and yellow colour signals. Nuptial tail elongation and red coloration have since evolved at least twice in distinct lineages, possibly as convergent responses to early established and directional sexual selection for increasingly exaggerated quality advertisements. This provides an interesting contrast to several recent findings of labile ornament evolution in birds and other animals.

Three different pigment profiles were identified in *Euplectes* feathers. Yellow colours primarily depend on dietary yellow carotenoids, while red hues result either from addition of metabolically derived red C4-keto-carotenoids, or from high concentrations of dietary and derived yellow pigments. A possible genetic constraint on colour evolution was also identified, as the southern red bishop *E. orix*, but not the yellow-crowned bishop *E. afer*, can manufacture red C4-keto-carotenoids (α-doradexanthin and canthaxanthin) from yellow dietary precursors (lutein and β-carotene).

Combined with previous work on adaptive signal functions in *Euplectes*, the phylogenetic and proximate analyses in this thesis provide an unusually complete picture of avian plumage diversification, and a useful framework for further exploration of both genetics and ecology of avian colour signalling.

KEYWORDS: Ploceidae, weaverbirds, stochastic character mapping, phylogenetic uncertainty, mate choice, status signalling, sexual dichromatism, C4-oxygenation

Sammanfattning / Swedish Abstract

Sexuell selektion av ornament och hotsignaler har dokumenterats hos många arter, men den enorma mångfalden av signalers design och uttryck är i stort sett oförklarad. I den här avhandlingen undersöks fylogenetiska, mekanistiska och ontogenetiska förklaringar till diversitet i två klassiska konditionsberoende signalegenskaper hos Afrikanska änkefåglar och biskopar (*Euplectes* ssp.): förlängda stjärtfjädrar (hos änkefåglar) och bjärt gula eller röda karotenoidfärger (mest framträdande hos biskopar).

En molekylär fylogeni av 33 *Euplectes*-underarter (representerande samtliga 17 arter) skattades med parsimoni-baserade och Bayesianska analyser av mitokondriella och nukleära DNA-sekvenser. Ett sammanvägt träd, eller ett stickprov av de mest sannolika Baysianska träden, användes sedan för parsimoni-, 'maximum likelihood'- och Bayesianska rekonstruktioner av signalernas evolutionära historia. Mer specifikt analyserades egenskaperna stjärtplym-förekomst (dvs. praktdräkts-ruggning av stjärtfjädrarna), kontinuerlig stjärtlängd, samt diskreta och kontinuerliga mått på färgnyans, baserade på objektiv reflektans-spektrometri. Proximata orsaker till mellanartsvariation i färg undersöktes också med vätskekromatografisk (HPLC-) analys av fjäder- och plasmapigment hos fem *Euplectes*-arter. Slutligen testades den relativa betydelsen av näringsmässiga och metaboliska begränsningar för förekomst av C4-keto-karotenoider, och därmed röd färg, inom *Euplectes*, genom dietmanipulation hos en gul och en röd biskopart.

Resultaten stöder monofyli för släktet *Euplectes*, men ej för grupperingarna 'änkor' eller 'biskopar'. Mest anmärkningsvärt är att arten rödkragad änka (*E. ardens*) tillhör en klad av kortstjärtade biskopar och inte de 'äkta' änkorna. Enligt de evolutionära rekonstruktionerna härstammar släktet *Euplectes* vidare från förfäder med korta stjärtplymer (som inte ruggades före häckning) och gul signalfärg. Långa stjärfjädrar och röda färgsignaler har sedan evolverat åtminstone två gånger i skilda grenar av släktträdet, troligen som konvergenta responser på tidigt uppkommen och riktad sexuell selektion av alltmer extrema kvalitets-indikatorer. Detta utgör en intressant kontrast mot tidigare rekonstruktioner av labil ornamentevolution hos fåglar och andra djur.

Tre olika pigmentprofiler identifierades i *Euplectes*-fjädrar. Gula färger orsakas främst av gula karotenoider från födan, medan röda nyanser antingen beror av metaboliskt modifierade röda C4-keto-karotenoider, eller av höga koncentrationer av gula pigment. En möjlig genetisk begränsning av färgevolutionen identifierades också, då den röda biskoparten *E. orix* men inte den gula *E. afer* kan tillverka röda C4-keto-karotenoider (α-doradexanthin and canthaxanthin) från gula födo-pigment (lutein and β-karoten).

I kombination med tidigare studier av adaptiva signalfunktioner hos *Euplectes*, erbjuder de fylogenetiska och proximata analyserna i den här avhandlingen en ovanligt komplett bild av dräktdiversifiering hos fåglar, samt en användbar utgångspunkt för vidare studier av genetik och ekologi bakom fåglars färgsignalering.

LIST OF PAPERS

This thesis is a summary of the following papers:

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

II   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.

III   Prager, M., Andersson, S. Convergent evolution of red carotenoid coloration in widowbirds and bishops (*Euplectes* spp.). Provisionally accepted for publication in Evolution.

IV   Andersson, S., Prager, M., Johansson, E.I.A., 2007. Carotenoid content and reflectance of yellow and red nuptial plumages in widowbirds (*Euplectes* spp.). Functional Ecology 21, 272-281.

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

CONTENTS

INTRODUCTION

Explaining the tremendous diversity of life is a fundamental challenge to biology, but may also be our best hope of preserving it, over the long term. One of the most striking and intensely researched aspects of biodiversity is the ornate and colourful plumages of birds, and this thesis is devoted to a fraction of this diversity: the elongated tails and bright carotenoid colours of African widowbirds and bishops (*Euplectes* spp.). Inspired by Tinbergen's (1963) four complementary categories of explanations for animal behaviour, the studies presented here build on previous tests of adaptive signal functions in *Euplectes*, but primarily approach signal diversity from mechanistic, ontogenetic and phylogenetic perspectives. In other words, focus will be on how different signals are produced, and how they have changed over evolutionary time within this genus of birds. Before exploring signal diversification in *Euplectes*, however, we first need to consider what is meant by sexual signals, and then take a closer look at tail ornamentation and carotenoid coloration.

SEXUAL SIGNALLING

Animal signals are behaviours or structures (e.g. ornaments or threat displays) that increase the fitness of senders by affecting the behaviour of receivers (Maynard Smith and Harper 2003). Signals can either be naturally selected characteristics (e.g. warning colours, contact calls), or elaborate displays that function to increase individual mating success (even at the expense of survival), and thus evolve in response to what Darwin (1871) termed sexual selection. Sexual selection on males can in turn operate via two different, though sometimes intertwined (Berglund et al. 1996), mechanisms: via female preferences for ornamented males, or via male success in contest competition over mating opportunity (Darwin 1871; M. Andersson 1994).

Whenever signal exaggeration is a good predictor of male ability to provide resources to females and offspring (see e.g. Griffith and Pryke 2006), or to fight rivals in aggressive encounters (see e.g. Senar 2006), discriminating receivers can gain *direct* benefits in terms of increased fecundity or survival. Direct fitness consequences of female mate choice is likely to be more important in socially monogamous species than in polygynous species with little or no paternal care (but see Reynolds and Gross 1990; Pryke and Lawes 2004). In both types of mating systems, however, choosy females may also acquire *indirect* benefits in the form of heritable attractiveness or quality to their offspring.

There are alternative hypotheses for the evolution of sexual signals in response to female selection for indirect benefits. Under Fisherian runaway models, genetic correlation leads to mutual reinforcement between male expression and female preference for an arbitrary, 'attractive', signal trait (Fisher 1930; Lande 1980, 1981; Kirkpatrick 1982). In contrast, quality indicator, or 'handicap' models (Zahavi 1975, 1977; Andersson 1982; Kodric-Brown and Brown 1984) emphasise female preference for condition-dependent (Andersson 1982; Grafen 1990; Johnstone 1995) or 'inherently revealing' (Hamilton and Zuk 1982; Iwasa et al. 1991) signal traits, functioning as honest indicators of male quality. Honesty is ensured since low-quality individuals either pay larger survival or fecundity costs for signal exaggeration (Grafen 1990; Kotiaho 2001), or are physically incapable of cheating (Hamilton and Zuk 1982), respectively. Other models of sexual selection assume that males evolve traits that exploit pre-existing sensory biases of female receivers, selected for in other circumstances (Ryan 1990; Ryan et al. 1990). Sensory bias,

Fisherian, and quality-indicator mechanisms are not necessarily incompatible, but could proceed simultaneously or sequentially (M. Andersson 1994; Backwell et al. 1995; Kokko et al. 2002; Garcia and Ramirez 2005).

This thesis focuses on two of the most familiar and well-established examples of quality-indicating signals, functioning both in mate choice and in agonistic contests over mates: extravagant tail plumes and conspicuous carotenoid colours.

TAIL ORNAMENTATION

Most birds have five or six pairs of tail feathers (i.e. rectrices), typically well adapted to aerodynamic functions, which include general stabilisation as well as helping the bird to turn and to manage slow flight (Thomas 1993). Ornamental elongation of tail feathers, however, seems to have evolved independently in many bird families and genera (M. Andersson 1994), and is arguably a suitable target for sexual selection for honest indicator traits, since condition-dependence is mediated both by aerodynamic hindrance and stressful growth.

Aerodynamic costs of tail elongation beyond the naturally selected length derive from increased drag forces, causing higher energy consumption during flight (Thomas 1993; Norberg 1995), but also involve effects on agility (i.e. max. turning speed) and manoeuvrability (i.e. min. turning radius, Thomas 1993; Evans 2004). The aerodynamic cost of tail elongation differs between commonly observed types of ornamental tails (Balmford et al. 1993). Specifically, graduated tail plumes, in which all or most rectrices are elongated, incur higher costs than for example forked tails (longer outer rectrices) or pintails (longer central rectrices), and they are also more strongly correlated with sexual dimorphism across taxa (Balmford et al. 1993).

Long tails are likewise stressful to produce, as indicated by the more pronounced fluctuating asymmetry (i.e. random deviations from bilateral symmetry) of ornamental tails, compared to non-ornamental tails of conspecifics or closely related taxa (Møller and Höglund 1991). Nutritional stress additionally reduces deposition of melanin pigments and structural keratin proteins into growing tail feathers, resulting in translucent 'fault bars' and even perforations across the feather vane (Grubb 1989, 1991; S. Andersson 1994). Since these, in turn, affect the incidence of feather breakage, elongated tails are not only costly indicators, but may also function as 'inherently revealing' signals of individual quality (Fitzpatrick and Price 1997).

Since honesty-maintaining costs of tail elongation are readily identified and measured (see above), and because the traits themselves are susceptible to manipulation, ornamental tails have become classic examples of sexual selection, originally in the long-tailed widowbird (*Euplectes progne*, Andersson 1982), and since then in several other avian taxa, such as barn swallows (Møller 1988; Smith and Montgomerie 1991), peacocks (Petrie et al. 1991), sunbirds (Evans and Hatchwell 1992), whydahs (Barnard 1990), flycatchers (Regosin and Pruett-Jones 2001) and sugarbirds (McFarlane et al. 2010).

CAROTENOID COLORATION

Most of the brilliant yellow, orange and red colours of birds and other animals, derive from deposition of carotenoid pigments into feather, beak or skin tissue (Fox and Vevers 1960; Brush 1978; Stradi 1998). There are approximately 700 known naturally occurring carotenoids, most of which are produced by and restricted to photosynthetic plants and micro-organisms (Britton 1991; Armstrong and Hearst 1996; Demmig-Adams and Adams 2002; Raila et al. 2002; McGraw 2006). The basic structure of carotenoids is a conjugated C40 hydrocarbon chain with or without

cyclic end groups (Britton 1995; Armstrong and Hearst 1996). Carotenoids are broadly divided into two major classes: carotenes, which are pure hydrocarbons, and xanthophylls, which have more or less oxygenated end rings (Isler et al. 1971). All carotenoids absorb strongly in the indigo-blue spectral region (400-500 nm) (Goodwin 1980), thereby creating yellow to red coloration of the reflective integument in which they are deposited (Andersson and Prager 2006).

Like other animals, birds acquire carotenoids exclusively through the diet (Brockmann and Völker 1934; Goodwin 1984; Hill and McGraw 2006), and carotenoid-based displays are therefore potentially limited by food intake (Endler 1980; Hill 1990). Furthermore, the uptake and expression of carotenoids can be affected by parasites (Hamilton and Zuk 1982; Milinski and Bakker 1990; Thompson et al. 1997; Zahn and Rothstein 1999), as well as direct allocation conflicts with immunological or antioxidant systems (Lozano 1994; von Schantz et al. 1999; Møller et al. 2000; Blount et al. 2003). Consequently, carotenoid coloration is commonly assumed to be an honest indicator of individual health and condition (Olson and Owens 1998; McGraw 2006; but see Hartley and Kennedy 2004).

Mating success or dominance is associated with redder (i.e. longer wavelength) colour hues in many carotenoid-pigmented birds (Shawcross and Slater 1983; Hansen and Rohwer 1986; Hill 1990; Evans and Hatchwell 1992; Wolfenbarger 1999; Pryke and Griffith 2006; Pryke 2007), and other vertebrates (Bakker and Sevenster 1983; Evans and Norris 1996). This suggests that red colours either make more efficient signals (Andersson 2000), e.g. by exploiting pre-existing sensory or cognitive biases of receivers (Endler and Basolo 1998), or that they are associated with higher production or maintenance costs, thus making them more reliable quality indicators than either yellow or orange displays (Hudon 1991; Hill 1996).

EXPLANATIONS OF SIGNAL DIVERSITY

Elaborate sexual signals provide some of the most spectacular examples of biodiversity (Darwin 1871; West-Eberhard 1983; M. Andersson 1994). Yet, whereas sexual selection through female choice or male contest competition is well documented in numerous species (see above), the extreme diversity in design and expression of sexual signals in many taxa is largely unexplained. Why, for example, do many related species differ markedly in terms of carotenoid colour signals? Is it because they ingest and deposit different types of pigments, or is it because fitness consequences of being colourful vary among species? Although these are two very distinct explanations of signal diversity, they do not preclude each other. Conceptually, they derive from Tinbergen's (1963) four complementary levels of analysis for explaining animal behaviour. These involve asking questions regarding the 1) adaptive value, 2) phylogeny (i.e. evolutionary history), 3) mechanism, and 4) ontogeny (i.e. individual history) of the trait in question. In the following section, Tinbergen's perspective is adopted to introducing different, but interlinked, explanations of interspecific diversity in sexual signal exaggeration.

Signal Adaptation

Adaptive explanations of signal diversity attempt to identify and quantify interspecific variation in social or ecological selection pressures acting on signal traits. Sexual signals, in focus here, are generally expected to evolve towards some optimum where mating benefits are balanced by viability costs (M. Andersson 1994). As regards mate choice signals, Fisherian processes (i.e. genetic correlations between signal and preference) may lead to bidirectional and even cyclic evolution of mate preferences (and accompanying oscillations between ornament exaggeration

and reduction), potentially causing rapid signal diversification among populations and taxa (Mead and Arnold 2004). In any scenario of Fisherian, honest indicator, or sensory bias forms of sexual selection, signal design and exaggeration are also adaptively shaped by signal conditions (e.g. light, background) or details of receiver biases (Endler 1992; Schluter and Price 1993; Andersson 2000; Boughman 2002). Finally, even when important adaptive effects (whether inherently divergent or ecologically determined) have been identified, much diversity typically remains unexplained. Rather than adding or refining adaptive hypotheses, this is where it becomes important to consider phylogenetic, mechanistic and ontogenetic constraints on adaptive processes.

Signal Phylogeny

Phylogenetic approaches to studying signal diversity recognise that phenotypic trait expression in contemporary taxa may, to varying extent, depend on historical adaptive (and stochastic) processes, i.e. on the evolutionary history of characters (Brooks and McLennan 1991; Harvey and Pagel 1991; Martins and Hansen 1997). In absence of fossil data (which is almost always the case), inferences of signal evolution rely on phylogenetic methods, basically involving two successive steps: phylogeny estimation (Huelsenbeck et al. 2001; Felsenstein 2004) and ancestral character state reconstruction (Swofford et al. 1992; Schluter et al. 1997; Ronquist 2004).

Phylogenies are tree diagrams showing the inferred evolutionary relationships among species, or other taxa, descended from a common ancestor. Estimations of these relationships build on the cladistic method of Hennig (1966), but are today typically based on patterns of similarity in biomolecular sequence data (i.e. DNA, RNA or protein), rather than in e.g. behavioural and morphological traits. Combined with data on the current distribution of phenotypic characteristics, however, phylogenies can be used to reconstruct the evolutionary history of e.g. signal expression. Such reconstructions seek the ancestral signal states (one for each branching point in the tree) that imply the fewest (parsimony methods, Kluge and Farris 1969; Farris 1970), or the most probable (likelihood or Bayesian methods, Schluter et al. 1997; Ronquist 2004), evolutionary changes to have occurred in the tree.

Interpreted with caution (Schluter et al. 1997; Cunningham et al. 1998; Losos 1999), reconstructions of signal evolution may reveal interesting macroevolutionary patterns, beyond the reach of the experimental approach, e.g. concerning ancestral and derived states of signal expression, and directions of evolutionary change, within a group of species (Omland and Lanyon 2000; Wiens 2001; Hofmann et al. 2006b). They can also help determine whether similarity in signal expression between taxa is due to shared ancestry (i.e. homology) or to convergent evolution in response to similar selection pressures (i.e. homoplasy). Accordingly, the prominent ornament diversity found in manakins (Pipridae, Prum 1997), bowerbirds (Ptilonorhynchidae, Kusmierski et al. 1997) and new world orioles (*Icterus* spp., Omland and Lanyon 2000; Hofmann et al. 2006b) seems to have originated from labile evolution of signal traits, including repeated convergence and loss of ornamentation.

Placing intraspecific experimental studies in a phylogenetic framework also allows us to examine the concordance between signal selection and expression across species. This provides possibilities for testing sensory bias models of sexual selection (reviewed by Shaw 1995), but can also help identify key innovations and phylogenetic constraints on selection (Harvey and Pagel 1991), as well as taxa of particular interest for future experiments (Omland and Kondo 2006).

Signal Mechanisms and Ontogeny

Proximate analyses of signal diversity focus on identifying interspecific variation in direct mechanisms behind signal expressions, as well as in the genetic-developmental processes underlying these (i.e. corresponding to questions 3 and 4, above). While interesting in its own right, such knowledge also constitutes a key element for understanding why particular signals are targeted by rivals or potential mates, and why species may differ in their response to such selection (see e.g. Hill and McGraw 2006). Ornamental carotenoid coloration may, for example, involve several different pigments with nutritional and metabolic constraints that may vary among species. In particular, and as is explored in this thesis, variation in colour hue can result from differences in dietary access to carotenoids (Hudon and Brush 1989; Hill 1992), or from differences in metabolic capacity to adjust the absorptance properties of ingested pigments (Brush 1981; McGraw et al. 2001).

Although carotenoid pigments typically absorb UV and blue light (350-500 nm; Goodwin 1980), the wavelength of maximum absorption (λ_{max}), and thus the hue of reflected light, depends on the number of conjugated double bonds present in the pigment molecule (Fox and Vevers 1960; Goodwin 1980). Carotenoid colour is therefore potentially affected by small structural re-arrangements of molecules, either shortening or elongating this chain of double bonds. Enzymatic conversion of ingested pigments has been documented in several avian taxa (Brush 1990; Latscha 1990; Stradi et al. 1997; Schiedt 1998). According to suggested metabolic pathways (Stradi et al. 1997), orange-red C4-keto-carotenoids in birds (e.g. α-doradexanthin and canthaxanthin) derive from enzymatic addition of a double-bonded oxygen atom to the C4 positions (C4-oxygenation) of dietary yellow precursors (e.g. lutein and β-carotene). Whether interspecific variation in metabolic capacity is an important factor behind avian colour diversity needs further investigation, however.

GENUS *EUPLECTES*: WIDOWBIRDS AND BISHOPS

A strikingly ornamented group of birds for which the adaptive functions (but neither evolutionary history nor proximate mechanisms) of sexual signals have been well documented, are the African widowbirds and bishops (*Euplectes* spp.). *Euplectes* is a genus of passerine birds in the weaver subfamily (Ploceinae, Sibley and Ahlquist 1990; alternatively family Ploceidae, Fry and Keith 2004), containing 17 'widowbird' and 'bishop' species (Fig. 1; Craig 1993a, b). These are all ecologically similar, medium-sized (13-45 g) weaverbirds, widely distributed across grasslands of sub-Saharan Africa (Hall and Moreau 1970; Fry and Keith 2004). Along with other Ploceinae, *Euplectes* are believed to have radiated from gregarious and savannah-dwelling seed eaters during the climatic fluctuations of the Pleistocene (Crook 1964; Craig 1980). Recent speciation seems to be likely given their close similarity in ecology and behaviour, and hybridization in captivity (Baily 1918; Gray 1958; Colahan and Craig 1981) suggests incomplete reproductive barriers. Based primarily on ecology and behaviour, the *Euplectes* genus has been hypothesized to be closer to queleas (*Quelea* spp.) and fodies (*Foudia* spp.) than to the 'true' weavers (*Ploceus* spp., Crook 1964).

As indicated by their short, conical bills, widowbirds and bishops primarily feed on grass seeds, but opportunistically also on nectar and insects, such as caterpillars and termites (Fry and Keith 2004). Successful territorial males typically attract and mate with several females, i.e. resource-defence polygyny seems to be the rule, with variable male participation in nest building (a domed nest with a side entrance) but never in incubation or chick-feeding (Craig 1980). The only exception to territorial polygyny is the lek mating system of Jackson's widowbird *E. jacksoni*,

where females visit male display courts solely for mating, and then fly off to nest on their own (e.g. van Someren 1946; Andersson 1989). Male territories otherwise vary in size from a few square meters in reed-nesting bishops, to more than a hectare in some montane widowbirds, and are defended vigorously against conspecific as well as congeneric males. Since breeding birds commonly join mixed species flocks to feed elsewhere, the primary function of the territory is not food supply, however, but rather to provide suitable nest sites (Craig 1980).

Fig. 1 15 of the 17 species of widowbirds and bishops (*Euplectes* spp.). Left panel shows males in breeding (nuptial) plumage; right panel females and non-breeding males. Not included: golden-backed bishop *E. aureus* and mountain marsh widowbird *E. psammocromius*. Illustrations by Dale A. Zimmerman.

Despite similar ecologies and general behaviour (Emlen 1957; Craig 1980), breeding *Euplectes* males show an extraordinary variation in tail ornamentation and carotenoid coloration, that have inspired classic studies on mating systems and sexual selection (Emlen 1957; Crook 1964; Lack 1968; Andersson 1982). In widowbirds, but not in bishops, males prenuptially (i.e. before breeding) replace their rectrices to grow more or less elongated black tails (7-50 cm, Andersson and Andersson 1994). Strong female preference for graduated, long tails has been experimentally demonstrated in three of the longest-tailed (20-50 cm) species: *E. progne* (long-tailed widowbird, Andersson 1982), *E. jacksoni* (Jackson's widowbird, Andersson 1992) and *E. ardens* (red-collared widowbird, Pryke and Andersson 2005), as well as in the relatively short-tailed (7 cm) *E. axillaris* (fan-tailed widowbird, Pryke and Andersson 2002). In the latter species, females showed a strikingly supernormal preference, i.e. preferred tails that were several standard

deviations outside the normal range (Pryke and Andersson 2002). Only in *E. macrourus* (yellow-mantled widowbird) did tail manipulations, albeit on few males, seem to affect male competition (in the form of territory retention) rather than the attraction of females (Savalli 1994). Finally, a recent experiment on the southern red bishop *E. orix* indicates a preference for long tails also in a lineage lacking nuptial tail ornamentation (Pryke and Andersson 2008).

All *Euplectes* species show dramatic sexual and seasonal dichromatism (i.e. colour variation, see Fig. 1): At the onset of the breeding season, adult males moult into black nuptial body plumage with highly contrasting yellow, orange or red patches produced by carotenoid pigments (Kritzler 1943) or, in a few taxa, white or brown (melanin-pigmented) patches. In contrast, females and nonbreeding males are sparrowy brown across all species, with the exception of a few in which adult males retain black remiges (i.e. wing feathers) or some carotenoid pigmentation also in the eclipse (i.e. nonbreeding) plumage. In breeding males, brightly coloured plumage regions are emphasized through posturing in agonistic and courtship interactions (Crook 1964). Behavioural observations and experiments have, furthermore, shown that the size and redness (hue) of colour patches function in male-male competition over territories in both *E. axillaris* (Pryke and Andersson 2003a, b) and *E. ardens* (Pryke et al. 2001b; Pryke et al. 2002).

AIMS OF THESIS

In this thesis, the evolutionary origins of plumage signal diversity in widowbirds and bishops (*Euplectes* spp.) are investigated by combining data on signal mechanisms and expression in a phylogenetic framework.

Specific aims are to:

- Infer the evolutionary relationships among extant widowbirds and bishops, and their placement within the Ploceinae subfamily, using DNA sequence data. In particular, the goal is to elucidate whether traditional morphologically and behaviourally based classifications of 'widowbirds' and 'bishops', as well as *Euplectes* as a whole, constitute natural (i.e. monophyletic) groups (Paper **I**).

- Use the derived molecular phylogeny to reconstruct the evolution of tail ornamentation (Paper **II**) and carotenoid coloration (Paper **III**) within the genus. In particular, the objective is to infer the tail length and colour hue of the most recent common ancestor of all widowbirds and bishops, and to investigate whether sexual selection for more extreme signals has led to directional evolution of these traits.

- Investigate whether differences in colour hue among *Euplectes* are caused by interspecific variation in carotenoid biochemistry. First, the pigmentary basis of colour variation in the genus (Paper **IV** and **V**) is explored. This is followed by a diet manipulation experiment to test whether observed differences in carotenoid pigment profiles between yellow and red species are caused by different abilities to enzymatically transform dietary yellow pigments into red ones (Paper **V**).

METHODS

Data used in this thesis were acquired from live birds in the field (Paper **I-V**) and in captivity at the University of Gothenburg (Paper **V**), as well as from skin specimens stored by the Natural History Museum at Tring, UK (Paper **II** and **III**). In addition to biometry and reflectance-based colour measurements, blood and feathers were also sampled for DNA and pigment analyses. Presence or absence of nuptial tail was scored according to Craig (1993a, b) and personal observations.

PHYLOGENY ESTIMATION (PAPER **I**)

In an initial step towards analysing plumage signal divergence in widowbirds and bishops, a molecular phylogeny of the genus and its placement within the subfamily Ploceinae was estimated from mitochondrial and nuclear DNA sequences. Representatives of all the 17 *Euplectes* species as well as eight Ploceinae outgroups from four genera (*Amblyospiza, Ploceus, Quelea and Foudia*) were included. To account for the considerable variation in plumage and morphology within many *Euplectes* species, samples also represented 31 of 51 suggested subspecies, some of which were additionally split geographically, resulting in a total of 33 *Euplectes* taxa in the phylogenetic analysis.

Following DNA extraction from blood, polymerase chain reaction (PCR) amplification and dye terminator sequencing procedures, retrieved mitochondrial (ATP6, cyt b, ND2 and ND3) and nuclear intron (G3PDH) sequences were aligned and concatenated into a matrix of 2557 base pairs (bp). Since no indications of phylogenetic incongruence between different DNA regions were found, the final bootstrapped parsimony, and Bayesian analyses were performed on this combined dataset, using separate models of evolution for each of the three codon positions and the nuclear intron region. Subsequent reconstructions of ancestral character states were either based on a sample of 10 000 most likely trees (Paper **III**) from Bayesian analysis, or on a fully resolved consensus tree summarised from these (Paper **II & III**).

SIGNAL QUANTIFICATION (PAPER **II-V**)

Under the well-founded assumption that the nuptial tails and colours of *Euplectes* are condition-dependent indicators of male quality, signal measurements aimed to quantify variation in signal dimensions that are 1) related to the honesty-maintaining mechanisms, i.e. the investments made by the sender, and 2) likely to be targets of sexual selection, via rival males or choosy females.

Tail Ornamentation

All elongated *Euplectes* tails have similar graduated shapes, why the simple linear measure of tail length was used to quantify tail exaggeration (Paper **II**), further motivated by its well-supported relationships with production and aerodynamic costs, as well as with female preferences. To separate sexually selected tail elongation from isometric (i.e. shape-preserving) scaling or naturally selected allometric scaling (i.e. shape-altering elongation determined by e.g. mechanic or aerodynamic principles), a 'body size adjusted' tail length measure was also constructed. This was calculated as the difference between male nuptial tail length, and tail length predicted by a linear regression of male non-breeding tail length on tarsus length. Tarsus length was used as the most reliable univariate measure of skeletal body size (Freeman and Jackson 1990), rather than for

example wing length, which may be confounded by secondary adaptation to tail length (Andersson and Andersson 1994).

Carotenoid Coloration

Although colour is a subjective and context-dependent sensation, reflectance (i.e. the ratio of reflected to incident light, as a function of wavelength), is a physical property of a surface, and therefore independent of both receivers and ambient light (Andersson and Prager 2006). Making a few general assumptions of vertebrate colour cognition, however, objective indices of the three universal dimensions of animal colour vision (Hailman 1977): brightness (intensity), hue (spectral location) and chroma (spectral purity), were derived from reflectance data. Specifically, λ_{R50} (wavelength at which reflectance is halfway between its minimum and its maximum, see Fig. 2; Andersson and Prager 2006), was used as a measure of carotenoid colour hue (Paper **III-V**). This colorimetric should be the best predictor of pigment concentration in saturated carotenoid colours (Andersson and Prager 2006), and has likewise been shown to correlate with dominance in *Euplectes* (Pryke et al. 2002; Pryke and Andersson 2003b). Continuous hue values (λ_{R50}) were both reconstructed directly, and partitioned into discrete categories using a cluster analysis procedure modified from Wang and Shaffer (2008).
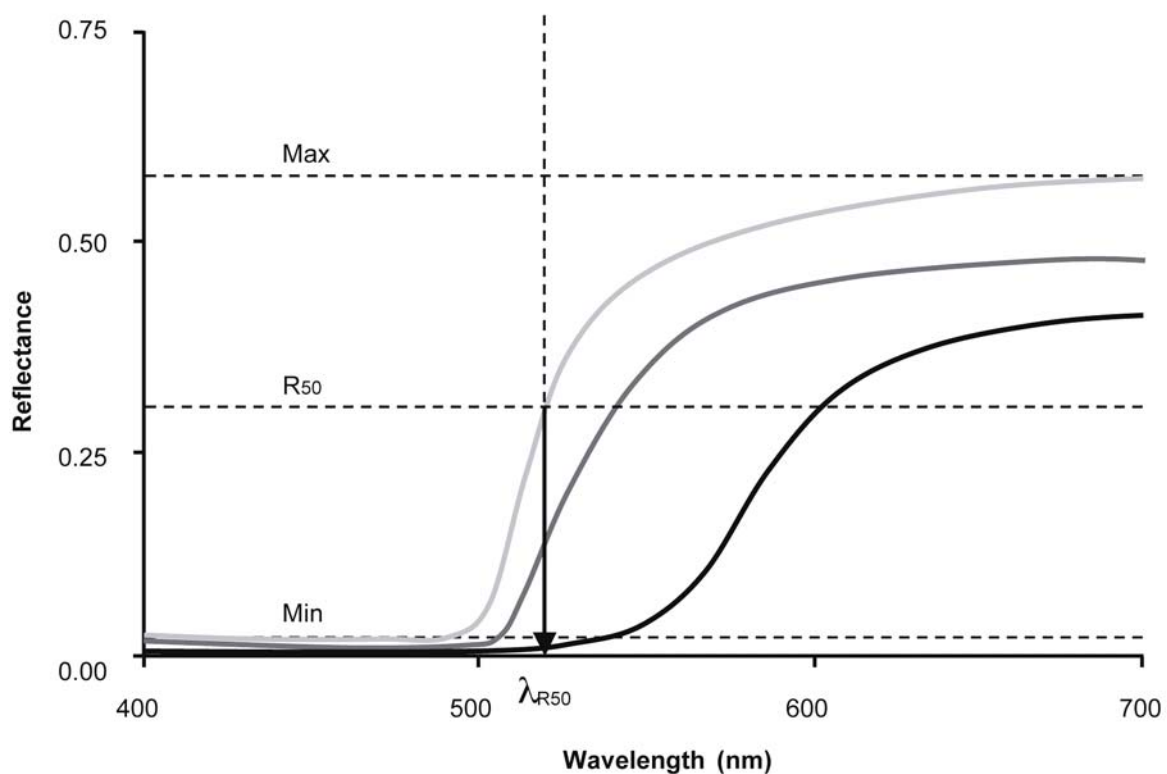
Fig. 2 Spectral reflectance functions typical of saturated carotenoid plumage pigmentation in *Euplectes*; yellow (light grey line), orange (dark grey line) and red (black line). The hue colorimetric, λ_{R50}, i.e. the wavelength at which reflectance is halfway between minimum and maximum (R_{50}), is illustrated for the shortest-wavelength (yellow) hue.

RECONSTRUCTIONS OF SIGNAL EVOLUTION (PAPER II-III)

In order to approach tail and colour diversity in *Euplectes* from a phylogenetic perspective, the evolution of both signal traits were reconstructed within the genus. The presence of nuptial tail, and discrete colour states were mapped onto the molecular tree(s) using parsimony, as well as likelihood and Bayesian algorithms, i.e. minimising the inferred number of state changes (e.g. from yellow to red) in the tree, or maximising the probability of the current state distribution among *Euplectes* taxa, respectively. Unlike parsimony, likelihood and Bayesian approaches are model-based methods that provide probability estimates for all reconstructed ancestral states. Through repeated sampling of alternative trees and transition rate parameters, Bayesian reconstruction (Paper **III**) furthermore allows for estimation of state probabilities that are independent of any particular branching pattern or evolutionary model setting being true.

Reconstruction methods for continuous trait measures were chosen based on likelihood comparisons of alternative evolutionary models, which suggested that both tail length and colour hue have evolved in a punctuated (rather than gradual) fashion. Following Hofmann *et al.* (2006a) linear parsimony (Farris 1970; Swofford and Maddison 1987) was considered to be the best correspondence to these punctuated models. However, in order to test the sensitivity of results to method choice, tail and colour evolution was also reconstructed using squared-change parsimony (Rogers 1984; Huey and Bennett 1987). The applied algorithms seek the set of ancestral character values that imply the smallest, absolute or squared, amount of evolutionary change in the tree, respectively.

PIGMENT IDENTIFICATION (PAPER IV-V)

Identification and quantification of carotenoid pigments is crucial for understanding signal mechanisms and constraints on colour evolution. High Performance Liquid Chromatography (HPLC) was thus used to analyse carotenoid pigments present in feathers and blood plasma. In this type of column chromatography, extracted analytes (here carotenoids) are dissolved in a moderately polar mobile phase (e.g. acetonitrile / methanol), and pumped through a non-polar stationary phase (a column packed with e.g. silica-bound alkyl chains), and subsequently a diode-array spectral absorption detector. The time required to travel through the column (i.e. retention time), and the shape of absorption spectra vary depending on compound polarity and molecular structure.

For all samples, two-dimensional (absorptance at 450 nm or 470 nm vs retention time) and three-dimensional (absorptance vs. wavelength and retention time) chromatograms were obtained and analysed. Peaks were identified first by comparisons to published accounts of relative retention times and spectral absorptance characteristics using similar methods (e.g. Britton 1995; Stradi et al. 1997; Stradi 1998), and quantified by comparisons to standard runs of the same or closely related carotenoids.

EXPERIMENTAL DIET MANIPULATION (PAPER V)

In order to investigate the relative importance of nutritional and metabolic constraints in determining the differential occurrence of red carotenoids and plumage colour in *Euplectes* (see Paper **III**-**V**), a diet supplementation experiment was performed at the University of Gothenburg, Sweden. Specifically, the experiment tested for differences in enzymatic capacity between yellow-crowned bishop *E. afer* and southern red bishop *E. orix*, regarding their ability to

produce red C4-keto-carotenoids (α-doradexanthin and canthaxanthin) from their presumed (but unconfirmed) yellow dietary precursors (lutein and β-carotene).

Three wild-caught *E. afer* and two *E. orix*, of unknown geographic origin, were purchased from an authorized distributor for zoo dealers (Imazo AB, Vara, Sweden). In addition, one *E. orix* male was brought to Gothenburg from KwaZulu-Natal, South Africa. To discriminate between potential constraints on carotenoid metabolism and deposition, respectively, carotenoids in both feathers and plasma were analysed. Reflectance-based colour and pigment samples were taken following 12 months of carotenoid-poor (couscous) diet, containing only small levels of lutein. A β-carotene supplement dispersed in water was then mixed into the diet. Diet supplementation continued for 3-19 weeks until a new prenuptial moult took place, after which measurements were repeated.

RESULTS AND DISCUSSION

PHYLOGENY OF WIDOWBIRDS AND BISHOPS (PAPER I)

Phylogenetic analyses of mitochondrial and nuclear DNA sequences from *Euplectes*, as well as Ploceinae outgroups, showed that widowbirds and bishops together constitute a monophyletic group, i.e. that this genus derive from a single ancestral population, and moreover include all living descendants from this ancestor (Fig. 3). Results also support a sister relationship between *Euplectes* and the genera *Quelea* and *Foudia*, and between these three genera and the main weaver genus *Ploceus*. This corresponds well with the DNA hybridization tree of Sibley and Ahlquist (1990) and a recent mtDNA phylogeny (Sorenson and Payne 2001), as well as with previous groupings based on the behaviour and ecology of Ploceinae genera (Crook 1964).

The traditional taxonomic distinction between widowbirds and bishops (Moreau 1960; Fry and Keith 2004) also received some phylogenetic support, since an early (but not basal) split into tail-ornamented widowbird species with relatively small colour patches ('true' widowbird clade, Fig. 3), and another clade of mostly short-tailed and extensively coloured bishops (red bishop clade, Fig. 3) was found. Interestingly, however, there are several important exceptions to this dichotomy:

First, a most striking deviation from traditional *Euplectes* taxonomy is the placement of the red-collared widowbird *E. ardens*. In spite of exhibiting the third longest tail plumes of all *Euplectes* taxa (see Paper **II**), *E. ardens* clearly belongs to a clade of red bishops, and not to the 'true' widowbirds as previously assumed based on its prenuptial tail moult. Close relatedness between *E. ardens* and the red bishops was also supported by HPLC analyses, showing marked similarity in carotenoid pigment profiles (see Paper **IV-V**).

Second, the yellow-crowned and golden-backed bishops, *E. afer* and *E. aureus*, represent lineages that separated from the ancestors of all other *Euplectes* before the main bishop-widowbird split. This means that red bishop species, in fact, are more closely related to the widowbirds (*E. ardens* in particular) than to any of the yellow bishops. What it does *not* mean (although erroneously suggested in e.g. Paper **I**) is that yellow bishops are in any way 'ancestral' or 'basal', since all extant taxa indeed are equally old. Neither does the tree topology, as such, imply that yellow bishops are closer in appearance (as regards tail length and colour) to the ancestor (Crisp and Cook 2005; Omland et al. 2008). By coincidence, however, these were in fact the results arrived at by ancestral state reconstruction (see Paper **II**-**III** below).
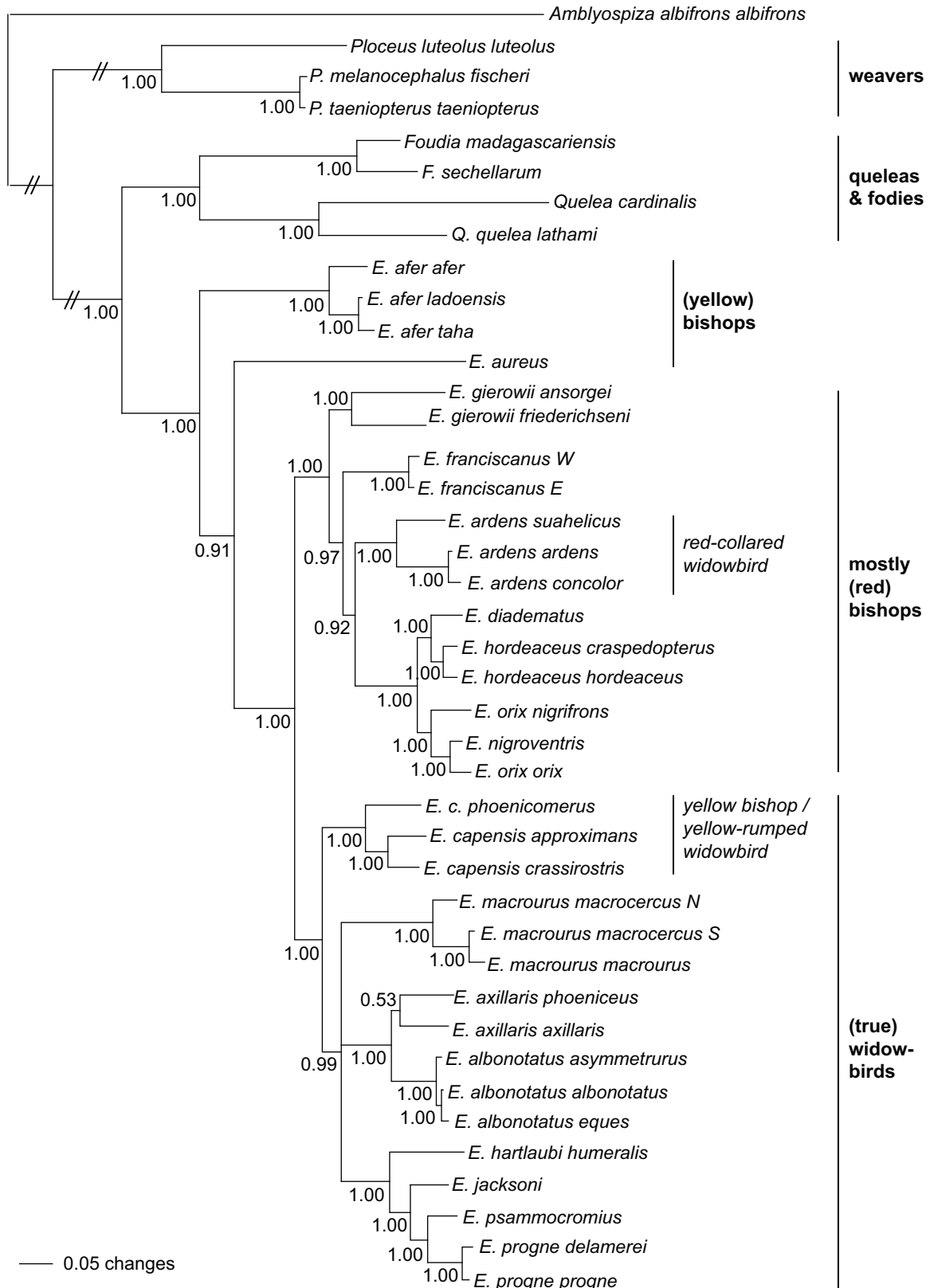
Fig. 3 Bayesian phylogeny estimate for *Euplectes* (species and subspecies), together with eight other Ploceinae species (Paper **I**). Branch lengths represent numbers of nucleotide changes (per DNA sequence position) between interlinked taxa. Numbers show (posterior) probablities of groupings being correct, and vertical lines delineate species (names in italics) or other taxa (bold) referred to in the text. Crossed branches have been shortened for display purposes.

12

Third, *E. capensis*, which has alternately been classified as a tail-moulting bishop (e.g. Howard and Moore 1994) or a short-tailed widowbird (Wolters 1975-82), as reflected by the conflicting common names yellow bishop (East Africa) and cape or yellow-rumped widowbird (Southern Africa), decidedly belongs within the 'true' widowbird clade.

In summary, the molecular phylogeny implies that neither 'bishops' nor 'widowbirds' reflect natural (evolutionary) groups within *Euplectes*. The main reason for this is that nuptial tail ornamentation, on which previous taxonomies were often based, probably has originated twice in this genus, causing close relatives to diverge and distant relatives to converge in this trait (see Paper **II**).

EVOLUTION OF TAIL ORNAMENTATION (PAPER **II**)

In paper **II**, the evolutionary history of tail ornamentation in *Euplectes* was reconstructed using the independently derived molecular phylogeny from Paper **I**, in combination with moult scores and biometry measurements from extant widowbirds and bishops. Specifically, the presence of nuptial tails (i.e. the inclusion of the tail in prenuptial moult) as a discrete ornamental trait, and tail length as a continuously varying trait, were examined.

Reconstruction results suggest that the common ancestor of the genus did not moult into ornamental black tail feathers before breeding, and had a short tail, similar to the bishop species of today (Fig. 4). Nuptials tails have subsequently been gained, and consistently elongated over evolutionary time, both in the red-collared widowbird *E. ardens*, and in the ancestor of the 'true' widowbirds. In both of these clades, previous studies have shown strong sexual selection for long tails through female mate choice (Andersson 1982; Andersson 1992; Pryke et al. 2001a; Pryke and Andersson 2002). Together with recent experimental evidence for female tail preferences also in a (short-tailed) bishop species (Pryke and Andersson 2008), this suggests that the first widowbird tails exploited a pre-existing sensory or cognitive bias. That is, female preferences for tail elongation may have evolved before the long tails, as a side effect of selection on other behaviours, e.g. preferences for larger (higher quality) males. However, as tails grow longer, they also become increasingly costly to produce and fly with, and thus are likely to become condition-dependent signals, as has been suggested for other male traits that supposedly originated as sensory traps (Backwell et al. 1995; Garcia and Ramirez 2005).

The reconstruction of a phylogenetically conserved, and directionally evolving, ornamental trait, differs from many recent suggestions of labile plumage ornaments in e.g. manakins (Pipridae; Prum 1997), bowerbirds (Ptilonorhynchidae; Kusmierski et al. 1997) and new world orioles (*Icterus* spp.; Omland and Lanyon 2000; Hofmann et al. 2006b). This is perhaps not so surprising, given that this study targets a specific display trait, subjected to a strong 'honest indicator' or 'sensory bias' form of sexual selection, rather than a whole suite of, possibly arbitrary, characters involved in Fisherian runaway processes. Nevertheless, the strong and directional exaggeration of a classic and documented sexual signal trait, in *Euplectes*, may serve as an important contrast to the prevailing view of sexual signal traits as particularly labile.
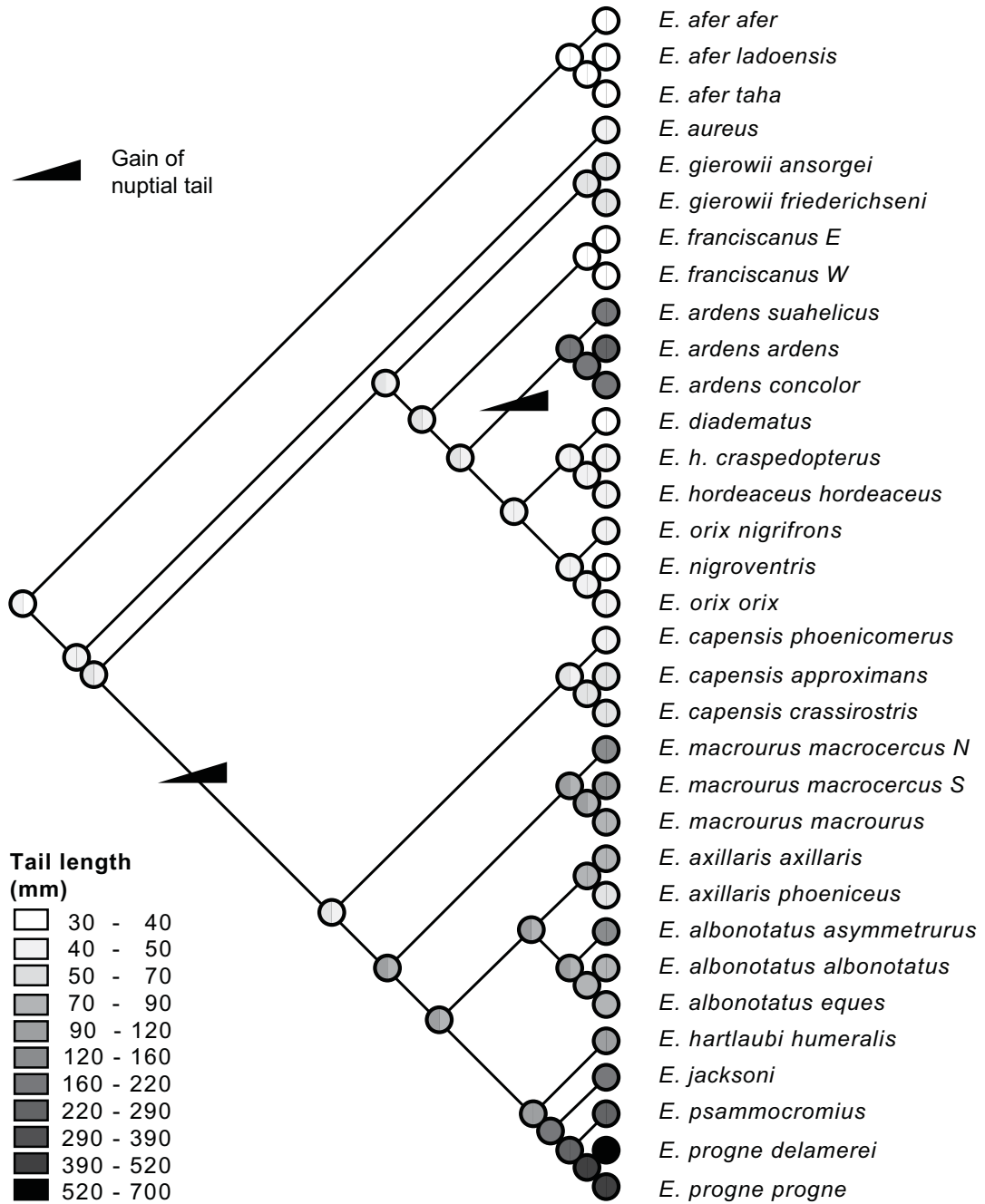
Fig. 4 Reconstructed evolution of tail ornamentation in *Euplectes* (Paper **II**). Triangular symbols represent discrete gains of a nuptial tail (i.e. inclusion of the tail in prenuptial tail moult), as inferred by maximum parsimony. Circles show linear parsimony estimates (single states, or intervals) of continuous tail length in millimeters.
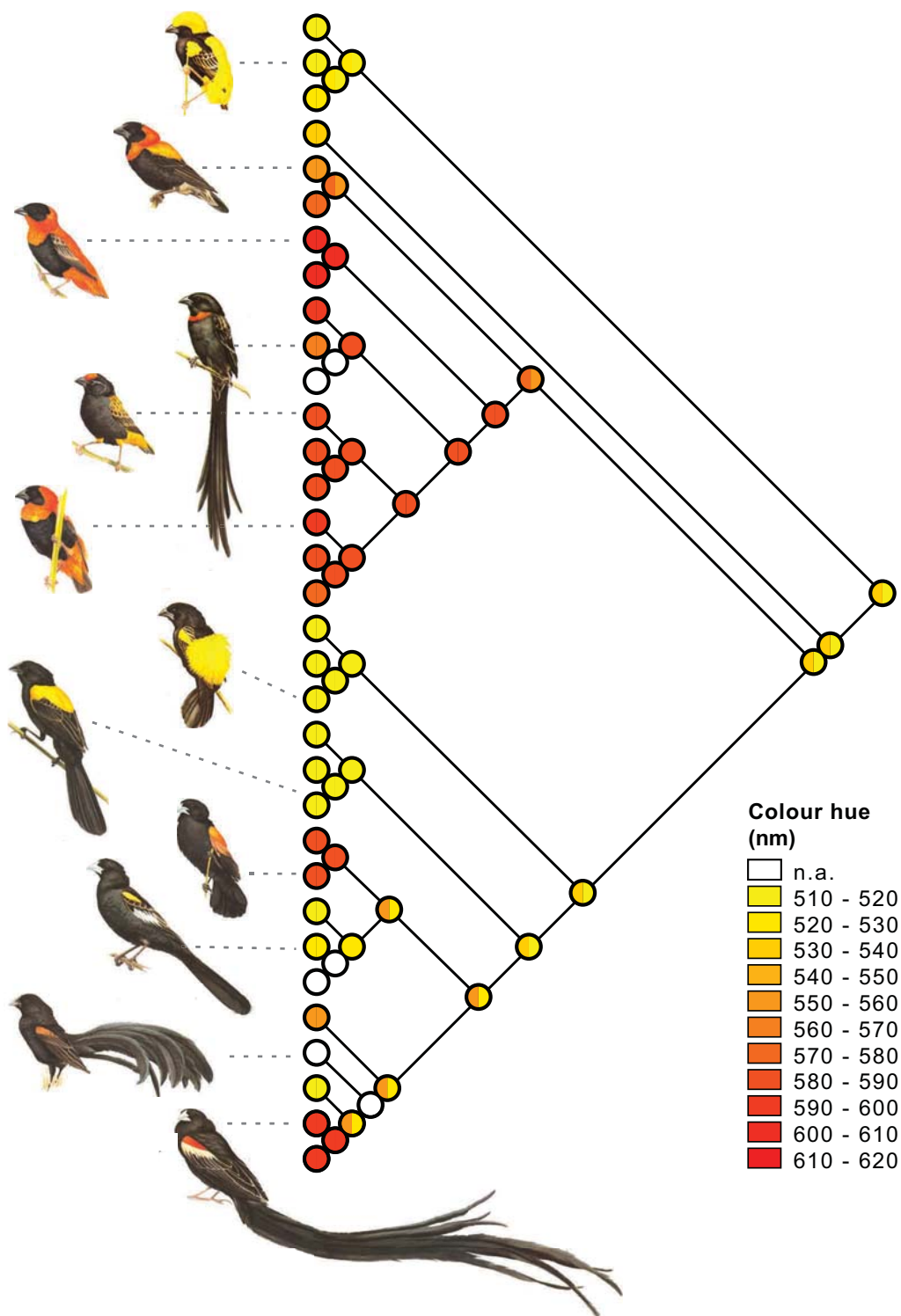
Fig. 5 Reconstructed evolution of carotenoid coloration in *Euplectes* (Paper **III**). Circles represent linear parsimony estimates (single states, or intervals) of continuous colour hue (λR50) in nanometers. For taxa displaying more than one colour, only the reddest (i.e. longest wavelength) hue is included. White circles denote taxa lacking carotenoid pigmentation, and ancestors of these taxa. Bird illustrations by Dale A. Zimmerman.

EVOLUTION OF CAROTENOID COLORATION (PAPER **III**)

Again using the molecular phylogeny from Paper **I**, but now in combination with reflectance-based colorimetry, Paper **III** deals with the evolution of carotenoid colour hue in *Euplectes* and outgroups.

Reconstructions suggest that extant widowbirds and bishops derive from a common ancestor with yellow plumage patches (i.e. with a hue in the 520-540 nm range, Fig. 5). Results furthermore imply that red coloration has evolved repeatedly and independently in the most recent common ancestor of the red bishops-ardens clade, and in the ancestors of the fan-tailed widowbird *E. axillaris* and the long-tailed widowbird *E. progne*. Distant relatives within *Euplectes* thus seem to have converged, not only in nuptial tail length (Paper **II**), but also in terms of carotenoid colour hue. Interestingly, a similar phylogenetic pattern, i.e. a yellow ancestor and subsequent convergent gains of red plumage coloration, was recently reconstructed in the American caciques (genus *Cacicus* and allies; Kiere et al. 2009).

In addition to convergent evolution of red colours, results also show recent losses of carotenoid pigmentation in three taxa, all of which are long-tailed widowbirds (Fig. 5). Given that elongated tails and red carotenoid coloration are both costly and both function to increase male mating success, one may assume an investment trade-off between these two signal traits. This has previously been demonstrated intraspecifically in *E. ardens ardens* (Andersson et al. 2002), but may also translate to a macroevolutionary trade-off responsible for the apparent negative relationship between nuptial tail elongation and coloration in the genus as a whole (Andersson et al. 2002).

Colour convergence in *Euplectes* may have resulted from a general selection pressure for redder (i.e. longer wavelength) colour hues in the genus. The effect of redness on social dominance and agonistic interactions has been well established for two phylogenetically relatively distant *Euplectes* species, i.e. *E. axillaris* (Pryke and Andersson 2003a, b) and *E. ardens* (Pryke et al. 2001b; Pryke et al. 2002). All widowbirds and bishops, as well as the *Quelea* and *Foudia* outgroups in this study, furthermore exhibit similar polygynous mating systems, as well as sexual and seasonal dichromatism (Fry and Keith 2004), suggesting a general sexual signalling role for coloration in the group.

Assuming a generalized selection pressure for redness in *Euplectes*, could yellow species be genetically or physiologically constrained from becoming red? This question was explored in Paper **IV** and **V**.

COLOUR MECHANISMS AND CONSTRAINTS (PAPER **IV** AND **V**)

In paper **IV** and **V**, the mechanistic (biochemical) basis of plumage colour variation in widowbirds and bishops was investigated using reflectance colorimetry, and High Performance Liquid Chromatography (HPLC) analyses of feather and plasma pigments.

Results confirm that the bright yellow, orange and red plumage colours of *Euplectes* are indeed produced by feather deposition of carotenoid pigments, as was previously suggested by Kritzler (1943). Analysing three widowbird and two bishop species, three distinctly different carotenoid profiles (pigment compositions) were found in the genus (Fig. 6):

The yellow plumage colours of yellow-mantled widowbird *E. macrourus* and yellow-crowned bishop *E. afer* primarily derive from the yellow pigments lutein and zeaxanthin (Fig. 6). Together with carotene and cryptoxanthin, these are the most abundant carotenoids in plants (Goodwin 1980), including grass seeds, which constitute the main diet of widowbirds (Craig
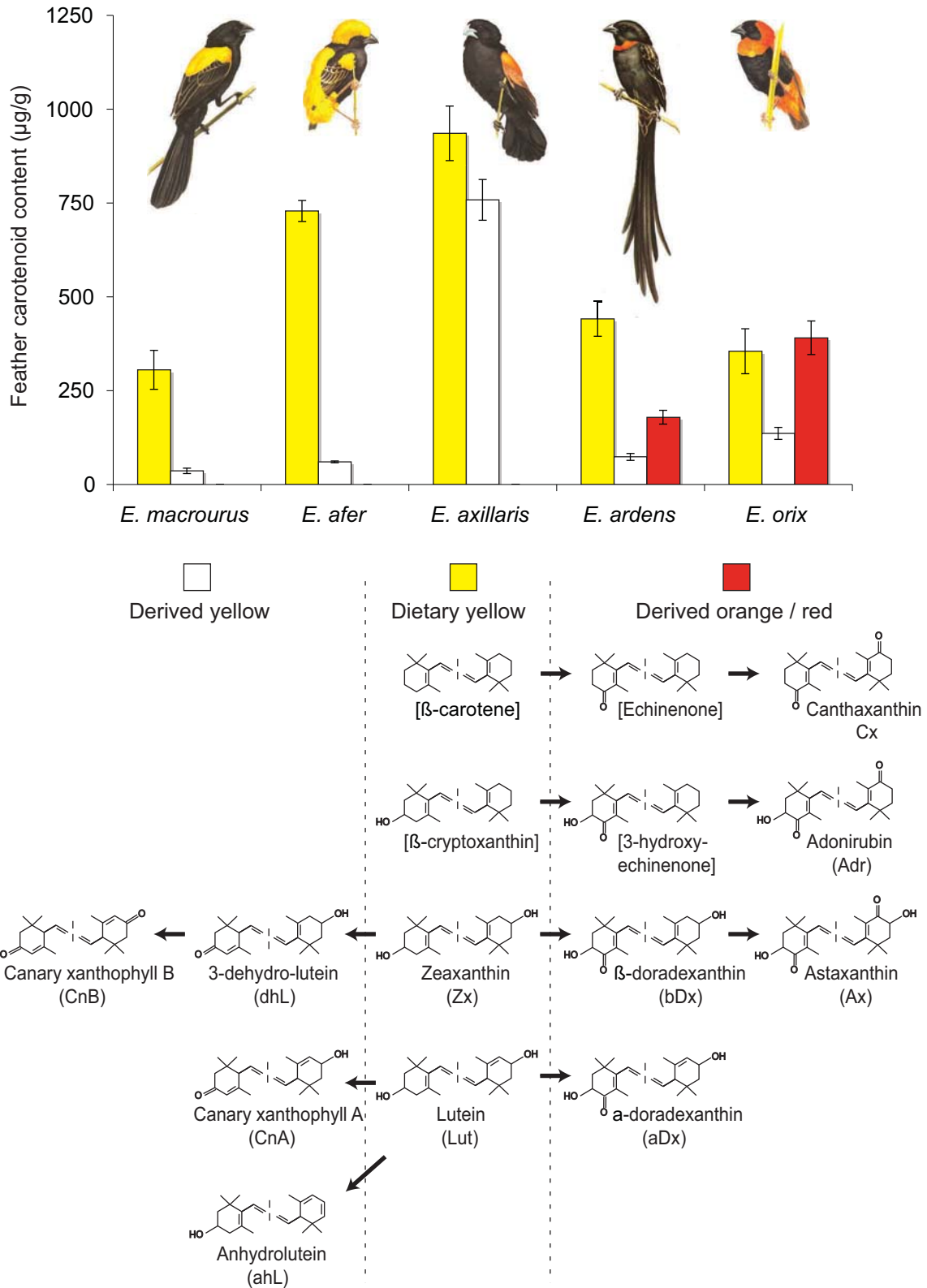
Fig. 6 Plumage carotenoids in five *Euplectes* species (Paper **IV**, **V**). Top: Average (±SE) concentrations of dietary (i.e. direct-deposited) yellow, and metabolically derived yellow and red pigments. Bottom: biochemical structures and metabolic pathways. Arrows pointing left, downwards and right indicate enzymatic dehydrogenation, dehydration and C4 oxygenation, respectively. Brackets indicate inferred but undetected precursors and intermediate derivatives. Bird illustrations by Dale A. Zimmerman.

1980). They are also common in plumages of other birds (Goodwin 1984; Stradi 1998; McGraw 2006). Feathers of *E. macrourus* and *E. afer* also contain small amounts of non-dietary yellow pigments, derived from enzymatic conversion of dietary carotenoids (Stradi 1998; McGraw 2006; Fig. 6).

In the red epaulette feathers of the fan-tailed (a.k.a. red-shouldered) widowbird *E. axillaris*, dietary yellow pigments lutein and zeaxanthin are complemented by large amounts of anhydrolutein. This yellow carotenoid has recently been found in the plumage of two estrildid finch species (McGraw et al. 2002; McGraw and Schuetz 2004), and presumably derives from dehydration of dietary lutein (Khachik et al. 1991; McGraw et al. 2002). Interestingly, *E. axillaris* lack red carotenoids altogether, why red colour in this species is most likely to result from deposition of a very high concentration of yellow pigments, as predicted and discussed by Andersson and Prager (2006). Alternatively, longer wavelength (i.e. red) hues may derive from formation of complexes between yellow carotenoid pigments and feather proteins (i.e. keratin, Stradi et al. 1995).

In contrast to *E. axillaris*, the red-collared widowbird *E. ardens* and the southern red bishop *E. orix* produce bright orange to red colours using relatively small amounts of red carotenoids: mainly α-doradexanthin, but also astaxanthin, canthaxanthin and adonirubin. As red carotenoids generally are scarce or absent in seed diets (Hill 1996) their presence in these plumages are likely to depend on metabolic modification of dietary precursors (see pathways in Fig. 6, and Stradi et al. 1997).

The relative importance of nutritional and metabolic constraints in determining the differential occurrence of red carotenoids and coloration in *Euplectes* was tested in a diet supplementation experiment (Paper **V**). The results confirm that *E. orix*, but not *E. afer*, can manufacture red carotenoids from yellow dietary precursors. Whether this means that yellow *Euplectes* taxa lack the gene coding for the C4 oxygenase enzyme present in the bishop-ardens clade (see Paper **I**), or if the expression of this gene varies among *Euplectes* taxa, either due to differences in sexual selection pressures or in for example energetic constraints, remains to be investigated.

CONCLUSIONS AND FUTURE PERSPECTIVES

This thesis addresses phylogenetic and proximate (i.e. mechanistic and developmental) aspects of tail and colour diversity in the African widowbirds and bishops (*Euplectes* spp.). Combined with several previous studies on adaptive signal functions, it thus provides a unique background for understanding signal diversification in a strikingly ornamented group of birds. Inevitably, results presented here also raise new questions that should be addressed, and will hopefully guide future investigation into signal diversity in this genus, as is suggested below.

In conclusion, widowbirds and bishops (*Euplectes* spp.) together constitute a monophyletic genus, likely to descend from an ancestral weaverbird population where breeding males lacked prenuptial tail moult, had short tails and displayed yellow plumage patches. In contrast, the intrageneric groupings of colourful bishops and long-tailed widowbirds are not monophyletic. Most notably, despite its extravagant tail plumes, the red-collared widowbird *E. ardens* belongs to a subclade of red bishops and not to the sister clade of 'true' widowbirds. Phylogenetic reconstructions accordingly show two convergent gains of nuptial tails and two or three gains of red carotenoid coloration in phylogenetically distant *Euplectes* lineages.

Furthermore, nuptial tails seem to have been consistently elongated over evolutionary time, both in *E. ardens*, and in the 'true' widowbirds.

Combined with previous empirical studies, phylogenetic reconstructions suggest convergent signal exaggeration in response to directional sexual selection for longer tails and redder colours (i.e. more honest quality signals). Whether these selection pressures are truly ubiquitous, and perhaps derive from sensory biases in this genus or in even earlier ancestors, needs to be investigated further, however. In particular, fitness consequences of experimental tail elongation and reddening in *E. afer* or *E. aureus*, both of which separated from remaining *Euplectes* before the evolutionary origins of nuptial tails and red colour hues, would be interesting to study in this respect.

Assuming similar sexual selection intensity, interspecific signal diversity in *Euplectes* is likely to derive from differential signalling conditions or constraints. While environmental influences on signal design and exaggeration is the focus of future investigations, a possible ontogenetic constraint to carotenoid coloration was identified in this thesis. Whereas yellow *Euplectes* colours primarily depend on dietary yellow carotenoids, convergently gained red colours result either from addition of small amounts of metabolically derived red C4-keto-carotenoids or from high concentrations of both dietary and derived yellow pigments. The results indicate that the southern red bishop *E. orix*, but not the yellow-crowned bishop *E. afer*, can manufacture red pigments from yellow dietary precursors. To determine whether these metabolic differences reflect variations in coding genes for relevant enzymes or in expression of these is an exciting ongoing project beyond the scope of this thesis.

ACKNOWLEDGEMENTS

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