Thesis for the degree of Doctor of Philosophy

PHYLOGENY AND SIGNAL DIVERSITY IN WIDOWBIRDS AND BISHOPS (*Euplectes* spp.)

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The oral defence of this thesis will take place at 10:00 am on Friday 12 March 2010, at the Department of Zoology, Medicinaregatan 18, Göteborg, Sweden. The opponent is Associate Professor Kevin Omland from the University of Maryland, Baltimore County, Department of Biological Sciences, Baltimore, MD 21250, USA.

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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 for 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

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