Thesis for the degree of Doctor of Philosophy

Colour Signalling
in Widowbirds and Bishops

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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.