

**The signal function of sexually selected male traits in satin bowerbirds**

*(Ptilonorhynchus violaceus)*

by

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## **ABSTRACT**

The prevalence of colour as a sexually selected trait is probably nowhere as widespread as it is in birds. In Chapter 1, I outline the differences between pigment-based and structurally determined plumage colours in birds and review research performed to date on the signal function of these different types of colour. I highlight the differences between avian and human colour vision, emphasizing the ability of birds to detect ultraviolet wavelengths. I then introduce the Hamilton and Zuk hypothesis of parasite-mediated sexual selection and review the research and controversy that surrounds this hypothesis. I identify bowerbirds as a model system for studies of sexual selection and, in particular, good genes models of parasite-mediated sexual selection. I introduce my study species, the satin bowerbird, and review what is known about its mating system, devoting particular attention to plumage colouration and bower elaboration. Chapter 2 summarizes my investigation of the signal function of sexually selected male traits in satin bowerbirds. I use spectrometry to quantify male plumage colouration in this species and I use standardized techniques to measure bower quality. I show that adult male plumage is highly reflective in the ultraviolet range in satin bowerbirds. I also demonstrate that plumage colouration and bower features signal various aspects of male quality, including parasite load, body size, and feather growth rate. I argue that plumage characters and bower features together constitute the extended phenotype of satin bowerbirds. In Chapter 3, I present an overview of my main findings and discuss the implications of my research, some limitations of my study, and potential avenues for future research.

## **CO–AUTHORSHIP**

The main data chapter (Chapter 2) of this thesis is written in the form of a scientific paper and has been submitted for publication. My supervisor, Dr. Robert Montgomerie, is co–author on that manuscript and I thank him for his contribution to ideas, study design, analysis, and editing. I am solely responsible for Chapters 1 and 3 of this thesis and as such, they are written in first person singular.

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# **Chapter 1**

**General Introduction and Literature Review**

## **Plumage colouration and sexual selection in birds**

Avian plumage ornaments may be one of the most notable examples of elaborate trait expression driven by sexual selection. According to Darwin (1871), “Secondary sexual characters are more diversified and conspicuous in birds than in any other class of animals.” While extreme examples of elaborate ornaments such as the trains of peacocks, the feather plumes of birds of paradise, and the elongated tails of widowbirds appear to be limited to a few taxa, the prevalence of colour as a sexually selected ornament is widespread (Owens and Hartley 1998). Plumage colouration in particular appears to be maintained by sexual selection in many species and a large body of research has been devoted to understanding the patterns of selection observable today (reviewed in Andersson 1994).

Plumage colouration can be separated into broad categories based on two causal mechanisms: pigmentation and reflective feather microstructure (Keyser and Hill 1999). Carotenoid pigments are responsible for the appearance of red, orange and yellow feathers, while melanin pigments produce black, brown and gray feathers (Fox 1976). On the other hand, colours such as ultraviolet, blue, green, and iridescence result from the organization of feather constituents. Light waves reaching the feathers are reorganized as they encounter the spongy keratin matrix of feather barbs. Through constructive interference, created by the periodicity and spatial distribution of keratin proteins and air spaces, only short wavelengths are reinforced, giving structural colours their ultraviolet or blue appearance (Prum et al. 1998, 1999). While carotenoid pigments can be important vitamin A precursors and antioxidants (Olson and Owens 1998) and melanin pigments

can be used in thermoregulation and abrasion resistance (Bonser 1995), structural colours appear to serve a strictly ornamental function.

### **Carotenoid–based plumage colouration**

Pigment–based colours have been disproportionately well studied (Andersson 1994). Within carotenoid–based signaling systems, for example, we now understand where carotenoids are obtained, how they are deposited in feathers, how the environment can influence carotenoid colouration, and what information is signaled to conspecifics with these colours (Olson and Owens 1998, Hill 1999). The house finch, *Carpodacus mexicanus*, has proven to be a remarkable model system for investigating these proximate and ultimate mechanisms (Olson and Owens 1998). In this sexually dichromatic species, males show conspicuous variation in hue from yellow to red, and females preferentially select the reddest males as mates (Hill 1990, 1991). Since carotenoids must be obtained from the diet (Olson and Owens 1998), only males with better access to resources or superior carotenoid uptake, transformation, or deposition mechanisms can become brightly coloured (Hill 1992, Hill et al. 1994). Furthermore, the reddest male house finches have been shown to be in superior nutritional condition (Hill and Montgomerie 1994), to have fewer feather mites and avian pox lesions (Thompson et al. 1997), and to be less likely to become infected by endoparasitic coccidia (Brawner et al. 2000). Thus, by choosing the reddest males as partners, females are choosing high quality males and may benefit from this choice directly (male provisioning; Hill 1991, Senar et al. 2002) and perhaps also indirectly (good genes; Hill 1991). Although much of the revolutionary work on the quality signaling potential of carotenoid colours has been developed in house

finches, many of the findings have been supported in other species such as yellowhammers, *Emberiza citrinella* (Sundberg 1995a, Sundberg and Dixon 1996), northern cardinals, *Cardinalis cardinalis* (Wolfenbarger 1999), American goldfinches, *Carduelis tristis* (McGraw and Hill 2000), collared widowbirds, *Euplectes ardens* (Pryke et al. 2001), and blue tits, *Parus caeruleus* (Senar et al. 2002).

### **Melanin-based plumage colouration**

The signal function of melanin pigmentation has similarly received considerable attention (Andersson 1994). In general, it appears that while carotenoid pigmentation is largely influenced by female choice, melanin pigmentation may be strongly influenced by male–male interaction (Badyaev and Hill 2000, but see Thusius et al. 2001). Over two decades ago, Rohwer (1975) proposed that melanin patches could be used as signals of social dominance in some species of birds (Status Signaling Hypothesis). It has since been shown that the size of melanin badges does reflect social rank in many species of birds (reviewed in Senar 1999). However, the mechanism whereby melanin badges signal social rank has yet to be clearly determined. Some studies suggest that, like carotenoid pigmentation, variation in melanin pigmentation may reflect individual condition. For example, Veiga and Puerta (1996) showed that levels of circulating blood protein were positively correlated with badge size in juvenile house sparrows, *Passer domesticus*. Similarly, Slagsvold and Lifjeld (1992) showed that nestling body mass was associated with increasingly melanized breeding plumage in pied flycatchers, *Ficedula hypoleuca*. However, some features of melanin pigmentation suggest that another mechanism may be responsible for regulating variation in badge size.

Melanin pigments differ from carotenoid pigments in that they do not need to be obtained externally; they can be synthesized within the body from basic amino acid precursors (Fox 1976). As such, melanin deposition in feathers should entail little physiological cost. Furthermore, melanin deposition appears to be largely under genetic control in some species (Møller 1989, Norris 1993, Roulin et al. 1998, but see Griffith et al. 1999). For these reasons, it has been suggested that melanin pigmentation should vary little with environmental stress and thus be a poor indicator of condition. This idea first received some support in house finches, where melanin pigmentation of tail feathers did not vary with experimental infection by coccidians (Hill and Brawnner 1998). However, tail feathers are not ornamental in house finches and thus may not be expected to vary with infection. More convincing evidence emerged from a recent study of American goldfinches in which experimental infection by coccidians had a significant negative effect on carotenoid-based yellow plumage but not on melanin-based black plumage (McGraw and Hill 2000). This latter study was the first to experimentally test the signal function of two different ornamental plumage regions with different colouration mechanisms. Finally, McGraw et al. (2002b) found that experimentally imposed nutritional stress during moult negatively influenced structural but not melanin-based plumage ornamentation in house sparrows and brown-headed cowbirds, *Molothrus ater*, suggesting that there may indeed be little physiological cost imposed by melanin deposition.

How can we explain the evolution of a plumage badge that signals rank but cannot be influenced by condition? Since melanin pigmentation signals social dominance, perhaps an individual's social environment during moult plays an important



role in determining melanin-based plumage ornamentation. In support of this argument, one recent study shows that melanin badge size increases with aggressiveness in house sparrows (McGraw et al. 2002a). Furthermore, in this study, the level of aggression between birds was a much better predictor of post-moult badge size than was pre-moult badge size (McGraw et al. 2002a). These recent findings suggest that social environment during moult may be an important determinant of the expression of melanin badges of status and may also provide a link between testosterone-mediated badge size and social dominance (Evans et al. 2000, Gonzalez et al. 2001). In summary, despite contention over the proximate mechanisms determining melanin-based badge size, there is general agreement that melanin-based plumage badges are reliable indicators of social status in some species (Senar et al. 1999).

### **Structural colours and avian colour vision**

Evolutionary biologists have recently become interested in an entirely different type of plumage colouration. Structural colours, which are produced by the microstructural arrangement of feather constituents, were first described decades ago (Auber 1957). Yet, despite the fact that the proximate basis for variation in structural plumage colouration allows for a unique suite of potential signaling mechanisms, structural colours have remained relatively unstudied until recently. The lack of attention devoted to structural plumage colouration may stem in part from the limitations of human vision; to humans, structurally-coloured traits appear to lack the extensive variation in hue described in the carotenoid colouration of some species (Hill 1991, Dale et al. 2001) and the variation in patch size described in the melanin colouration of other species (Järvi

and Bakken 1984, Møller 1987, Otter and Ratcliffe 1999, Thusius et al. 2001). However, this apparent lack of variation likely arises from the limitations of human vision.

Bird colour vision is perhaps the most sophisticated visual system among vertebrates and far exceeds the capabilities of human vision (Cuthill et al. 2000). First, while humans have only three types of retinal cone photoreceptors (blue, red and green), most birds have a fourth type of retinal cone that is usually sensitive to ultraviolet (UV) wavelengths (300–400 nm; Cuthill et al. 2000). Together with UV-transparent ocular media, the fourth retinal cone photoreceptor confers birds with considerable UV photosensitivity. This visual system provides birds with the ability to detect ultraviolet light and also allows for enhanced discriminatory capability at all shorter wavelengths from ultraviolet to blue (Cuthill et al. 2000). Another factor differentiating between avian and human vision is that, in birds, each cone type is associated with a pigmented oil droplet that narrows the waveband to which each cone is maximally sensitive, thereby decreasing the overlap in spectral sensitivity between cone types. The narrowed spectral sensitivity of cone types is thought to enhance colour saturation and hue discrimination and to improve colour constancy (Vorobyev et al. 1998). Colour constancy is the phenomenon that allows individuals to perceive an object's colour as the same under changing light conditions and may be important when the spectral quality of light is variable (Cuthill et al. 2000). Therefore, bird colour vision is inherently different from human vision, particularly from the short wavelength range of the visual spectrum to the ultraviolet range. Consequently, traditional human-based assessment of bird plumage colouration may not be an adequate approximation of patterns perceptible to birds, particularly with respect to structural colours.

Spectrometry, the technique that uses a spectrometer to quantify the amount of light reflected by an object at specific wavelengths, has proven to be an ideal tool for the objective measurement of animal colour patterns (Endler 1990). The use of spectrometry to measure bird plumage colours first emerged from a need to quantify colour rather than make qualitative comparisons of colour chips (Bennett et al. 1994), and was further driven by an interest in identifying ‘cryptic’ ultraviolet patterns (Bennett and Cuthill 1994, Andersson 1996, Hunt et al. 1998). For example, Hunt et al. (1998) showed that seemingly sexually monochromatic blue tits are actually dichromatic when an assessment of plumage colouration includes the ultraviolet range. While these cryptic signals are interesting, they are probably uncommon (Bennett and Cuthill 1994). However, these early studies of cryptic ultraviolet signals paved the way for studies of individual variation in structural plumage colouration. While humans perceive little variation in structural plumage colouration (e.g. Borgia and Collis 1989), the use of spectrometry has revealed that in many species, structural plumage colouration is surprisingly variable (Andersson and Amundsen 1997, Bennett et al. 1997, Hunt et al. 1998, Keyser and Hill 1999). For example, Keyser and Hill (1999) describe individual variation in the structural plumage colouration of blue grosbeaks, *Guiraca caerulea*, that is comparable to the conspicuous variation in the carotenoid colouration of house finches (Hill 1991).

Individual variation in structural plumage characters appears to be maintained by sexual selection through female choice in many species, including blue tits (Andersson et al. 1998, Hunt et al. 1998, Sheldon et al. 1999), bluethroats, *Luscinia svecica*, both in captivity (Andersson and Amundsen 1997) and in the wild (Johnsen et al. 1998), and European starlings, *Sturnus vulgaris*, (Bennett et al. 1997). The role of structural plumage

colouration for intrasexual signaling remains largely unexplored, although some studies suggest that structural colours could potentially serve as status signals in male–male competition (Keyser and Hill 2000).

While it is becoming clear that structural plumage colouration may be a sexually selected male trait, hypotheses on the signal function of individual variation in structural colour are just beginning to emerge. In one comparative study, the degree of structurally–based sexual dichromatism among passerines was positively associated with rates of extra–pair paternity (Owens and Hartley 1998). Intraspecific studies suggest multiple signal functions. For example, in blue grosbeaks, male blueness was shown to be partially dependent on nutritional condition (Keyser and Hill 1999). In a follow–up study, the bluest male grosbeaks were larger, defended larger territories with higher prey abundances, and tended to feed their nestlings more often than did duller males (Keyser and Hill 2000). In blue tits, the saturation of the ultraviolet colouration of the crest was shown to predict survival to the following breeding season, suggesting that structural colouration could be an honest indicator of viability (Sheldon et al. 1999). Finally, in blue–black grassquits, *Volatinia jacarina*, the brightness of structural plumage colouration was shown to be related to nutritional condition (Doucet 2002), as in blue grosbeaks. While these studies indicate that structural plumage colour is associated with indicators of male quality, a proximate link between structural plumage colouration and individual quality remains to be established. One potential proximate mechanism, the influence of parasites on plumage colouration, has yet to be explicitly investigated in relation to structural plumage colouration.

## **Parasites and plumage colouration in birds**

It is now generally understood that in some species, females prefer to mate with brightly coloured individuals (Andersson 1994); however, the mechanism maintaining this female preference is still subject to much debate. Hamilton and Zuk (1982) proposed a controversial theory linking female preference for bright males and a good genes model of sexual selection; they argued that plumage brightness might be associated with heritable parasite resistance (parasites considered in the broadest evolutionary sense; Hamilton and Zuk 1982). Thus, by choosing brightly coloured males, females could acquire parasite resistance genes for their offspring. If brilliant colours evolved to reveal parasite resistance, it follows that those species most susceptible to parasites would evolve bright plumage because of increased pressure to reveal freedom from parasites. Within a species, males with fewer parasites should be brighter. In support of their hypothesis, Hamilton and Zuk (1982) found that across North American passerines, there was a positive association between plumage brightness and incidence of infection from blood parasites.

Since its initial proposition, the Hamilton–Zuk hypothesis has generated a large body of research (reviewed in Read 1988, Clayton 1991). The Hamilton–Zuk hypothesis has received some support from both interspecific and intraspecific studies. For example, Pruett–Jones et al. (1990) showed that across species of birds of paradise, there was a positive association between relative parasite intensity and showiness in males. Similarly, in a study of North American passerines John (1995) showed that when overt polygynists were excluded, there was a positive relationship between plumage brightness and the

occurrence of haematozoan parasites. Some predictions of the Hamilton–Zuk hypothesis have also been supported intraspecifically. For example, Sundberg (1995b) showed that in yellowhammers, plumage brightness was negatively associated with the intensity of haematozoan parasitic infection and that more parasitized males produced fewer fledgelings. Similarly, Thompson et al. (1997) showed that in house finches, ectoparasitic feather mite burdens and endoparasitic avian pox infections during moult were associated with reduced expression of bright male plumage. Finally, Figuerola et al. (1999) showed that in ciril buntings, *Emberiza cirilus*, higher blood parasite infection intensities were associated with a reduction in carotenoid–based patch size. Evidence from experimental studies also supports the Hamilton–Zuk hypothesis: in American goldfinches, experimental infection with endoparasitic coccidians during moult was shown to reduce the expression of carotenoid–based plumage ornamentation (McGraw and Hill 2000).

Despite the fact that some studies have generally supported predictions of the Hamilton–Zuk hypothesis, many others have found inconclusive or even contradicting results. For example, Garvin and Remsen (1997) showed that nest height was a better predictor of blood parasite prevalence than either plumage brightness or degree of sexual dichromatism. They argued that brightly coloured species, which tend to nest at greater heights than do dull species, are more susceptible to ornithophilic vectors known to be more common in the canopy. Similarly, Walther et al. (1999) found no relationship between ectoparasite abundance and male brightness among 122 species of neotropical birds. Furthermore, among non–passerine species there was a significant negative relationship between parasite abundance and showiness (Walther et al. 1999), a direction opposite to that predicted by Hamilton and Zuk (1982). Not surprisingly, the authors also

found that brighter species nested in higher forest strata than drab species (Walther et al. 1999). Some intraspecific studies have also failed to show support for the Hamilton–Zuk hypothesis. For example, in pied flycatchers there was no clear relationship between male plumage brightness and blood parasite infection (Dale et al. 1996).

While the studies described above represent only a small subset of the large body of research devoted to testing the Hamilton–Zuk hypothesis, they are representative of the research in this field and of the controversy that continues to surround the hypothesis. Some points of criticism of the hypothesis persist throughout the literature. For example, in comparative studies, the fact that parasite abundances vary both temporally and geographically within a species is often identified as a potentially confounding factor (Merila et al. 1995, Yezerinac and Weatherhead 1995). Also, as indicated in the research described earlier, plumage colouration may be related to foraging stratum or mating system, variables that may make some species more susceptible to parasites independent of plumage colouration (John 1995, Garvin and Remsen 1997, Walther et al. 1999). For these reasons, it may be most appropriate to investigate the Hamilton–Zuk hypothesis intraspecifically.

In a meta-analysis of 199 tests of the Hamilton–Zuk hypothesis, intraspecific studies generally show less support for the hypothesis than comparative studies (Hamilton and Poulin 1997). However, just as a negative association between parasites and plumage brightness does not show conclusive support for the Hamilton–Zuk hypothesis, the lack of a relationship does not necessarily refute the hypothesis. First, it is important for researchers to clearly distinguish between the different types of

parasite-mediated sexual selection under investigation. Females may use secondary sexual characters to select parasite-free individuals for reasons other than acquiring good genes for their offspring as the Hamilton–Zuk model suggests. For example, females may avoid parasitized males in order to avoid the direct transmission of parasites to themselves or to their offspring (Clayton 1991). Alternatively, females may choose unparasitized males who are more likely to provide resources such as help with parental care (Clayton 1991). Thus, in order to test the Hamilton–Zuk hypothesis appropriately, one should ideally investigate a host species in which males provide no resources and a parasite species that is not transmitted through host proximity (Clayton 1991). Another important point to consider is that male showiness should be measured using sensory modes relevant to the host and not the investigator (Endler and Lyles 1989, Clayton 1991). Thus, brightness measures of showiness should be used in species in which visual communication is important in mate choice, and brightness should be quantified objectively. These restrictions may in part explain the lack of support for the Hamilton–Zuk hypothesis in some intraspecific studies. Furthermore, these restrictions identify one group of birds as ideal candidates for investigations of both general sexual selection theory and good genes models of parasite-mediated sexual selection: the bowerbirds of Australia and New Guinea.

### **Bowerbirds and sexual selection**

The bowerbirds form a monophyletic family endemic to Australia and New Guinea (Kumierski et al. 1997). They are unique among birds in that they build display structures, called bowers, which are used strictly as mating arenas. Darwin (1871) quoted



the ornithologist John Gould as saying: “These highly decorated halls of assembly must be regarded as the most wonderful instances of bird–architecture yet discovered.”

Bowers, which are often associated with cleared display courts decorated with colourful objects, are subject to intense sexual selection. Females prefer to mate with males who construct larger, better quality, and more highly decorated bowers (Borgia 1985, Borgia and Mueller 1992, Lenz 1994). Given that bower quality can be easily quantified and manipulated, bowerbirds are ideal species for both intraspecific and comparative investigations of the evolution of sexually selected male traits (Borgia 1985, Kumierski et al. 1997, Humphries and Ruxton 1999). The bowerbird species to have received the most research attention to date is the satin bowerbird, *Ptilonorhynchus violaceus*. We owe much of our current understanding of the mating system of satin bowerbirds to research undertaken by Gerald Borgia and his colleagues at the University of Maryland. Gerald Borgia and his students have devoted over two decades to the long–term study of one particular population of satin bowerbirds.

### **Study species: the satin bowerbird**

Satin bowerbirds are large, sexually dichromatic passerines. They inhabit rainforest and wet sclerophyll forest along the eastern coast of Australia (figure 1). Their distribution is divided into two widely separated populations that correspond to different races of satin bowerbird; the race *minor* is limited to the Atherton Tablelands of northeast Queensland while the race *violaceus* ranges from southeast Queensland to eastern Victoria (figure 1). Gerald Borgia’s work has largely focused on a New South Wales population of satin bowerbirds, while my study population was located near Atherton,

Queensland (figure 2). In satin bowerbirds, adult male plumage consists of an iridescent blue that varies from almost black in low light conditions to bright lilac in direct sunlight (figure 3a). Females and juveniles, on the other hand, are green above with scalloped beige and brown patterning on the breast (figure 3b). Young males retain their cryptic green plumage until their seventh year. During their first six years, immature males are subordinate to adult birds at feeding sites and spend much of their time observing adult birds or practicing bower building and displaying when bower owners are away (Collis and Borgia 1992, S. Doucet personal observation). Once they reach adult plumage, males can start to build and maintain their own permanent bower sites (Collis and Borgia 1992).

The bower of the satin bowerbird is an avenue-type bower consisting of two parallel walls that are slightly curved toward the inside of the avenue (figure 4). It is constructed from fine twigs woven into place on a cleared display court which is covered with pale yellow twigs. Satin bowerbirds decorate their bowers with a variety of natural and human-manufactured objects including blue feathers, snail shells, blue berries, blue or yellow flowers, insect exoskeletons, small mammal skulls and other bones, and pieces of blue plastic (Marshall 1954, Gilliard 1969, S. Doucet personal observation). Some of these objects are uncommon in the rainforest, and males often steal decorations from each other's bowers; Borgia and Gore (1986) suggest that male satin bowerbirds obtain most of the feathers adorning their bowers by pilfering other males' bowers. Satin bowerbirds are also renowned for their preference for blue bower decorations and those located near human habitation have been reported to include blue laundry bags and children's blue toys in their bowers (Marshall 1954, Gilliard 1969). In fact, Australian government

agencies discourage the use of blue flagging tape and the manufacture of blue milk bottle caps has been discontinued in some states.

To demonstrate that colour preference is not merely incidental to the preference for specific objects, Borgia et al. (1986) showed that male satin bowerbirds would decorate their bowers with white flowers that were experimentally dyed blue, but not those dyed red. An experiment I performed further supported Borgia et al.'s (1986) findings. I allowed male satin bowerbirds to choose between five different colours of dyed feathers for which I had obtained detailed spectral measurements. I then visited bowers every hour until males chose at least one colour, after which I visited the bowers every two hours over the course of two days. Of the ten males that integrated the experimental decorations into their bowers, all incorporated blue feathers in their first choice (table 1). Males tended to choose yellow and green feathers second and one male even chose the orange feathers, but no male selected the red feathers. Only blue feathers were ever stolen by other males. Thus, male satin bowerbirds clearly prefer blue decorations for their bowers even when controlling for decoration type.

As with most bowerbirds, satin bowerbirds engage in a polygynous mating system. Females visit males at their respective bowers and observe the males display from within the walls of the bower avenue (Borgia 1986b). During the display, a male usually picks up a decoration with his beak, often a yellow leaf, and performs highly ritualized courtship behaviours which include prancing, wing beating, producing mechanical calls and mimicking other species' songs (Borgia 1986b). An approving female will allow the male to mount her and copulate from within the bower avenue. The female is entirely responsible for nest building and parental care duties (Borgia 1986b).

In investigations by Borgia (1985) and Uy et al. (2001), a few males in their population obtained a disproportionately high number of matings while some bower–holding males did not mate at all.

### **Parasites and satin bowerbirds**

Satin bowerbirds appear ideally suited for investigations of the good genes model of parasite–mediated sexual selection of plumage colouration (Hamilton and Zuk 1982). First, males are conspicuously sexually dichromatic and display bright, iridescent structural plumage colouration (figure 3). Second, males provide only gametes to females; thus, good genes models can be investigated without potentially confounding factors such as increased paternal care from parasite–free males. Finally, satin bowerbirds are infected by a number of species of parasites that can be quantified relatively easily. It is therefore not surprising that satin bowerbirds have been the focus of investigations of parasite–mediated sexual selection (Borgia 1986a, Borgia and Collis 1989, Borgia and Collis 1990).

Borgia (1986a) first showed that there was no relationship between mating success and ectoparasite load in satin bowerbirds and therefore failed to support predictions of parasite–mediated sexual selection theory. However, only three of 20 bower–holding males were infected with ectoparasites in his investigation. In a second study, Borgia and Collis (1989) found that there was a negative relationship between ectoparasite load and mating success in their population. Borgia and Collis (1989) also attempted to score male plumage colouration visually, but given the limitations of human

vision they could find no consistent differences between males. Given that ectoparasites are quite visible in satin bowerbirds, Borgia and Collis (1989) suggested that their findings favored a parasite avoidance model of parasite-mediated sexual selection. However, as they pointed out themselves, the fact that females had more parasites than males was not consistent with the parasite avoidance model. In a third study, Borgia and Collis (1990) pooled their data from the two previous studies and revisited the predictions of the good genes model, the correlated infection model, and the parasite avoidance model of parasite-mediated sexual selection. Again, the parasite avoidance model was favored (Borgia and Collis 1990).

I believed that the Hamilton–Zuk hypothesis of parasite-mediated sexual selection warranted further investigation in satin bowerbirds for several reasons. First, the key intraspecific prediction of the Hamilton–Zuk hypothesis is a negative correlation between plumage brightness and parasite load (Hamilton and Zuk 1982). Due to lack of necessary tools, previous researchers could not measure plumage colouration and therefore could not assess a fundamental prediction of the hypothesis they were testing (Borgia 1986a, Borgia and Collis 1989, Borgia and Collis 1990). Second, as they point out themselves, the investigators considered only ectoparasite load, despite the fact that ectoparasites are not the kind of parasite Hamilton and Zuk (1982) predicted to be important in shaping mating preferences (Borgia and Collis 1990). The investigators suggest that perhaps ectoparasite load is correlated with the intensity of infection by endoparasites (Borgia and Collis 1989), but I found no such relationship in my own data (Doucet, unpublished results). Third, as mentioned above, the fact that females have more parasites than males is not consistent with the bright male hypothesis. Thus, I felt that by

using the appropriate tools to measure plumage colouration, and by quantifying more than one type of parasite, I could improve on previous studies of parasite-mediated sexual selection in satin bowerbirds.

### **Thesis outline**

The purpose of my thesis was to investigate the signal function of sexually selected male traits in satin bowerbirds. It has been well established that bower quality is an important feature of mate choice in this species (Borgia 1985), but I was curious to learn what specific information females might obtain from assessing bower quality. I was also particularly interested in quantifying plumage colouration in this species. I wondered how plumage colouration covaried with bower quality and other aspects of male quality. Finally, I felt that the satin bowerbird was an ideal species within which to test good genes models of parasite-mediated sexual selection, given that males provide no parental care and are differentially infected with quantifiable parasite species. The main chapter of this thesis details the relationship between plumage colouration, bower quality, and parasite abundance in adult male satin bowerbirds.

### **References**

- Andersson, M. B. 1994. *Sexual Selection*. Princeton, Princeton University Press.
- Andersson, S. 1996. Bright ultraviolet colouration in the Asian whistling-thrushes (*Myiophonus* spp.) *Proceedings of the Royal Society of London B* 263: 843–848.
- Andersson, S. and Amundsen, T. 1997. Ultraviolet colour vision and ornamentation in Bluethroats. *Proceedings of the Royal Society of London B* 264: 1587–1591.

- Andersson, S., Örnborg, J., and Andersson, M. 1998. Ultraviolet sexual dimorphism and assortative mating in blue tits. *Proceedings of the Royal Society of London B* 263:843–848.
- Auber, L. 1957. The distribution of structural colours and unusual pigments in the class Aves. *Ibis* 99:463–476.
- Badyaev, A. V. and Hill, G. E. 2000. Evolution of sexual dichromatism: contribution of carotenoid– versus melanin–based plumage coloration. *Biological Journal of the Linnean Society* 69: 153–172.
- Bennett, A. T. D. and Cuthill, I. C. 1994. Ultraviolet vision in birds: what is its function? *Vision Research* 34: 1471–1478.
- Bennett, A. T. D., Cuthill, I. C., and Norris, K. J. 1994. Sexual selection and the mismeasure of colour. *American Naturalist* 144: 848–860.
- Bennett, A. T. D., Cuthill, I. C., Partridge, J. C., and Lunau, K. 1997. Ultraviolet plumage colors predict mate preferences in starlings. *Proceedings of the National Academy of Sciences, USA* 94: 8618–8621.
- Bonser, R. H. C. 1995. Melanin and the abrasion resistance of feathers. *Condor* 97: 590–591.
- Borgia, G. 1985. Bower quality, number of decorations and mating success of male satin bowerbirds (*Ptilonorhynchus violaceus*): an experimental analysis. *Animal Behaviour* 33: 266–271.
- Borgia, G. 1986a. Satin bowerbird parasites: a test of the bright male hypothesis. *Behavioral Ecology and Sociobiology* 19: 355–358.
- Borgia, G. 1986b. Sexual selection in bowerbirds. *Scientific American* 254: 70–79.
- Borgia, G. and Collis, K. 1989. Female choice for parasite–free male satin bowerbirds and the evolution of bright male plumage. *Behavioral Ecology and Sociobiology* 25: 445–454.
- Borgia, G. and Collis, K. 1990. Parasites and bright male plumage in the satin bowerbird (*Ptilonorhynchus violaceus*). *American Zoologist* 30: 279–285.
- Borgia, G. and Gore, M. A. 1986 Feather stealing in the satin bowerbird (*Ptilonorhynchus violaceus*): male competition and the quality of display. *Animal Behaviour* 34: 727–738.

- Borgia, G. and Mueller, U. 1992. Bower destruction, decoration stealing and female choice in the spotted bowerbird *Chlamydera maculata*. *Emu* 92: 11–18.
- Borgia, G., Kaatz, I. M., and Condit, R. 1986. Flower choice and bower decoration in the satin bowerbird *Ptilonorhynchus violaceus*: a test of hypotheses for the evolution of male display. *Animal Behaviour* 35:1129–1139.
- Brawner, W. R. III, Hill, G. E., and Sunderman, C. A. 2000. Effects of coccidial and mycoplasmal infections on carotenoid-based plumage pigmentation in male house finches. *Auk* 177: 952–963.
- Clayton, D. H. 1991. The influence of parasites on host sexual selection. *Parasitology Today* 7: 329–334.
- Collis, K. and Borgia, G. 1992. Age-related effects of testosterone, plumage, and experience on aggression and social dominance in juvenile male satin bowerbirds (*Ptilonorhynchus violaceus*). *Auk* 109: 422–434.
- Cuthill, I. C., Partridge, J. C., Bennett, A.T. D., Church, S. C., Hart, N. S., and Hunt, S. 2000. Ultraviolet vision in birds. *Advances in the Study of Behavior* 29: 159–214.
- Dale, S., Kruszewicz, A., and Slagsvold, T. 1996. Effects of blood parasites on sexual and natural selection in the pied flycatcher. *Journal of Zoology, London* 238: 373–393.
- Dale, J., Lank, D. B., and Reeve, H. K. 2001. Signaling individual identity versus quality: a model and case studies with ruffs, queleas, and house finches. *American Naturalist* 158:75–86.
- Darwin, C. 1871. *The descent of man and selection in relation to sex*. London. Murray.
- Doucet, S. M. 2002. Structural plumage coloration, male body size, and condition in the blue-black grassquit. *Condor* 104: 30–38.
- Endler, J. A. 1990. On the measurement and classification of colour in studies of animal colour patterns. *Biological Journal of the Linnean Society* 41: 315–352.
- Endler, J. A. and Lyles, A. M. 1989. Bright ideas about parasites. *Trends in Ecology and Evolution* 4: 246–248.
- Evans, M. R., Goldsmith, A. R., and Norris, S. R. A. 2000. The effects of testosterone on antibody production and plumage coloration in male house sparrows (*Passer domesticus*). *Behavioral Ecology and Sociobiology* 47: 156–163.



- Figuerola, J., Munoz, E., Gutierrez, R., and Ferrer, D. 1999. Blood parasites, leucocytes and plumage brightness in the ciril bunting, *Emberiza cirilus*. *Functional Ecology* 13: 594–601.
- Fox, D. L. 1976. *Animal biochromes and structural colors*. Berkeley, University of California Press.
- Garvin, M. C. and Remsen, J. V. Jr. 1997. An alternative hypothesis for heavier parasite loads of brightly colored birds: exposure at the nest. *Auk* 114: 179–191.
- Gilliard, E. T. 1969. *Birds of paradise and bowerbirds*. London, Weidenfeld and Nicholson.
- Gonzalez, G., Sorci, G., Smith, L. C., and de Lope, F. 2001. Testosterone and sexual signalling in male house sparrows (*Passer domesticus*). *Behavioral Ecology and Sociobiology* 50: 557–562.
- Griffith, S. C., Owens, I. P. F. and Burke, T. 1999. Environmental determination of a sexually selected trait. *Nature* 400: 358–360.
- Hamilton, W. J. and Poulin, R. 1997. The Hamilton and Zuk hypothesis revisited: A meta-analytical approach. *Behaviour* 134: 299–320.
- Hamilton, W. D. and Zuk, M. 1982. Heritable true fitness and bright birds: A role for parasites? *Science* 218: 384–387.
- Hill, G. E. 1990. Female house finches prefer colourful males: sexual selection for a condition-dependent trait. *Animal Behaviour* 40: 563–572.
- Hill, G. E. 1991. Plumage coloration is a sexually selected indicator of male quality. *Nature* 350: 337–339.
- Hill, G. E. 1992. Proximate basis of variation in carotenoid pigmentation in male house finches. *Auk* 109: 1–12.
- Hill, G. E. 1999. Mate choice, male quality, and carotenoid-based plumage colouration. *In Proceedings of the 22<sup>nd</sup> International Ornithological Congress, Durban* (Adams, N. J. and Slotow, R. H. eds). pp. 1654–1658. Johannesburg. BirdLife South Africa.
- Hill, G. E. and Brawner, W. R. III. 1998. Melanin-based plumage coloration in the house finch is unaffected by coccidial infection. *Proceedings of the Royal Society of London B* 265: 1105–1109.

- Hill, G. E. and Montgomerie, R. 1994. Plumage colour signals nutritional condition in the house finch. *Proceedings of the Royal Society of London B* 258: 47–52.
- Hill, G. E., Montgomerie, R., Inouye, C. Y., and Dale, J. 1994. Influence of dietary carotenoids on plasma and plumage colour in the house finch: Intra- and intersexual variation. *Functional Ecology* 8:343–350.
- Humphries, S. and Ruxton, G. D. 1999. Bower-building: coevolution of display traits in response to the costs of female choice? *Ecology Letters* 2:404–413.
- Hunt, S., Bennett, A. T. D., Cuthill, I.C., and Griffiths, R. 1998. Blue tits are ultraviolet tits. *Proceedings of the Royal Society of London B* 265: 451–455.
- Järvi, T. and Bakken, M. 1984. The function of the variation in the breast stripe of the great tit (*Parus major*). *Animal Behaviour* 32: 590–596.
- John, J. L. 1995. Haematozoan parasites, mating systems and colourful plumages in songbirds. *Oikos* 72: 395–401.
- Johnsen, A., Andersson, S., Örnborg, J., and Lifjeld, J.T. 1998. Ultraviolet plumage ornamentation affects social mate choice and sperm competition in bluethroats (*Aves: Luscinia s. svecica*): a field experiment. *Proceedings of the Royal Society of London B* 264: 1587–1591.
- Kumierski, R., Borgia, G., Uy, A., and Crozier, R. H. 1997. Labile evolution of display traits in bowerbirds indicates reduced effects of phylogenetic constraints. *Proceedings of the Royal Society of London B* 264: 307–313.
- Keyser, A. J. and Hill, G. E. 1999. Condition-dependent variation in the blue-ultraviolet coloration of a structurally based plumage ornament. *Proceedings of the Royal Society of London B* 266: 771–777.
- Keyser, A. J. and Hill, G.E. 2000. Structurally based plumage coloration is an honest signal of quality in male blue grosbeaks. *Behavioral Ecology* 11: 202–209.
- Lenz, N. 1994. Mating behaviour and sexual competition in the regent bowerbird *Sericulus chrysocephalus*. *Emu* 94: 263–272.
- Marshall, A. J. 1954. *Bower-birds: their displays and breeding cycles*. Oxford, Clarendon Press.
- McGraw, K. J. and Hill, G. E. 2000. Differential effects of endoparasitism on the expression of carotenoid- and melanin-based ornamental coloration. *Proceedings of the Royal Society of London B* 267:1525–1532.

- McGraw, K. J., Dale, J., and Vonnegut, E. A. 2002a. Social environment during molt predicts the expression of melanin-based plumage pigmentation in male house sparrows (*Passer domesticus*). Behavioral Ecology and Sociobiology. In review.
- McGraw, K. J., Vonnegut, E. A., Dale, J., and Hauber, M. E. 2002b. Different plumage colors reveal different information: how nutritional stress affects the expression of melanin- and structurally based ornamental coloration. Journal of Experimental Biology. In review.
- Merila, J., Bjorklund, M., and Bennett, G. F. 1995. Geographic and individual variation in haematozoan infections in the greenfinch, *Carduelis chloris*. Canadian Journal of Zoology 73: 1798–1804.
- Møller, A. P. 1987. Variation in badge size in male house sparrows *Passer domesticus*: evidence for status signaling. Animal Behaviour 35:1637–1644.
- Møller, A. P. 1989. Natural and sexual selection on a plumage signal of status and on morphology in house sparrows, *Passer domesticus*. Journal of Evolutionary Biology 2: 125–140.
- Norris, K. 1993. Heritable variation in a plumage indicator of viability in male great tits *Parus major*. Nature 362: 537–539.
- Olson, V. A. and Owens, I. P. F. 1998. Costly sexual signals: Are carotenoids rare, risky or required? Trends in Ecology and Evolution 13: 510–514.
- Otter, K. and Ratcliffe, L. 1999. Relationship of bib size to age and sex in the black-capped chickadee. Journal of Field Ornithology 70: 567–577.
- Owens, I. P. F. and Hartley, I. R. 1998. Sexual dimorphism in birds: why are there so many different forms of dimorphism? Proceedings of the Royal Society of London B 265: 397–407.
- Pruett-Jones, S. G., Pruett-Jones, M. A., and Jones, H. I. 1990. Parasites and sexual selection in birds of paradise. American Zoologist 30: 287–298.
- Prum, R. O., Torres, R., Williamson, S., and Dyck, J. 1998. Constructive interference of light by blue feather barbs. Nature 396: 28–29.
- Prum, R. O., Torres, R., Williamson, S., and Dyck, J. 1999. Two-dimensional Fourier analysis of the spongy medullary keratin of structurally coloured feather barbs. Proceedings of the Royal Society of London B 266: 13–22.

- Pryke, S. R., Lawes, M. J. and Andersson, S. 2001. Agonistic carotenoid signaling in male red-collared widowbirds: Aggression related to the colour signal of both the territory owner and model intruder. *Animal Behaviour* 62:695–704.
- Read, A. F. 1988. Sexual selection and the role of parasites. *Trends in Ecology and Evolution* 3: 97–102.
- Roulin, A., Richner, H. and Ducrest, A. L. 1998. Genetic, environmental, and condition dependent effects on female and male ornamentation in the barn owl *Tyto alba*. *Evolution* 52: 1451–1460.
- Rohwer, S. 1975. The social significance of avian winter plumage variability. *Evolution* 29: 593–610.
- Senar, J. C. 1999. Plumage coloration as a signal of social status. *In* Proceedings of the 22<sup>nd</sup> International Ornithological Congress, Durban (Adams, N. J. and Slotow, R. H. eds). pp. 1669–1686. Johannesburg, BirdLife South Africa.
- Senar, J. C., Figuerola, J., and Pascual, J. 2002. Brighter yellow blue tits make better parents. *Proceedings of the Royal Society of London B*. In press.
- Sheldon, B. C., Andersson, S., Griffith, S. C., Örnborg, J., and Sendecka, J. 1999. Ultraviolet colour variation influences blue tit sex ratios. *Nature* 402: 874–877.
- Slagsvold, T. and Lifjeld, J. T. 1992. Plumage color is a condition-dependent sexual trait in male pied flycatchers. *Evolution* 46: 825– 828.
- Sundberg, J. 1995a. Female yellowhammers (*Emberiza citrinella*) prefer yellower males: a laboratory experiment. *Behavioral Ecology and Sociobiology* 37: 275–282.
- Sundberg, J. 1995b. Parasites, plumage coloration and reproductive success in the yellowhammer, *Emberiza citrinella*. *Oikos* 74: 331–339.
- Sundberg, J. and Dixon, A. 1996. Old, colorful male yellowhammers, *Emberiza citrinella*, benefit from extra-pair copulations. *Animal Behaviour* 52: 113–122.
- Thompson, C. W., Hillgarth, N., Leu, M., and McClure, H. E. 1997. High parasite load in house finches (*Carpodacus mexicanus*) is correlated with reduced expression of a sexually selected trait. *American Naturalist* 149: 270–294.
- Thusius, K. J., Peterson, K. R., Dunn, P. O., and Whittingham, L. A. 2001. Male mask size is correlated with mating success in the common yellowthroat. *Animal Behaviour* 62: 435–446.

- Uy, J. A. C., Patricelli, G. L., and Borgia, G. 2001. Complex mate searching in the satin bowerbird *Ptilonorhynchus violaceus*. *American Naturalist* 158: 530–542.
- Veiga, J. P. and Puerta, M. 1996. Nutritional constraints determine the expression of a sexual trait in the house sparrow. *Passer domesticus*. *Proceedings of the Royal Society of London B* 263: 229–234.
- Vororbyev, M., Osorio, D., Bennett, A. T. D. Marshall, N. J., and Cuthill, I.C. 1998. Tetrachromacy, oil droplets and bird plumage colours. *Journal of Comparative Physiology A* 183: 621–633.
- Walther, B. A., Clayton, D. H., and Gregory, R. D. 1999. Showiness of neotropical birds in relation to ectoparasite abundance and foraging stratum. *Oikos* 87: 157–165.
- Wolfenbarger, L. L. 1999. Red coloration of male northern cardinals correlates with mate quality and territory quality. *Behavioral Ecology* 10: 80–90.
- Yezerinac, S. M. and Weatherhead, P. J. 1995. Plumage coloration, differential attraction vectors and haematozoa infections in birds. *Journal of Animal Ecology* 64: 528–537.

Table 1. Experimental feather choice by adult male satin bowerbirds, *Ptilonorhynchus violaceus*. Males were allowed to choose between blue, green, yellow, orange and red feathers over a period of 48 hours.

<b>Bower number</b>	<b>First choice</b>	<b>Second choice</b>	<b>Third choice</b>
<b>1</b>	blue		
<b>2</b>	blue	yellow, green	
<b>3</b>	blue		
<b>4</b>	no choice		
<b>5</b>	blue	yellow, green	orange
<b>6</b>	blue		
<b>7</b>	blue	yellow	
<b>8</b>	blue	yellow	
<b>9</b>	blue, yellow, green		
<b>10</b>	no choice*		
<b>11</b>	blue, green		
<b>12</b>	blue		

\* Blue experimental choice feathers were stolen by male at bower number 6.

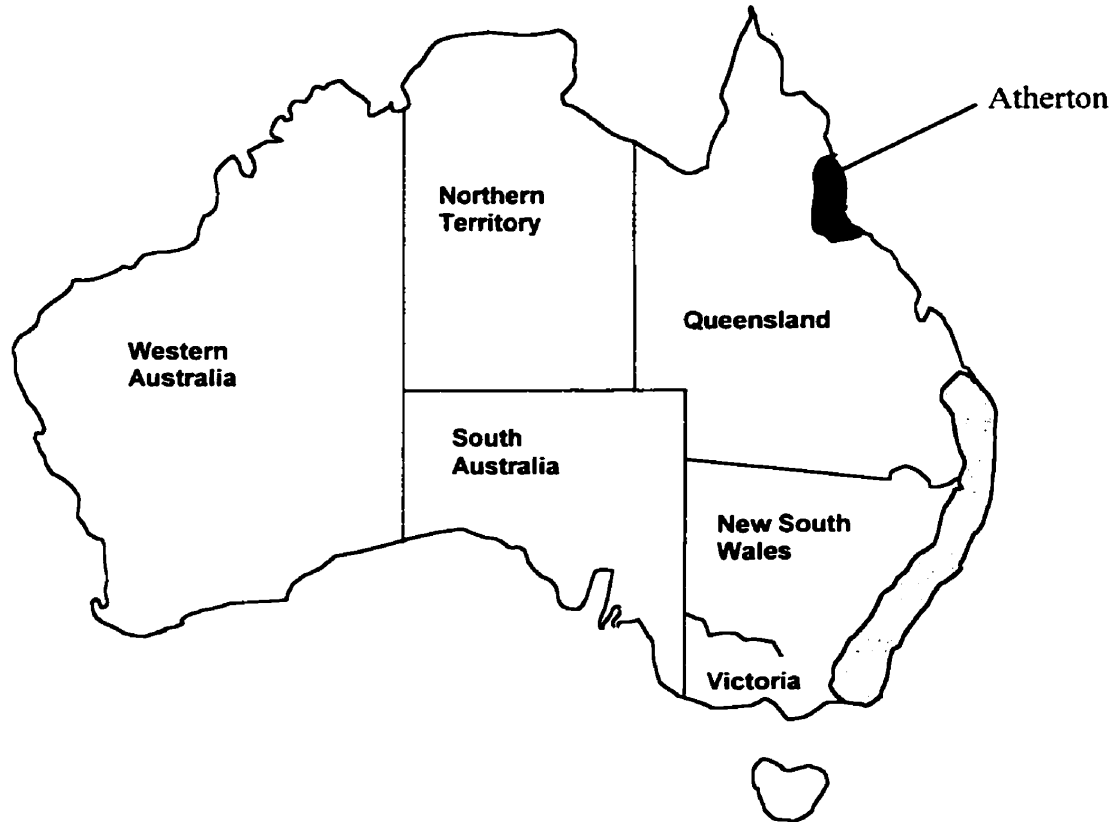


Figure 1. The distribution of satin bowerbirds, *Ptilonorhynchus violaceus*, in Australia.

The northern population (dark shading) represents the distribution of the race *minor* while the southern population (light shading) represents the distribution of the race *violaceus*.

The location of my study site in Atherton, Queensland is identified.

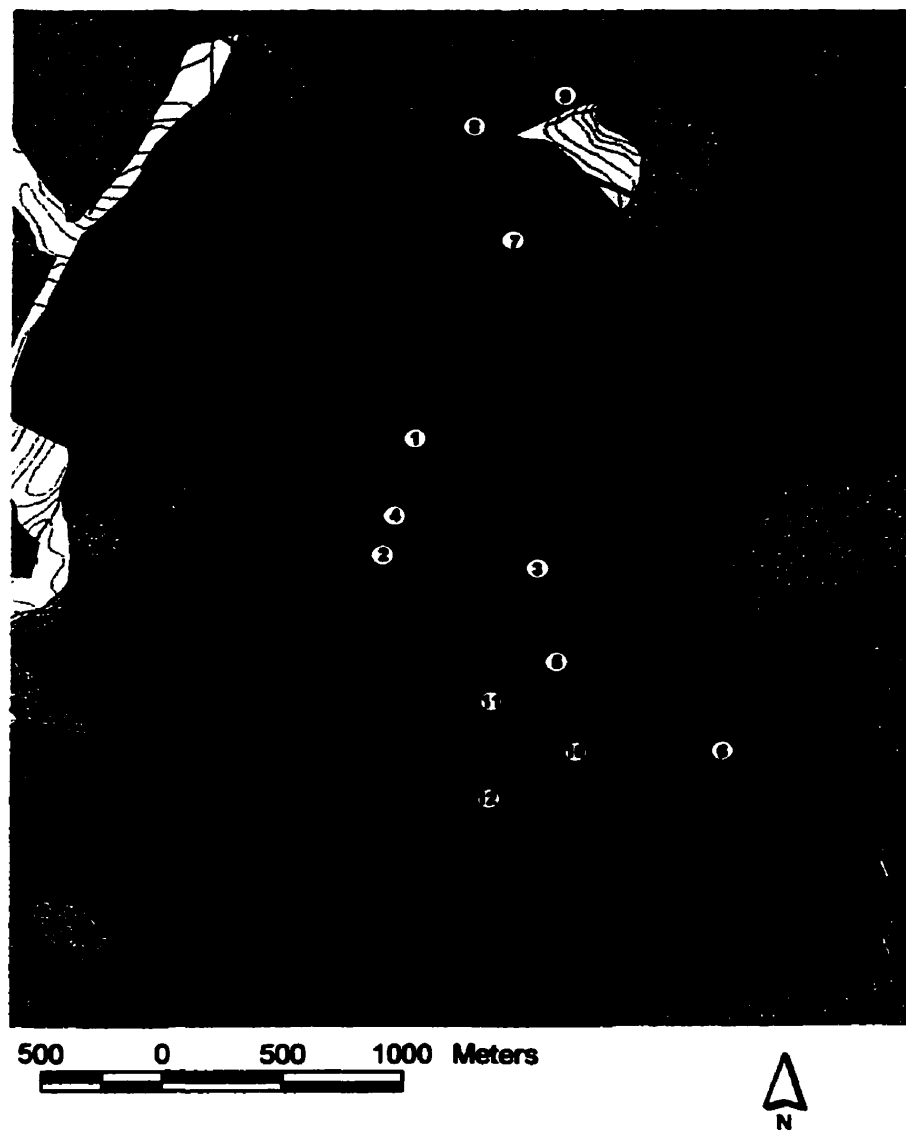


Figure 2. Topographic map of my study site at Mount Baldy State Forest near Atherton, Queensland, Australia. The access road is identified in red. Satin bowerbird bower locations are identified by numbers. The different background colours identify different types of habitat: green represents rainforest and pink represents wet sclerophyll forest, while the other colours represent intermediate habitats.





Figure 3. Adult male satin bowerbird (a) showing structurally–based iridescent blue plumage colouration and bright yellow bill. Adult females (b) are cryptic green with a dark bill.

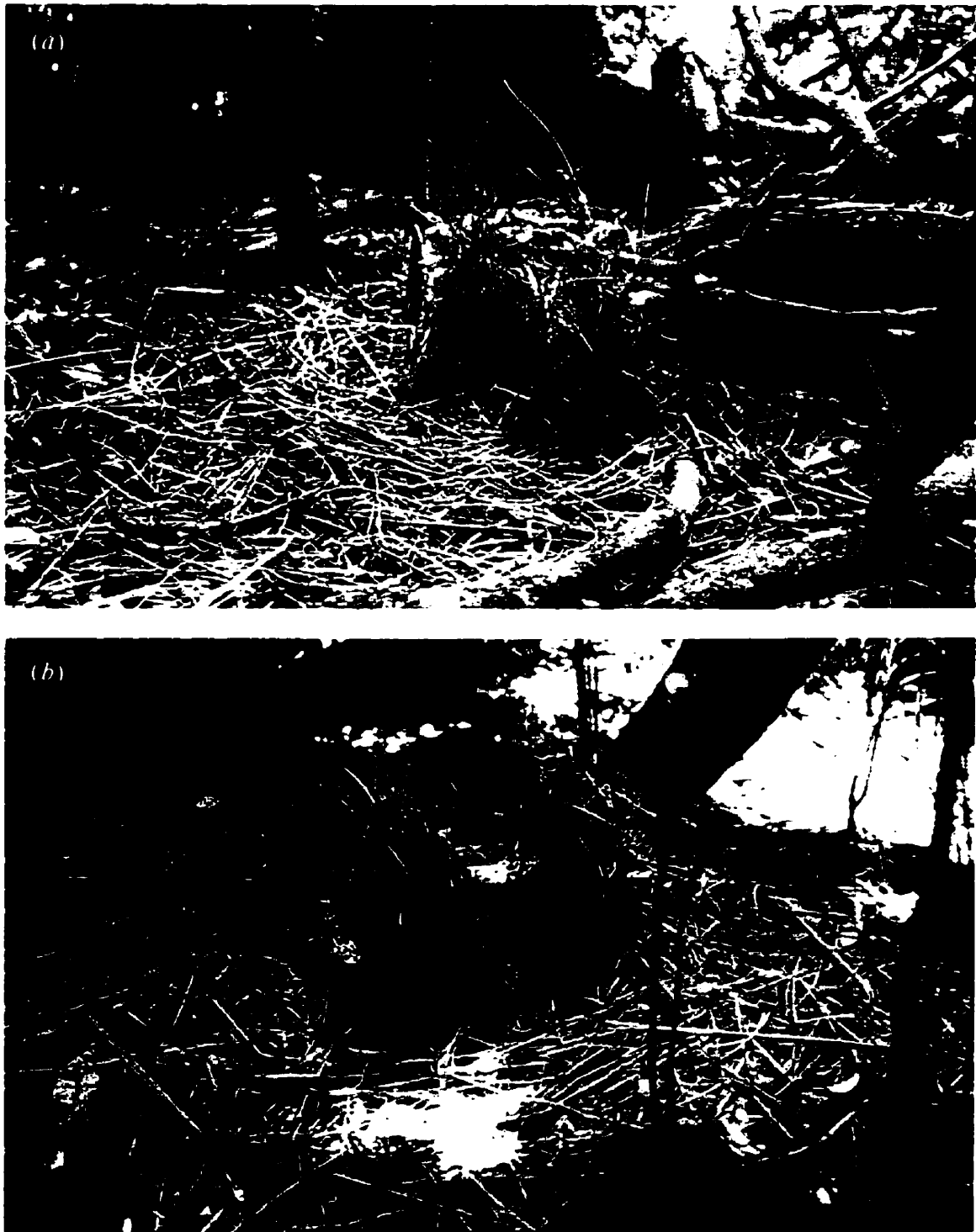


Figure 4. Typical satin bowerbird bowers with few (a) and several (b) decorations. Note the bower platform, upon which are built the two curved bower walls that form the avenue.

# Chapter 2

**The extended phenotype of satin bowerbirds: bowers and plumage colouration signal different aspects of male quality**

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**ABSTRACT**

Though male mating success is related to the quality of display bowers constructed by male satin bowerbirds, *Ptilonorhynchus violaceus*, it remains unclear exactly why bower features influence female preference, and whether female mate choice may also involve the direct assessment of male phenotypic traits. We investigated the relationship between bower features and male plumage colouration in satin bowerbirds to determine whether these traits could reveal aspects of male quality. To do this, we located the bowers of 10 male satin bowerbirds in rainforest in Queensland, Australia, and quantified the quality of bower construction and the level of bower decoration. We then captured bower owners and used spectrometry to measure the plumage colouration of several ornamental body regions. We found that bower quality and male plumage colouration were intricately related, and that together these traits could be used to predict ectoparasite load, body size, and feather growth rates. However, only rump plumage colouration was a significant predictor of the intensity of infection by blood parasites. We conclude that female satin bowerbirds can obtain a general impression of male quality by evaluating their bowers, and then refine this assessment by directly observing the ultraviolet plumage colouration of males.

**Keywords:** bowerbirds; male quality; parasites; plumage colouration; sexual selection; ultraviolet

## INTRODUCTION

Nearly all bowerbird species clear display courts and build bowers, elaborate structures constructed from twigs and decorated with a variety of colourful natural and human-manufactured objects (Marshall 1954; Gilliard 1969). The evolution and adaptive significance of these bowers has intrigued evolutionary biologists for some time (Darwin 1871; Marshall 1954; Gilliard 1956; Borgia 1995; Humphries & Ruxton 1999). It is now thought that bowers may have evolved from display courts in polygynous species, where the male has been liberated from parental duties (Humphries & Ruxton 1999). Bowers with barriers separating females from aggressively displaying males may have favored the construction of walls on the bowers of avenue builders and the elaboration of saplings on the bowers of maypole builders. For example, threat reduction seems to be a current function of bowers in the avenue building bowerbird, *Chlamydera maculata*, where females observe aggressive male displays through one of two straw walls (Borgia & Presgraves 1998).

Despite an emerging understanding of the mode of bower evolution (Borgia 1995; Humphries & Ruxton 1999), many unanswered questions persist with respect to current selective pressures on these complex structures (Humphries & Ruxton 1999): the elaborate decoration of bowers, for example, cannot be explained by the threat reduction hypothesis. Bower decoration is more likely to be influenced by sexual selection through female preference. For example, in the satin bowerbird, *Ptilonorhynchus violaceus*, extensive individual variation in both the quality of construction of bowers and the numbers and types of decorations adorning the bower platform is known to affect female choice of copulation partners, as measured by male mating success (Borgia 1985b).

However, it remains unclear why bowers influence mate choice, and whether female satin bowerbirds also assess males beyond evaluating their bower. Bower features together explained 37% of the variation in male mating success in one population of satin bowerbirds (Borgia 1985b), thus it seems likely that other factors may influence female choice.

In an extensive study of mate searching patterns in satin bowerbirds, Uy *et al.* (2001) found that females made courtship visits to multiple males, and returned to mate with the most attractive male (attractiveness measured as mating success). These findings suggest that females directly assess a pool of males and make mate choices based on traits that they can compare between males. The fact that females intently observe complex male displays also suggests that they are assessing males directly (Lofredo & Borgia 1986; Borgia 1995). For example, Lofredo & Borgia (1986) provide evidence that females pay attention to male display, as male mating success was related to age-correlated features of courtship vocalizations, yet this association between mating success and song was limited to a few of the many variables tested. In the present study, we investigated the relationship between male plumage ornamentation and bower features in the satin bowerbird to determine the relative contribution of these traits in signaling male quality.

## **METHODS**

This study was conducted from September to December 2000 in Mount Baldy State Forest in Queensland, Australia. The dominant vegetation type consisted of rainforest with a sharp transition to wet sclerophyll forest at the northeastern edge of our study

population. We located 10 satin bowerbird bowers by listening for male advertisement calls, usually given near bowers, and systematically searching the area for active bowers. We assessed bower quality by evaluating bower construction and quantifying the number of decorations used. Following Borgia (1985b), two observers independently evaluated four features of bower construction, each feature on a scale from 1 (poor) to 4 (excellent): overall symmetry of the structure, stick size, stick density, and overall quality of construction. For each bower, these scores were summed, and we used an average of the two observers' totals as a bower quality score. To assess levels of bower decoration, we regularly visited bowers from mid October to late November ( $n = 3$  to 7 visits per bower) and recorded the number of each type of decoration present on the bower. For our analyses, we used the mean number of decorations recorded at each bower.

We caught 11 adult males near display sites using mist nets baited with blue objects. Captured individuals were fitted with a unique combination of two colour bands and one Australian Bird and Bat Banding Scheme (ABBBS) stainless steel band. We measured the wing chord, tarsus length, head–bill length, and tail length (to nearest 0.1 mm), and mass (to nearest gram) of each bird. We also assessed each male's fat score on a scale of 0 to 5 (Helms & Drury 1960). We noted whether feathers were predominantly old, new, or moulting, and we removed the right outer rectrix to assess daily feather growth rate.

We quantified plumage reflectance using an Ocean Optics S2000 spectrometer illuminated by a pulsed xenon lamp (PX–2; Ocean Optics, Dunedin, Florida, USA). Measurements were taken with a fibre–optic metal probe that provided illumination from the light source and transferred the reflected light to the spectrometer. The probe was

mounted in a hard rubber cover that excluded external light from the measurement area (*ca.* 3 mm<sup>2</sup>) and held the probe perpendicular to the feather surface. All colour measurements were expressed as a proportion of reflectance relative to the reflectance of a Spectralon<sup>®</sup> white standard, an almost perfect reflector measured before measuring each bird. We measured plumage reflectance on eight body regions for each individual: wing coverts, wing primaries, breast, nape, mantle, rump, tail, and crown, taking five readings for each region, and moving the probe at least 5 mm before each new reading. We restricted spectral analyses to wavelengths between 300 nm and 700 nm, as most birds are sensitive to ultraviolet (UV) wavelengths (300 – 400 nm; Cuthill *et al.* 2000) and 700 nm is likely the upper limit of the vertebrate visual spectrum (Jacobs 1981).

We summarized reflectance data by calculating four colour variables: total brightness, UV brightness, intensity, and contrast. Brightness is a measure of the total light reflected from the feather surface. Brightness was calculated as the sum of reflectance values from 300 nm to 700 nm (Endler 1990; Andersson 1999) and UV brightness as the sum of reflectance values in the UV region (300 – 400 nm). We identified the intensity as the maximum reflectance reached (Keyser & Hill 1999). Contrast, which we calculated as the difference between the maximum and minimum reflectance across the 300 – 700 nm range, describes the spectral saturation of the colour, such that higher contrast indicates a richer colour (Keyser & Hill 1999).

We also calculated an overall ornamental colour score using Principal Components Analysis (PCA). We first calculated the mean of each colour variable for each of four blue body regions: the rump, wing coverts, mantle and breast. Measurements of wing primaries and tail feathers were not used in the ornamental colour score because



these regions were spectrally distinct (see figure 1) and are not likely to be ornamental in this species. The crown and nape measurements were also not included in the analyses as they were highly variable within individuals due to excessive movement of the bird during these measurements. Thus, we performed a PCA using the mean UV brightness, intensity, and contrast averaged over the four remaining body regions. We did not include total brightness in the PCA given that ornamental satin bowerbird plumage reaches maximum reflectance in the UV, and UV brightness was highly correlated with total brightness ( $r = 0.98$ ,  $n = 11$ ,  $p < 0.0001$ ). The first principal component (PC1) explained >80 % of the variation in colour, and all three calculated colour variables had strong positive loadings on PC1 (eigenvectors from 0.54 to 0.60). Therefore, males with high PC1 scores displayed an overall intense, highly saturated, and UV-bright ornamental plumage colouration.

We assessed ectoparasite load by counting the number of *Myrsidea ptilonorhynchi* lice on the head and especially near the eyes of each male. This louse is the only common ectoparasite on satin bowerbirds, and it is found mainly around the head and eyes where the bird cannot easily preen (Borgia 1986; Borgia & Collis 1989, 1990). This louse belongs to a suborder in which species are known to consume feathers and feed on the blood and skin of their hosts; thus, they are subject to specific immune response and can have a considerable effect on host fitness (Clayton 1991a, b).

To assess the intensity of infection from blood parasites we collected a small amount of blood from each male by piercing the brachial vein, drawing blood into a capillary tube, and thinly smearing it onto a glass slide. We prepared the slides according to the Hema 3™ staining procedure (Fisher Scientific). We then observed the stained

slides under oil immersion at 1250 X magnification and scanned each slide for haemosporidian parasites until 10 000 red blood cells had been surveyed, identifying each parasite to genus (Campbell 1988). All but one of the blood parasites identified were *Hemoproteus*, thus only mature (intra-erythrocytic) *Hemoproteus* parasites are considered in the following analyses. All slides were scored by the same observer, blind to the identity of the bird being scored.

We assessed feather growth rates by measuring the width of alternating dark and light bars on the right outer rectrix of each male. Each pair of bars represents one day's growth (Michener & Michener 1938), and the width of these bars has been associated with nutritional condition in several species (Grubb 1989, 1991; Jenkins *et al.* 2001). We measured the width of six pairs of bars on either side of the midpoint of the feather, from which we calculated a 12-d average daily growth rate for each male (see Hill & Montgomerie 1994).

One purpose of our study was to determine the relative contribution of bower features and plumage colouration in predicting quality. We sought to predict four dependent quality variables: ectoparasite load, intensity of haemosporidian infection, feather growth rates, and body size. To do this, we constructed four backward stepwise multiple regression models (one for each dependent variable) using bower quality, number of decorations, and the UV brightness of the rump, mantle, breast, and wing coverts, as independent (predictor) variables in each model, setting probabilities to leave and enter each model at 0.05 and 0.10 respectively.

## RESULTS

### (a) Plumage colouration

The rump, mantle, breast and wing coverts of male satin bowerbirds reflect most strongly in the ultraviolet and deep blue regions of the spectrum, while the darker wing and tail primaries are mostly black and not particularly reflective (figure 1). There was considerable variation in male plumage characteristics, among both males and body regions within males, even when we excluded the darker plumage regions. For example, the coefficients of variation (CV) for UV brightness ranged between 0.26 and 0.37 for the wing coverts, mantle, breast, and rump. Further, mean UV brightness was significantly different across the four blue body regions (ANOVA,  $F_{3,40} = 5.94$ ,  $p = 0.002$ ) despite looking similar to us.

### (b) Plumage colouration and bower characteristics

Measures of bower quality and male plumage colouration were also intricately associated in the satin bowerbird. Ornamental plumage colour (PC1) was significantly positively related to male bower quality (figure 2a). Ornamental plumage colouration was similarly positively related to the average number of decorations adorning bowers (figure 2b). Thus, the satin bowerbird's bower provides females with a useful index of a male's appearance, even in his absence, with quality score and number of decorations together explaining about 62% of the variation in ornamental plumage colouration.

### (c) Parasites

To determine whether plumage colouration and bower features reveal aspects of male quality, we compared these attributes to the degrees of infection from ecto- and endo-parasites. In a stepwise multiple regression analysis, the quality of bower construction emerged as the only significant predictor of ectoparasite load among the variables tested (table 1, figure 3). That is, males with high quality bowers had fewer ectoparasites, and bower quality explained more than 50% of the variation in ectoparasite load. On the other hand, variation in the intensity of endoparasite infection was best explained by the UV brightness of the rump (table 1, figure 3); males with the brightest rumps had the lowest intensity of infection by *Hemoproteus sp.* blood parasites, with rump UV brightness explaining 57% of the variation in the intensity of infection.

### (d) Feather growth rate

None of the variables in the regression model were significant predictors of feather growth rates (table 1), although the average number of decorations on the bower was weakly associated with feather growth rate ( $R^2 = 0.34$ ,  $\beta = -0.58$ ,  $F = 4.41$ ,  $p = 0.08$ ). Additionally, when we compared feather growth rates to our measure of overall ornamental plumage colouration (PC1), we found a significant negative relationship between these two traits (figure 3; Model II regression,  $y = 3.31 - 0.14x$ ;  $r^2 = 0.51$ ,  $n = 11$ ,  $p = 0.01$ ), a relationship in the opposite direction to that expected.

**(e) Body size**

Rump UV brightness, bower quality score, and number of bower decorations were all significant predictors of body size as measured by tarsus length (table 1, figure 3), together explaining >80 % of the variation in tarsus length. Rump UV brightness was the best predictor of tarsus length, explaining >40 % of the variation (table 1). Rump UV brightness and average number of bower decorations were positive predictors of tarsus length, while bower quality score was a negative predictor, although bower quality explained only a small amount (<10%) of the variation in body size.

**DISCUSSION**

Our study shows that male plumage colouration and bower quality features are intricately related in the satin bowerbird and that, together, these attributes reveal important aspects of male quality. The relationship between male ultraviolet plumage colouration and bower characteristics provides indirect support for Gilliard's (1956) transferal hypothesis, which predicted that the focus of sexual display in bowerbirds was transferred from male traits to bowers over the course of evolution, with the least sexually dimorphic species building the most elaborate bowers. Thus, satin bowerbirds appear to represent an intermediate step in this evolutionary pathway, as males are brightly coloured and highly dichromatic, while their bowers are moderately elaborate. Accordingly, it is not surprising that male plumage traits are so highly correlated with bower features and that both reveal male quality. Thus, bowers are an extension of the male phenotype in this species.

As we have shown, the signal function of decorated bowers and bright plumage in the satin bowerbird may be explained in part by their association with an important indicator of male quality: parasite load. Parasites are known to reduce fitness in several species (Clayton 1991b), and signals revealing parasite loads should be important to choosy females. In Hamilton & Zuk's (1982) model of parasite-mediated sexual selection, showy male traits, such as bright plumage colouration, are preferred by females because of their capacity to reveal parasite burdens (see also Read 1988, Clayton 1991b). Hence females may acquire heritable parasite resistance (good genes) for their offspring by mating with bright males (Hamilton & Zuk 1982). Satin bowerbirds are an ideal species within which to investigate good genes models of parasite-mediated sexual selection since males provide no parental care, only gametes. Here, we provide indirect support for the Hamilton–Zuk hypothesis by two means. First, we show that the quality of bower construction is a significant predictor of ectoparasite load in this population. Thus, females could potentially assess male ectoparasite load by assessing bower quality, even in the absence of the bower owner (figure 3). It should be noted, however, that females may also be able to assess male ectoparasite load directly through careful scrutiny (Borgia & Collis 1989, 1990). In fact, male ectoparasite load is negatively correlated with mating success in another population of satin bowerbirds, despite a lack of association between ectoparasites and bower features in that population (Borgia & Collis 1989). Nevertheless, evidence of male ectoparasite burdens should remain important to females irrespective of the source of the information and regardless of whether the potential benefits are heritable resistance for their offspring (Hamilton & Zuk 1982) or direct avoidance of parasite transmission, as suggested by other models (Borgia

& Collis 1989, 1990; Loehle 1997). Second, we show that rump plumage colouration can reveal the intensity of male endoparasitic infection. Should parasite burden be an important feature of male quality, as indicated in many studies (Andersson 1994), female satin bowerbirds could assess male endoparasite infection intensities by evaluating rump plumage brightness during male display (figure 3). Since the intensity of *Hemoproteus* infection is not correlated with bower features, females must evaluate males directly to obtain information about their endoparasite burdens.

We also found that rump plumage colouration, average number of bower decorations, and quality of bower construction were significant predictors of male body size (tarsus length). The association between the number of decorations and body size is perhaps best explained in the context of male choice of bower decorations. Male satin bowerbirds preferentially decorate their bowers with blue feathers, flowers, and berries, as well as small mammal skulls and other bones, all of which are relatively rare in the surrounding environment. As a consequence, theft from other males appears to be a primary means of obtaining these decorations (Borgia & Gore 1986; S. Doucet, personal observation). Larger males may have a competitive advantage during theft-related confrontations, allowing them to steal more decorations from other males, and defend their own decorations from thieving neighbours. In fact, Borgia (1985a) found that more aggressive males destroyed other males' bowers more frequently, a behaviour often associated with the theft of decorations. Thus, larger bowerbirds may defend and maintain more elaborate bowers, resulting in the observed association between body size and bower decoration.

The negative relationship between feather growth rate and overall plumage colouration was not expected. Growth rates have traditionally been used as indicators of condition at the time of moult (Grubb 1989, 1991; Jenkins *et al.* 2001) and positive associations between feather growth rate and quality–indicating plumage colouration have been found in several species (Hill & Montgomerie 1994; Keyser & Hill 1999; Doucet 2002). Possibly, high quality males spend so much energy building and maintaining their bowers and defending them from thieving neighbours during the breeding season (Borgia 1985a, Borgia & Gore 1986) that they become nutritionally stressed and grow their feathers more slowly during the subsequent moult, which begins in the final stages of the breeding season (Vellenga 1980). Alternatively, the microstructure required to achieve the brightest reflectance in structurally coloured plumage (Prum *et al.* 1998, 1999) may require slower feather growth, a costly process that is perhaps limited to high quality males.

This is the first study to show an association between bower features and a male epigamic trait, and thus that bowers are an extension of the male phenotype that can be used by females in assessing male quality. Bower features and male plumage colouration explained considerable variation in four potential quality indicators: ectoparasite load, haematozoa infection intensity, feather growth rate, and body size. Thus, female satin bowerbirds could assess male quality using both bower features and male plumage colouration (see figure 3) to obtain better information than is available from either trait alone. It is already known that male mating success is related to bower quality in this species (Borgia 1985b), and our study associates bower quality with ectoparasite load and body size. Despite this, only the UV brightness of the rump was useful in predicting



endoparasitic infection intensities. Thus, if freedom from endoparasites is also an important feature of male health and vigor, discriminating females may need to look beyond the bower and directly assess displaying males. Interestingly, female satin bowerbirds appear to have relatively large brains compared to their male counterparts (Madden 2001). While male brain capacity is probably essential to building complex bowers, searching for bower decorations, and decorating bowers appropriately, female brain size may be as important in searching for potential males (Uy *et al.* 2000) and assessing complex bowers, male plumage, and elaborate male displays. Thus, female satin bowerbirds may be particularly well suited to evaluate the impressive array of signals of quality discovered so far in this species, from bower features and male plumage colouration to song and perhaps even display complexity.

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**REFERENCES**

- Andersson, M. B. 1994 *Sexual Selection*. Princeton: Princeton University Press.
- Andersson, S. 1999 Morphology of UV reflectance in a whistling-thrush: implications for the study of structural colour signalling in birds. *J. Avian Biol.* **30**, 193–204.
- Borgia, G. 1985a Bower destruction and sexual competition in the satin bowerbird (*Ptilonorhynchus violaceus*). *Behav. Ecol. Sociobiol.* **18**, 91–100.
- Borgia, G. 1985b Bower quality, number of decorations and mating success of male satin bowerbirds (*Ptilonorhynchus violaceus*): an experimental analysis. *Anim. Behav.* **33**, 266–271.
- Borgia, G. 1986 Satin bowerbird parasites: a test of the bright male hypothesis. *Behav. Ecol. Sociobiol.* **19**, 355–358.
- Borgia, G. 1995 Why do bowerbirds build bowers? *Am. Sci.* **83**, 542–547.
- Borgia, G. & Collis, K. 1989 Female choice for parasite-free male satin bowerbirds and the evolution of bright male plumage. *Behav. Ecol. Sociobiol.* **25**, 445–454.
- Borgia, G. & Collis, K. 1990 Parasites and bright male plumage in the satin bowerbird (*Ptilonorhynchus violaceus*). *Amer. Zool.* **30**, 279–285.
- Borgia, G. & Gore, M. A. 1986 Feather stealing in the satin bowerbird (*Ptilonorhynchus violaceus*): male competition and the quality of display. *Anim. Behav.* **34**, 727–738.
- Borgia, G. & Presgraves, D. C. 1998 Coevolution of elaborated male display traits in the spotted bowerbird: an experimental test of the threat reduction hypothesis. *Anim. Behav.* **56**, 1121–1128.

- Campbell, T. W. 1988 *Avian Hematology and Cytology*. Ames, IO: Iowa State University Press.
- Clayton, D. H. 1991a Coevolution of avian grooming and ectoparasite avoidance. In *Bird–parasite interactions* (ed. J. E. Loye & M. Zuk), pp. 258–289. Oxford: Oxford University Press.
- Clayton, D. H. 1991b The influence of parasites on host sexual selection. *Parasitology Today* **7**, 329–334.
- Cuthill, I. C., Partridge, J. C., Bennett, A. T. D., Church, S. C., Hart, N. S. & Hunt, S. 2000 Ultraviolet vision in birds. *Advances in the Study of Behavior* **29**, 159–214.
- Darwin, C. 1871 *The Descent of Man and Selection in Relation to Sex*. London: Murray.
- Doucet, S. M. 2002 Structural plumage coloration, male body size, and condition in the Blue–black Grassquit. *Condor* **104**, 30–38.
- Endler, J. A. 1990 On the measurement and classification of colour in studies of animal colour patterns. *Biol. J. Lin. Soc.* **41**, 315–352.
- Gilliard, E. T. 1956 Bower ornamentation versus plumage characters in Bowerbirds. *Auk* **73**, 450–451.
- Gilliard, E. T. 1969 *Birds of Paradise and Bowerbirds*. London: Weidenfeld & Nicholson.
- Grubb, T. C. Jr. 1989 Ptilochronology: feather growth bars as indicators of nutritional status. *Auk* **106**, 314–320.
- Grubb, T. C. Jr. 1991 A deficient diet narrows growth bars on induced feathers. *Auk* **108**, 725–727.

- Hamilton, W. D. & Zuk, M. 1982 Heritable true fitness and bright birds: a role for parasites? *Science* **218**, 384–387.
- Helms, C. W. & Drury, W. H. 1960 Winter and migratory weight and fat: field studies of North American buntings. *Bird-Banding* **31**, 1–40.
- Hill, G. E. & Montgomerie, R. 1994 Plumage colour signals nutritional condition in the house finch. *Proc. R. Soc. Lond. B* **258**, 47–52.
- Humphries, S. & Ruxton, G. D. 1999 Bower-building: coevolution of display traits in response to the costs of female choice? *Ecology Letters* **2**, 404–413.
- Jacobs, G. H. 1981 *Comparative Color Vision*. New York: Academic Press.
- Jenkins, K. D., Hawley, D. M., Farabaugh, C. S. & Cristol, D. A. 2001 Ptilochronology reveals differences in condition of captive White-throated Sparrows. *Condor* **103**, 579–586.
- Keyser, A. J. & G. E. Hill. 1999 Condition-dependent variation in the blue-ultraviolet coloration of a structurally based plumage ornament. *Proc. R. Soc. Lond. B* **266**, 771–777.
- Loehle, C. 1997 The pathogen transmission avoidance theory of sexual selection. *Ecol. Modeling* **103**, 231–250.
- Lofredo, C. A. & Borgia, G. 1986 Male courtship vocalizations as cues for mate choice in the satin bowerbird (*Ptilonorhynchus violaceus*). *Auk* **130**, 189–195.
- Madden, J. 2001. Sex, bowers and brains. *Proc. R. Soc. Lond. B* **268**, 833–838.
- Marshall, A. J. 1954 *Bower-birds: Their Displays and Breeding Cycles*. Oxford: Clarendon Press.
- Michener, H. & Michener, J. R. 1938 Bars in flight feathers. *Condor* **40**, 149–160.

- Prum, R. O., Torres, R., Williamson, S. & Dyck, J. 1998 Constructive interference of light by blue feather barbs. *Nature* **396**, 28–29.
- Prum, R. O., Torres, R., Williamson, S. & Dyck, J. 1999 Two-dimensional Fourier analysis of the spongy medullary keratin of structurally coloured feather barbs. *Proc. R. Soc. Lond. B* **266**, 13–22.
- Read, A. F. 1988 Sexual selection and the role of parasites. *TREE* **3**, 97–102.
- Uy, J. A. C., Patricelli, G. L. & Borgia, G. 2000 Dynamic mate-searching tactic allows female satin bowerbirds *Ptilonorhynchus violaceus* to reduce searching. *Proc. R. Soc. Lond. B* **267**, 251–256.
- Uy, J. A. C., Patricelli, G. L., & Borgia, G. 2001 Complex mate searching in the satin bowerbird *Ptilonorhynchus violaceus*. *Am. Nat.* **158**, 530–542.
- Vellenga, R. E. 1980 The moults of the satin bowerbird *Ptilonorhynchus violaceus*. *Emu*. **80**, 49–54.

Table 1. *Significant predictors of male quality in satin bowerbirds from backward stepwise multiple regression models. Each model was initially constructed using bower and plumage features as independent variables.*

Dependent variables	Significant predictors	$R^2$	$\beta$	$F$	$p$
I. Ectoparasites	Bower quality score	0.51	-0.72	8.39	0.02
II. Endoparasites	Rump UV brightness	0.57	-0.64	10.87	0.01
III. Feather growth rate	No significant predictor	–	–	–	–
IV. Body size	Whole Model	0.82		9.08	0.01
	Rump UV brightness	0.43	0.84	12.57	0.006
	Bower quality score	0.09	-0.94	11.49	0.01
	Number of decorations	0.30	0.81	10.03	0.02

The independent variables included in the model were: bower quality score, average number of bower decorations, and the UV brightness of the rump, wing coverts, mantle and breast. Only variables that were significant predictors of each quality indicator are reported here.

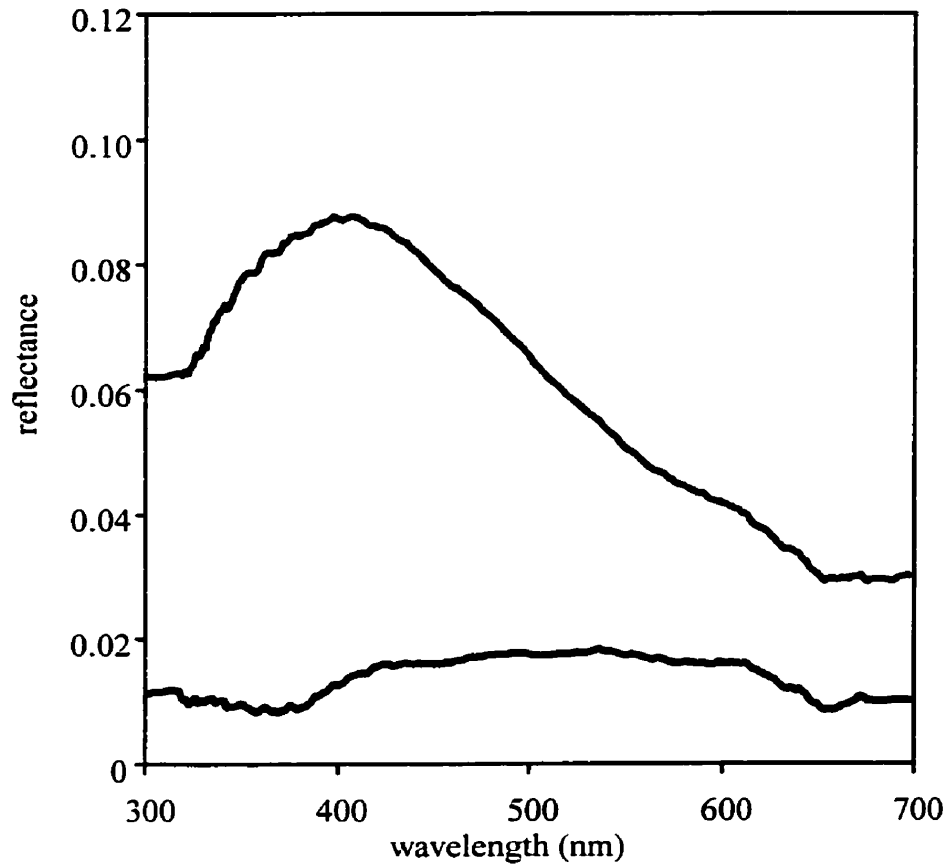


Figure 1. Representative spectral reflectance curves for blue regions (upper curve; average of wing coverts, breast, mantle, rump) and black regions (lower curve; average of wing and tail primaries) of one male satin bowerbird's plumage.

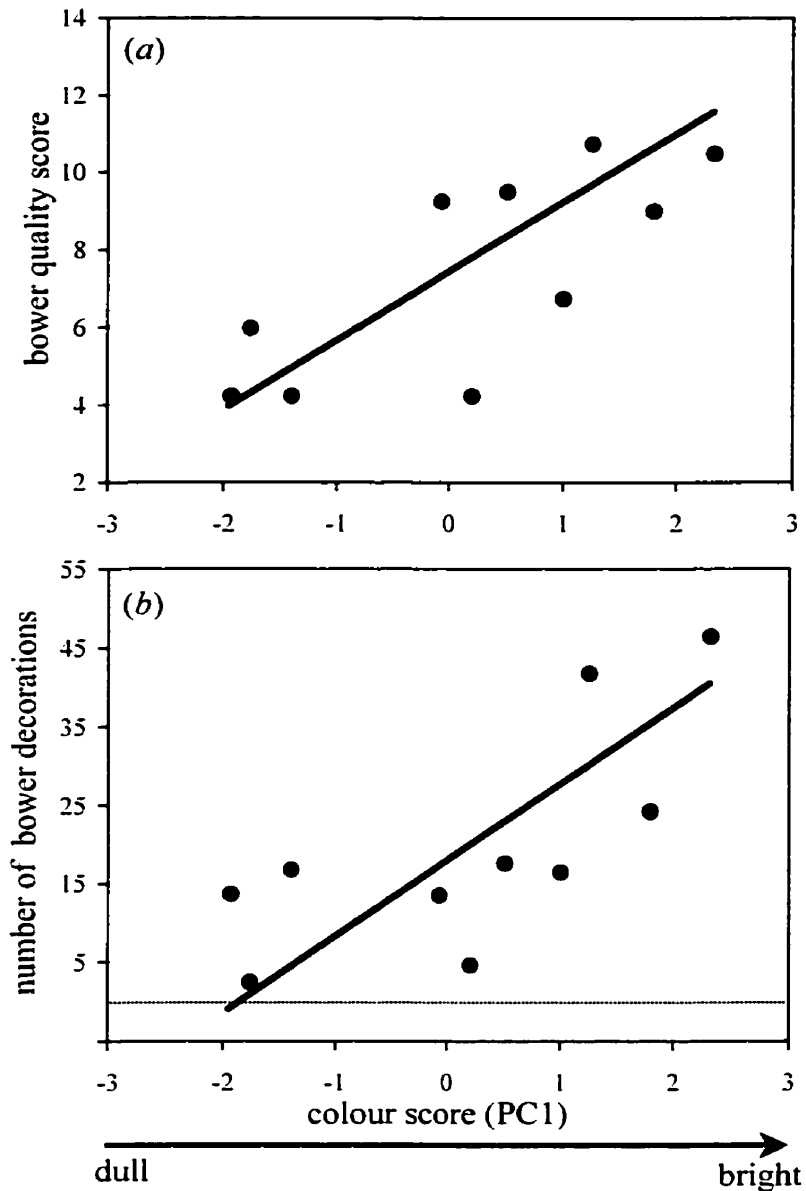


Figure 2. Relations between plumage colouration and (a) the quality of bower construction ( $y = 7.45 + 1.78x$ ;  $r^2 = 0.57$ ,  $n = 10$ ,  $p = 0.01$ ) and (b) average number of bower decorations ( $y = 17.99 + 9.7x$ ;  $r^2 = 0.51$ ,  $n = 10$ ,  $p = 0.02$ ) in male satin bowerbirds. Males with high PC1 scores have UV-bright, intense, and highly contrasting structural plumage colouration. Trend lines are from Model II regressions.



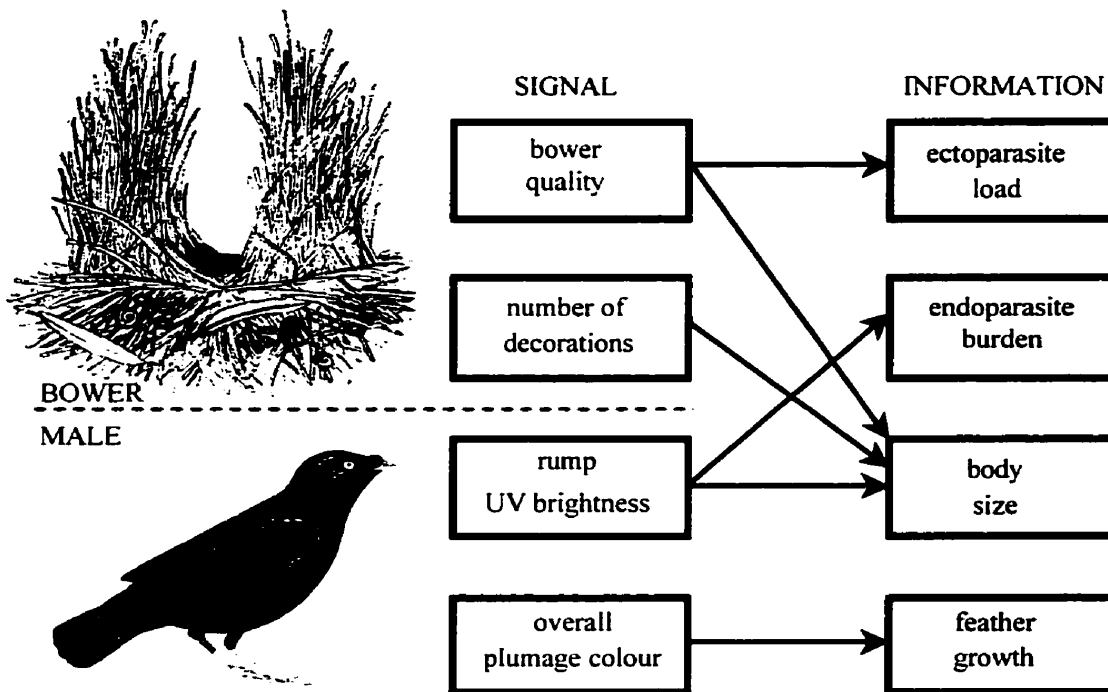


Figure 3. Associations between four male attributes potentially used by females in mate choice (bower quality, number of bower decorations, overall plumage colour, and rump UV brightness), and four indicators of male quality in the satin bowerbird. Arrows show variables that significantly ( $p < 0.05$ ) predicted each target quality indicator in regression models.

# Chapter 3

**General Discussion**

## Overview and implications of main findings

In this thesis, I investigated the signal function of sexually selected male traits in satin bowerbirds, *Ptilonorhynchus violaceus*. To do this, I objectively quantified the plumage ornamentation of males with a spectrometer and assessed each male's bower quality (as in Borgia 1985). I found that ultraviolet reflectance was a major component of male plumage colouration, and that plumage ornamentation was associated with both bower quality and the number of decorations adorning a male's bower. This relationship between bower quality and plumage colouration is congruent with Gilliard's (1956) suggestion that over the course of bower evolution, there has been a transfer of sexual selection pressure from plumage ornamentation to bower elaboration. My findings show a clear relationship between these two sexually selected male traits. Together, plumage colouration and bower quality features comprise the extended phenotype of male satin bowerbirds.

A second important aspect of my study is the discovery that structural plumage colouration and bower features signal different aspects of male quality in satin bowerbirds. While bower quality reflects ectoparasite load and body size, plumage colouration reveals the intensity of infection by blood parasites, feather growth rate, and body size. My findings suggest that if female satin bowerbirds use these traits to assess potential sires, an integrative approach whereby females assess both bower features and male characteristics would be most beneficial. This idea was supported by a recent investigation of mate searching patterns in female satin bowerbirds (Uy et al. 2001). Uy et al. (2001) found that female courtship visits to bowers were not randomly distributed

in their population. While this finding may in part be explained by past mating experience (Uy et al. 2000), the authors also suggest that assessment of the bower may allow females to pre-select a subset of males to court with and evaluate further (Uy et al. 2001). In the same study, Uy et al. (2001) found that even among males visited for courtship, the distribution of matings differed significantly from that expected by chance. Thus females assessed a subset of males and selected only the highest quality males as copulation partners (Uy et al. 2001). The female mate searching patterns discovered in Uy et al.'s (2001) study support the idea that females could use bowers to first select a subset of males to visit for courtship and refine this assessment by directly evaluating features of male courtship, which could conceivably include brilliant plumage colouration.

The results of my study can also be evaluated in context of multicomponent signaling theory. In many species, elaborate sexual displays involve a combination of several distinct signals such as plumage ornamentation, song, and display behaviour. In satin bowerbirds, females could potentially assess males based on bowers (Borgia 1985), song (Lofredo and Borgia 1986), plumage characteristics (this study) or quality of display. Four hypotheses have been proposed to explain the evolution of multiple signals (Møller and Pomiankowski 1993, Savalli 1995). According to the Multiple Messages Hypothesis, each trait can vary on a different time scale and/or represent a different quality attribute of the signaler. The Redundant Signal Hypothesis argues that if individual traits can only partially represent condition, receivers will benefit by using multiple traits to assess condition. The Unreliable Signal Hypothesis proposes that some traits are not variable enough to be functionally significant and remain associated with

attractiveness because of weak receiver preference and low cost. Finally, the Multiple Receiver Hypothesis argues that multiple traits result from selection by different receivers. My findings seem to support the Multiple Messages Hypothesis. Plumage colouration in satin bowerbirds may reflect male condition at time of moult (eg. Hill and Montgomerie 1994, Doucet 2002), while bower decorations can change on a daily basis (Borgia 1985, S. Doucet personal observation) and more likely signal current condition. From a different perspective, plumage colouration may be related to heritable parasite resistance and thus may reflect genetic quality, while bower features, which are subject to intense male–male competition, may be related to male fighting ability or dominance.

My study is the first to explicitly test predictions of the Hamilton–Zuk hypothesis in a species displaying structural plumage colouration. My finding that structural plumage brightness varies negatively with the intensity of infection by blood parasites supports a key prediction of the hypothesis (Hamilton and Zuk 1982). The signal function of individual variation in structural plumage colouration has only been investigated in a handful of studies (Sheldon et al. 1999, Keyser and Hill 1999, 2000, Doucet 2002). Only one of these attempted to assess how structural plumage colouration varied with parasite load, but parasite burden did not vary between males in that study (Keyser and Hill 2000). Thus, my study provides the first evidence that parasites may influence structural plumage colouration, while also making a general contribution to our understanding of the signal function of structural colours.

### **Limitations of study**

My study provides important insight into the signal function of sexually selected male traits in satin bowerbirds, but it is worth considering some potential shortcomings of this work. For example, my study is largely observational and relies on correlational analyses; as such, the results should be interpreted cautiously. Thus, the fact that males with high blood parasite intensities have duller plumage colouration does not necessarily imply that parasites cause dull plumage in males. High parasite intensities could simply reflect general poor condition in males; thus plumage colouration may only be indirectly related to parasites. A more convincing test would include an experimental manipulation of parasite intensities during moult while controlling for other factors such as access to food. However, because satin bowerbirds are a protected species in Australia and cannot be held in captivity, such controlled experimental manipulations are not possible in this species.

In addition, while plumage colouration was shown to signal aspects of male quality, female preference for bright males was not assessed. Thus, I cannot conclusively argue that individual variation in male brightness is maintained by female preference. However, based on evidence from other recent studies of structural plumage colouration (eg. Bennett et al. 1997, Andersson and Amundsen 1997, Andersson et al. 1998), the prominence of male plumage during courtship display in satin bowerbirds (Marshall 1954), and the potential for plumage to reveal parasite burdens, it is likely that females do use plumage colouration in mate assessment. Certainly, my findings hinting at the signal function of bower elaboration complement past studies which showed that females preferentially mate with males decorating high quality bowers (Borgia 1985).

While my study supports a key prediction made by Hamilton and Zuk (1982), it is by no means meant to be a thorough investigation of their hypothesis. A comprehensive intraspecific study of the Hamilton–Zuk hypothesis should test the following predictions: (1) Male plumage colouration is related to parasite load, (2) Females preferentially choose males based on plumage characters, (3) Hosts coevolve with parasites so that resistance remains in part heritable, and (4) Parasites have an appreciable effect on host fitness. A study evaluating all of these predictions would provide a sound test of the Hamilton–Zuk hypothesis while also distinguishing between the good genes model and the two other models of parasite–mediated sexual selection (transmission avoidance and resource provisioning; Clayton 1991). To my knowledge, no study has been able to investigate all four predictions, and field studies are particularly limiting for this level of analysis. An ideal study system would involve a species in which both laboratory and field manipulations are possible.

Finally, all contemporary researchers of plumage colouration face the difficult task of deciding which characteristics of colour are important as visual signals to the organism under study. While some broad patterns of importance can probably be inferred from receiver perceptual ecology (Endler 1990, Cuthill et al. 2000), signal origin and design might also influence which colour characteristics are biologically meaningful. Thus, it may be impossible to outline a small set of colour variables that every study should investigate. For example, in species with distinct patches of colour, patch size is likely an important signal component. Likewise, in species where hue is highly variable, such as in house finches, *Carpodacus mexicanus* colour analysis should include an assessment of hue. However, hue and patch size variation are not ubiquitous across

brightly coloured species. For example, in American goldfinches, *Carduelis tristis*, colour saturation appears to be the variable under selection in males (McGraw and Hill 2000). Alternatively, in blue–black grassquits, *Volatinia jacarina*, brightness is the most likely candidate signal (Doucet 2002). In fact, brightness may be a particularly important component of achromatic colours (white, gray, and black) and iridescent colours, like the iridescent structural plumage colouration of satin bowerbirds.

### **Directions for future research**

The findings of my study elicit as many exciting questions as they provide answers. I feel that my study would be best complemented by an investigation of female preference for secondary sexual traits in satin bowerbirds. Of the suite of elaborate male traits that could be used by female satin bowerbirds in mate choice, only bower quality (Borgia 1985) and song (Lofredo and Borgia 1986) have been investigated. A detailed study of female choice in satin bowerbirds should incorporate an assessment of all prominent features of ritualized male courtship: display behaviour, song characteristics, and elaborate plumage. Female preference can be assessed in satin bowerbirds by positioning movement–activated video cameras at the bower (Borgia 1985, Uy et al. 2000, 2001). Thus, through video observations, one could assess which males received the most female visits and which visits resulted in successful copulation. By simultaneously quantifying male plumage characteristics, song rate and quality, and male display characteristics, one could develop a more complete picture of the intricacies of female choice in satin bowerbirds.



Another interesting avenue for future research could involve an investigation of the choice of decorations used by male satin bowerbirds. We know that satin bowerbirds prefer to decorate their bowers with blue objects (Marshall 1954, Borgia et al. 1986, this study), but they also tend to incorporate other colours in their bowers. Is there one unifying link between these different types of decoration? One interesting hypothesis might be that males select decorations based on ultraviolet reflectance. Another possibility is that males choose colours that maximize contrast between bowers and the environment, bowers and plumage colouration, or between different types of bower decorations. I have collected experimental data on choice of UV-reflecting versus UV-absorbing decorations, spectral reflectance of bower decorations, and plumage reflectance of males which should allow me to test these hypotheses in the near future.

## References

- Andersson, S. and Amundsen, T. 1997. Ultraviolet colour vision and ornamentation in bluethroats. *Proceedings of the Royal Society of London B* 264: 1587–1591.
- Andersson S., Örnborg, J., and Andersson, M. 1998. Ultraviolet sexual dimorphism and assortative mating in blue tits. *Proceedings of the Royal Society of London B* 263:843–848.
- Bennett, A. T. D., Cuthill, I.C., Partridge, J. C., and Lunau, K. 1997. Ultraviolet plumage colors predict mate preferences in starlings. *Proceedings of the National Academy of Sciences, USA* 94: 8618–8621.
- Borgia, G. 1985. Bower quality, number of decorations and mating success of male satin bowerbirds (*Ptilonorhynchus violaceus*): an experimental analysis. *Animal Behaviour* 33: 266–271.
- Borgia, G., Kaatz, I. M., and Condit, R. 1986. Flower choice and bower decoration in the satin bowerbird *Ptilonorhynchus violaceus*: a test of hypotheses for the evolution of male display. *Animal Behaviour* 35:1129–1139.

- Clayton, D. H. 1991. The influence of parasites on host sexual selection. *Parasitology Today* 7: 329–334.
- Cuthill, I. C., Partridge, J. C., Bennett, A. T. D., Church, S. C., Hart, N. S., and Hunt, S. 2000. Ultraviolet vision in birds. *Advances in the Study of Behavior* 29: 159–214.
- Doucet, S. M. 2002. Structural plumage coloration, male body size, and condition in the blue–black grassquit. *Condor* 104: 30–38.
- Endler, J. A. 1990. On the measurement and classification of colour in studies of animal colour patterns. *Biological Journal of the Linnean Society* 41: 315–352.
- Gilliard, E. T. 1956. Bower ornamentation versus plumage characters in bowerbirds. *Auk* 73: 450–451.
- Hamilton, W. D. and Zuk, M. 1982. Heritable true fitness and bright birds: a role for parasites? *Science* 218: 384–387.
- Hill, G. E. and Montgomerie, R. 1994. Plumage colour signals nutritional condition in the house finch. *Proceedings of the Royal Society of London B* 258: 47–52.
- Keyser, A. J. and Hill, G. E. 1999. Condition–dependent variation in the blue–ultraviolet coloration of a structurally based plumage ornament. *Proceedings of the Royal Society of London B* 266: 771–777.
- Keyser, A. J. and Hill, G. E. 2000. Structurally based plumage coloration is an honest signal of quality in male blue grosbeaks. *Behavioral Ecology* 11: 202–209.
- Lofredo, C. A. and Borgia, G. 1986 Male courtship vocalizations as cues for mate choice in the satin bowerbird (*Ptilonorhynchus violaceus*). *Auk* 130: 189–195.
- Marshall, A. J. 1954. *Bower–birds: their displays and breeding cycles*. Oxford, Clarendon Press.
- McGraw, K. J. and Hill, G.E. 2000. Differential effects of endoparasitism on the expression of carotenoid– and melanin–based ornamental coloration. *Proceedings of the Royal Society of London B* 267: 1525–1532.
- Møller, A. P., and Pomiankowski, A. 1993. Why have birds got multiple sexual ornaments? *Behavioral Ecology and Sociobiology* 32: 167–176.
- Savalli, U. M. 1995. The evolution of bird coloration and plumage elaboration. *In Current Ornithology* (Power, D. M. ed). pp 145–190. Plenum, New York.

Sheldon, B. C., Andersson, S., Griffith, S. C., Örnborg, J., and Sendecka, J. 1999.

Ultraviolet colour variation influences blue tit sex ratios. *Nature* 402: 874–877.

Uy, J. A. C., Patricelli, G. L. & Borgia, G. 2000 Dynamic mate–searching tactic allows female satin bowerbirds *Ptilonorhynchus violaceus* to reduce searching.

*Proceedings of the Royal Society of London B* 267: 251–256.

Uy, J. A. C., Patricelli, G. L., and Borgia, G. 2001. Complex mate searching in the satin bowerbird *Ptilonorhynchus violaceus*. *American Naturalist* 158: 530–542.

## **SUMMARY**

1. I show that in satin bowerbirds, male plumage colouration is particularly reflective in the ultraviolet region of the electromagnetic spectrum.
2. Male plumage colouration was positively correlated with both the quality of bower construction and the average number of decorations adorning a male's bower.
3. While bower characteristics significantly predicted ectoparasite load and body size, plumage colouration significantly predicted the intensity of infection from blood parasites, feather growth rate, and body size.
4. My finding that parasite intensity was negatively correlated with male brightness supports an intraspecific prediction of the Hamilton and Zuk model of parasite-mediated sexual selection.
5. Overall, my findings suggest that female satin bowerbirds would benefit most by evaluating bower features to make general assessments of male quality and by directly evaluating displaying males to refine this assessment.
6. Given that plumage colouration and bower features are regulated by different mechanisms and reveal different aspects of quality, my findings support the Multiple Messages Hypothesis of the evolution of multiple signals of quality in satin bowerbirds.