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Female choice for parasite-free male satin bowerbirds and the evolution of bright male plumage

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Summary. Hamilton and Zuk proposed that bright male plumage may have evolved in males of polygynous species as a result of female preferences for males that are able to demonstrate their resistance to disease. They predicted an inverse correlation between female mating preferences and the level of parasitic infection of males. We found such a correlation between the level of infection by a common ectoparasite (*Myrsidea ptilonorhynchi*: Menoponidae) and mating success of male satin bowerbirds (*Ptilonorhynchus violaceus*). In addition, we tested and were able to confirm three other predictions derived from their model: that (1) older males had fewer parasites than their younger counterparts, (2) levels of individual parasitic infection are highly correlated between years, and (3) that individuals resighted in successive years are less parasitized than those that fail to return. These results support the bright male model, but they are also consistent with two other hypotheses that may explain plumage dimorphism based on the level of parasitic infection. The correlated infection model suggests that females choose males with few ectoparasites because of a correlation between the level of ectoparasitic infection and heritable resistance to internal infections. In the parasite avoidance model, females favor parasite-free males because it lowers their own prospects for parasitic infection. Our data did not show the predicted relationship between parasite numbers with plumage quality that is needed to support the bright male hypothesis, nor did it show the inverse correlation between male condition and parasite numbers that is predicted by both the bright male and correlated infection hypotheses. Our results are most consistent with the parasite avoidance hypothesis.

Introduction

Recently there has been much attention directed at the problem of how extreme sex-limited displays evolve in males of polygynous species. Numerous hypotheses have been developed to explain the evolution of these traits (Fisher 1930; Zahavi 1975; Borgia 1979; Lande 1981; Parker 1983; Seger 1985), but no consensus has formed to support any set of models (see Bradbury and Andersson 1987). This may be due to a paucity of empirical tests of these hypotheses. Among the most frequently discussed of these models is Hamilton and Zuk's (1982) bright male hypothesis. It proposes that only healthy males can develop bright plumage and that females use differences in the brightness of male plumage as an indicator of a male's resistance to disease. Then, by choosing bright males as sires for their offspring, females are more likely to produce disease resistant offspring. Recent models have described the conditions under which this process might work (e.g., Pomiankowski 1987a, b; Charlesworth 1988; but see Kirkpatrick 1986).

Hamilton and Zuk (1982) supported their model with an interspecific comparison in which they obtained a positive correlation between the brightness of male plumage and the number of parasites found in a species. They argued that species with high levels of endoparasitic infection are more likely to evolve bright males because there is intense selection on females to gain more from assessing male disease resistance. This test has been criticized for two reasons. First, selection for bright males could produce the opposite result if female selection of male brightness has increased population resistance thereby lowering the level of infection in the population. Second, their result could be due to a correlation with another variable (Borgia 1986a; Read 1987; Partridge and Harvey 1986). For example, it has long been recognized that male brightness is associated with polygyny (Darwin 1871). Thus, the correlation between male brightness and parasitic infection might occur because diseases are transmitted more readily in polygynous species that have been selected to have bright males for other reasons. Read (1987) tested this possibility and concluded that mating system had no effect on level of infection in his sample. However, the relatively small sample sizes in his comparison and questions about the scoring of birds plumage (Read and Harvey 1989) leave the issue of correlated effects unresolved.

Hamilton and Zuk proposed a more straightforward test of their model using intraspecific comparisons. They predicted an inverse correlation between male mating success and the number of parasites carried by males. We used this prediction as a focus for testing the bright male and related models with data from our study of the satin bowerbird.

Satin bowerbirds are well-suited for testing models of plumage dimorphism. This is a polygynous species in which males provide no parental care or other material benefits. Males build and defend twig structures called bowers where courtship and matings occur and which can be monitored using cameras controlled by an infrared detection system (Borgia 1985a). Males 7 years and older have a shiny blue-black plumage that differs from the mottled green plumage of females and young males (Vellenga 1980). The plumage of adult males refracts sunlight in a way that generates bright flashes when males flick their wings during courtship displays (Borgia 1986b).

In 1984 we found significant differences between age and sex classes in numbers of ectoparasites on males such that older age classes had fewer parasites (Borgia 1986a). These data were consistent with predictions of the bright male model, but comparisons among mating males did not show the predicted inverse correlation between the number of parasites and male mating success. Our inability to show this result was due to the overall scarcity of lice on bower-holding males in 1984.

Here we report data from our 1985 and 1986 field work. We evaluate several predictions that can be developed from the Hamilton and Zuk model. In addition, we consider two other hypotheses that may explain the evolution of plumage dimorphism in satin bowerbirds. Both of these hypotheses state that the dark plumage of male satins functions to make the light-colored ectoparasites easier to see, thereby making it easier for females to gauge the level of male infection.

The "correlated infection" model suggests that females are selected to avoid males with ectoparasitic infection because the presence of ectoparasites serves as an indicator of low male resistance to disease. Marshall (1981) has noted that levels of endo- and ectoparasitic infection are often correlated. By inspecting males for ectoparasites, females might then gain information about male resistance to ecto- and endoparasites. Like the bright male hypothesis, if this resistance is heritable, then females may benefit from choice of parasite-free males by having offspring with enhanced disease resistance.

The "parasite avoidance" model suggests that females prefer to avoid males with ectoparasites because this reduces the likelihood that they will be infected by their mate. This infection could come directly from the ectoparasite or from another disease that males carry that is correlated with the level of ectoparasitic infection. Both models suggest that there has been selection for dark-plumed males in order to make ectoparasites easier to see. The bright male and correlated infection models suggest that choosy females gain from producing more parasite resistant young. The parasite avoidance model suggests a more immediate payoff (proximate benefit) for females in lowering their own risk of infection. The parasite avoidance and correlated infection models do not require a correlation between adult male plumage quality and the degree of parasitic infection.

Methods

This study was carried out at Wallaby Creek, in the Beaury State Forest, 120 km NW of Lismore, New South Wales, Australia. An area 1.5 km in each direction from capture sites was thoroughly surveyed for bowers, and the identity of the owner was determined for each bower. Marking of birds began in 1976 and intensive study of parasitic infection started in 1984. The bulk of observations reported here were made from September through December in 1985 and 1986. Birds were captured in baited traps and removed immediately. The birds were color-banded (if not previously captured), scored for plumage characters and numbers of ectoparasites, weighed, measured for wing length, and immediately released. Plumage characters and measurements of wing length allowed sexing and aging of birds (Vellenga 1980). Our records allowed us to assign males to age classes according to when they obtained adult plumage (see Borgia 1986a, b). Plumage comparisons were made among adult males in an attempt to score for differences in plumage quality. The louse *Myrsidea ptilonorhynchi* is the only abundant ectoparasite found on satin bowerbirds. It was restricted to the head, mostly in the areas immediately above and around the eyes. Counts of this parasite on males were used to test hypotheses. The data reported here include only parasite counts on the heads of birds. Initially, parasites were counted over the entire bird, but it was determined that lice were found regularly only on the heads of birds where they could not preen. Occasionally, hippoboscid flies (*Ornithophilia metallica* and *Ornithomya fuscipennis*) were found in the plumage on other parts of the bird, but their tendency to fly off the bird after we captured it made our counts unreliable. We found that these flies regularly carried *M. ptilonorhynchi* attached to their abdomen and are likely vectors for the transfer of lice between birds (Borgia 1986a). Birds designated as bower holders were birds that held a permanent bower site, that is, a site where a bower was maintained through the entire mating season the previous year. Each permanent bower site was monitored by a camera controlled by an infrared device that triggered the camera when birds entered the bower (see Borgia 1985a, 1986b). Matings occur in the bower and our camera system allows us to determine male mating success. Matings were scored by review of films from cameras that monitored bowers. Statistical comparisons are by Kendall (r_k) and Spearman (r_s) rank correlations, t-tests, and LSD multiple comparison tests (Sokal and Rohlf 1981; Wilkinson 1986).

Results

Age and sex class differences

As in 1984, males in 1985 and 1986 tended to have fewer parasites than females (1985: $t=-1.35$, $N=217$, $P=0.09$; 1986: $t=-1.76$, $N=224$, $P=0.04$), and older males had fewer parasites than younger males (Table 1). Overall, there was an inverse relationship between infection and age among all males (Table 1) and among bower holders in 1985 ($r_k=-0.44$, $N=22$, $P=0.026$); however, this was not the case in 1986.

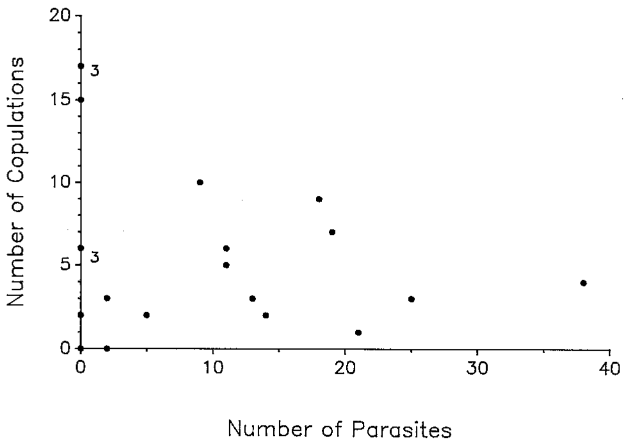

Fig. 1. A plot of the number of ectoparasites (*Myrsidea ptilonorhynchi*) on a male satin bowerbird versus male mating success. Numbers indicate multiple data points

Mating success

In 1985 we were able to support Hamilton and Zuk's prediction with the finding of a significant inverse correlation between the number of lice and the number of matings by bower holding males ($r_k=-0.31$, $N=22$, $P=0.03$; Fig. 1). In 1986 we did not find a significant correlation. However, because of extraordinary conditions that year, this was not unexpected. There was a very low number of matings associated with extreme drought and a severe cold period during which some males uncharacteristically abandoned their bowers.

Table 1. Number of lice (*Myrsidea ptilonorhynchi*) for six sex- and age-classes of the satin bowerbird in 1985 and 1986. [In an earlier paper (Borgia 1986) this parasite was misidenitified as *Cuclotogaster sp.*]

	Years							
	1985				1986			
Class	$\bar{X}$	S.E.	N	Sig.*	$\bar{X}$	S.E.	N	Sig.*
Adult plumage males with bowers	7.6	2.4	22	a	5.7	1.7	21	a
Adult plumage males without bowers	11.4	1.9	63	a	16.6	4.5	25	ab
Males with mixed adult and juvenile plumage	18.1	3.6	28	ab	18.2	4.8	19	ab
Juvenile plumage males	24.0	4.0	31	b	25.1	4.0	39	b
Females	18.4	2.5	75	b	23.5	2.3	120	b

* Classes with different letters have significantly different means using Fisher's Protected LSD ($P<0.05$)

Table 2. Between year comparison of ectoparasite number on individual satin bowerbirds; years 1984 with 1985 and 1985 with 1986 (one-tailed p values)

Class	1984–1985	1985–1986
All birds	$N=65$ $r_s=0.391$ $P=0.0009$	$N=79$ $r_s=0.468$ $P<0.0005$
Females	$N=7$ $r_s=0.427$ $P=0.15$	$N=13$ $r_s=0.819$ $P=0.002$
All males	$N=58$ $r_s=0.346$ $P=0.004$	$N=66$ $r_s=0.351$ $P=0.002$
All juvenile plumage males (Dark-billed, yellow-billed, and mixed plumage males)	$N=16$ $r_s=0.401$ $P=0.06$	$N=30$ $r_s=0.416$ $P=0.01$
Dark-billed males	$N=6$ $r_s=0.714$ $P=0.05$	$N=14$ $r_s=0.527$ $P=0.03$
Transitional plumage males (Yellow-billed and mixed plumage males)	$N=10$ $r_s=0.152$ $P>0.25$	$N=16$ $r_s=0.330$ $P=0.10$
All adult plumage males	$N=42$ $r_s=0.175$ $P=0.13$	$N=36$ $r_s=0.275$ $P=0.05$
Adult plumage males with bowers	$N=17$ $r_s=-0.091$ $P>0.50$	$N=13$ $r_s=0.298$ $P=0.15$
Adult plumage males without bowers	$N=25$ $r_s=0.148$ $P=0.23$	$N=23$ $r_s=0.200$ $P=0.17$

Between-year comparisons

The bright male hypothesis predicts that the level of infection of birds is heritable. Although we could not directly test the heritability of parasite resistance, we were able to test a related hypothesis. That is, if there is a heritable component to parasite resistance, then we expect a positive between-year correlation in levels of individual infection. We were able to confirm this prediction for both sexes (Table 2). We also found between-year correlations in levels of individual infection within different age classes of males. This result is significant because it shows that the predicted pattern persists when the effects of age are eliminated.

Falconer (1981) provides a measure of the upper limit to heritabilities as shown by a measure he calls repeatability (r), which is the proportion of the total phenotypic variation that is explained by between-individual variation. The value of r we obtained from our sample was 0.71, which suggests that the potential for a high heritability exists.

Bower holding males have different behaviors than other males, and it is possible that they contribute to differences in levels of infection (Borgia 1986a). These differences, however, do not lead to obvious biases in our expectations about levels of infection in different classes of males. For example, established bower holders court considerably fewer males in practice displays than younger males; some bower holders court many females and thereby may suffer a similar overall level of exposure to ectoparasitic infection. To test the hypothesis that age groupings differ in their exposure to parasites, we examined patterns of infection of initially uninfected individuals in each group. Pooling data across years showed no obvious between-class differences among uninfected birds in their likelihood of becoming infected in the following year (juvenile plumage males, 6/12; blue nonbower holders, 5/8; bower holders, 12/25). Although these results are based on a small sample, they suggest that male age and related differences in where they reside have no dramatic effect on the tendency to become infected.

The observed between-year correlations may not be due to intrinsic resistance of birds but rather to a low rate of infection such that uninfected birds tended to stay uninfected. In our comparisons, 51% of uninfected birds were infected the next year, and 22% of the birds that had been infected were not infected the next year. These results show that there are large changes in the membership of the class of uninfected birds between years and indicate that the probability of becoming infected is quite high. Eliminating initially uninfected birds from year to year, comparisons still showed significant between-year correlations in levels of infection (Table 3). This result indicates that uninfected birds are not critical for establishing year to year correlations in levels of individual infection. It is also consistent, however, with the hypothesis that the correlation in the levels of infection between years is due to the history of ectoparasite numbers on the bird. We cannot directly test this hypothesis, but it seems unlikely for the following reason. Lice have relatively high reproductive rates (Marshall 1981); therefore, we would expect that over the course of a year numbers of lice have the potential to change dramatically on any bird. If this is true, then population numbers of lice on an infected bird should be less important in determining numbers in subsequent years than the bird's capacity to control the growth of ectoparasites.

Differences in age-related infection could also be explained by differences in contact with conspecifics. We compared the number of contacts by males during aggressive interactions at feeding sites

Table 3. Between year comparison of ectoparasite and number on individual satin bowerbirds that were not infected in the first year of each comparison; years 1984 with 1985 and 1985 with 1986 (one-tailed p values)

Class	1984–1985	1985–1986
All birds	$N=44$ $r_s=0.391$ $P=0.005$	$N=52$ $r_s=0.427$ $P=0.001$
Females	$N=5$ $r_s=-0.200$ $P>0.50$	$N=8$ $r_s=0.575$ $P=0.06$
All males	$N=39$ $r_s=0.364$ $P=0.01$	$N=44$ $r_s=0.320$ $P=0.02$
All juvenile plumage males (Dark-billed, yellow-billed, and mixed plumage males)	$N=14$ $r_s=0.326$ $P=0.12$	$N=23$ $r_s=0.330$ $P=0.06$
Dark-billed males	$N=5$ $r_s=0.800$ $P=0.05$	$N=9$ $r_s=0.239$ $P=0.25$
Transitional plumage males (Yellow-billed and mixed plumage males)	$N=9$ $r_s=0.012$ $P>0.25$	$N=14$ $r_s=0.377$ $P=0.09$
All adult plumage males	$N=25$ $r_s=0.290$ $P=0.08$	$N=21$ $r_s=0.221$ $P=0.16$
Adult plumage males with bowers	$N=5$ $r_s=0.344$ $P=0.24$	$N=6$ $r_s=-0.015$ $P>0.50$
Adult plumage males without bowers	$N=20$ $r_s=0.236$ $P=0.15$	$N=15$ $r_s=0.260$ $P=0.17$

Table 4. Comparisons of ectoparasite number with number of birds contacted and total number of interactions at a feeding site in 1986 (two-tailed p values)

Class	Number of birds interacted with vs parasite number	Number of total interactions vs parasite number
All birds	$N=103$ $r_s=-0.045$ $P>0.50$	$N=103$ $r_s=-0.075$ $P>0.50$
Females	$N=26$ $r_s=0.140$ $P>0.40$	$N=26$ $r_s=0.064$ $P=>0.50$
All males	$N=77$ $r_s=0.027$ $P>0.50$	$N=77$ $r_s=-0.010$ $P>0.50$
All juvenile plumage males (Dark-billed, yellow-billed, and mixed plumage males	$N=38$ $r_s=0.300$ $P=0.07$	$N=38$ $r_s=0.232$ $P=0.17$
Dark-billed males	$N=23$ $r_s=0.333$ $P=0.13$	$N=23$ $r_s=0.234$ $P>0.30$
Transitional plumage males (Yellow-billed and mixed plumage males)	$N=15$ $r_s=0.254$ $P>0.30$	$N=15$ $r_s=0.204$ $P>0.40$
All adult plumage males	$N=39$ $r_s=-0.297$ $P=0.07$	$N=39$ $r_s=-0.296$ $P=0.07$
Adult plumage males with bowers	$N=23$ $r_s=-0.256$ $P>0.20$	$N=23$ $r_s=-0.265$ $P>0.20$
Adult plumage males without bowers	$N=16$ $r_s=-0.461$ $P=0.08$	$N=16$ $r_s=-0.385$ $P=0.15$

and the level of infection. Our results (Table 4) show no overall relationship between infection with either the number of birds interacted with or with the total number of interactions. Among juvenile plumage birds there is a marginally significant tendency in the predicted direction but a similar comparison among adult plumage males shows the pattern in the opposite direction.

Survivorship

If parasite resistance affects survivorship, then the observed age-related changes in levels of infection might be explained by a greater loss of non-resistant individuals. Also, if these ectoparasites impose a direct cost, then infection should be positively related to mortality. We tested these hypotheses by comparing the number of parasites on individuals in two groups: those that were and those that were not resighted in the following year. Observers sighting birds were not aware of the level of infection of birds in the previous year. In accordance with out predictions, we found that birds that reappeared had significantly fewer parasites than those that did not (1985: $t=3.37$, $N=268$, $P=0.0004$; 1986: $t=1.19$, $N=217$, $P=0.12$; combined $P<0.001$). An alternative explanation for this result is that the lower level of infection among returned individuals occurred because that group contained a disproportionately large number of older males that had a low level of infection. By excluding adult plumage males from our comparison this effect could be eliminated. We found a trend in the predicted direction in each year, but it was not significant in either case (1985: $t=1.35$, $N=204$, $P=0.09$; 1986: $t=0.90$, $N=132$, $P=0.19$). Thus, there is limited support for the hypotheses that ectoparasitic infection affects the survival of satin bowerbirds, but we were not able to eliminate the possibility that this pattern was due to a differential return rate among different classes of birds.

Table 5. Comparisons of a measure of condition (weight/wing) with ectoparasite number on individual birds across years (one-tailed p values)

Class	1984	1985	1986
All birds	$N=275$ $r_s=0.0006$ $P>0.50$	$N=229$ $r_s=0.007$ $P>0.50$	$N=232$ $r_s=0.065$ $P>0.50$
Females	$N=157$ $r_s=0.098$ $P>0.50$	$N=75$ $r_s=0.060$ $P>0.50$	$N=121$ $r_s=0.088$ $P>0.50$
All males	$N=118$ $r_s=-0.020$ $P>0.25$	$N=154$ $r_s=0.002$ $P>0.50$	$N=111$ $r_s=0.067$ $P>0.50$
All juvenile plumage males (Dark-billed, yellow-billed, and mixed plumage males)	$N=54$ $r_s=0.095$ $P>0.50$	$N=72$ $r_s=0.155$ $P>0.50$	$N=64$ $r_s=0.084$ $P>0.50$
Dark-billed males	$N=38$ $r_s=0.215$ $P>0.50$	$N=44$ $r_s=0.175$ $P>0.50$	$N=45$ $r_s=0.011$ $P>0.50$
Transitional plumage males (Yellow-billed and mixed plumage males)	$N=16$ $r_s=-0.281$ $P=0.14$	$N=28$ $r_s=0.199$ $P>0.50$	$N=19$ $r_s=0.384$ $P>0.50$
All adult plumage males	$N=64$ $r_s=-0.038$ $P>0.25$	$N=82$ $r_s=-0.024$ $P>0.25$	$N=47$ $r_s=0.003$ $P>0.50$
Adult plumage males with bowers	$N=29$ $r_s=-0.046$ $P>0.25$	$N=37$ $r_s=-0.088$ $P>0.25$	$N=25$ $r_s=0.336$ $P>0.50$
Adult plumage males without bowers	$N=35$ $r_s=-0.064$ $P>0.25$	$N=45$ $r_s=0.016$ $P>0.50$	$N=22$ $r_s=-0.285$ $P=0.10$

Table 6. Comparisons of ectoparasite number with measures of bower quality and the number of different decorations found on individual bowers in 1984, 1985, and 1986 (one-tailed p values). Low bower quality scores represent high quality bowers

Measures	1984	1985	1986
Symmetry of bower	$N=19$ $r_s=0.190$ $P=0.21$	$N=20$ $r_s=0.246$ $P=0.14$	$N=18$ $r_s=-0.089$ $P>0.50$
Bower stick size	$N=19$ $r_s=0.188$ $P=0.21$	$N=20$ $r_s=0.275$ $P=0.11$	$N=18$ $r_s=-0.043$ $P>0.50$
Bower stick density	$N=19$ $r_s=0.300$ $P=0.10$	$N=20$ $r_s=-0.037$ $P>0.50$	$N=18$ $r_s=0.037$ $P>0.25$
Overall quality of bower	$N=19$ $r_s=0.208$ $P=0.19$	$N=20$ $r_s=0.110$ $P=0.32$	$N=18$ $r_s=-0.103$ $P>0.50$
Yellow leaves	$N=19$ $r_s=0.013$ $P>0.50$	$N=20$ $r_s=-0.025$ $P>0.25$	$N=18$ $r_s=-0.105$ $P>0.25$
Yellow straw	$N=19$ $r_s=-0.258$ $P=0.14$	$N=20$ $r_s=0.181$ $P>0.50$	$N=18$ $r_s=0.053$ $P>0.50$
Blue feathers	$N=19$ $r_s=-0.339$ $P=0.07$	$N=20$ $r_s=0.019$ $P>0.50$	$N=18$ $r_s=0.582$ $P>0.50$
Snail shells	$N=19$ $r_s=-0.114$ $P>0.25$	$N=20$ $r_s=0.554$ $P>0.50$	$N=18$ $r_s=0.030$ $P>0.50$
Blue blossoms	$N=19$ $r_s=-0.173$ $P=0.23$	$N=20$ $r_s=0.029$ $P>0.50$	$N=18$ $r_s=-0.059$ $P>0.25$
Yellow blossoms	$N=19$ $r_s=-0.037$ $P>0.25$	$N=20$ $r_s=-0.066$ $P>0.25$	$N=18$ $r_s=0.326$ $P>0.50$
Cicada skins	$N=19$ $r_s=-0.109$ $P>0.25$	$N=20$ $r_s=-0.010$ $P>0.25$	$N=18$ $r_s=0.233$ $P>0.50$
Man-made objects	$N=19$ $r_s=-0.396$ $P=0.05$	$N=20$ $r_s=-0.081$ $P>0.25$	$N=18$ $r_s=0.170$ $P>0.50$
Natural objects	$N=19$ $r_s=-0.216$ $P=0.18$	$N=20$ $r_s=-0.002$ $P>0.25$	$N=18$ $r_s=0.255$ $P>0.50$

Male condition

We tested the hypothesis that male condition affects levels of infection by comparing the relative weights (weight/wing length) of birds to levels of infection. We found no correlation between relative weight and number of parasites (Table 5). Elsewhere, (Borgia 1985a, b) we have shown that aggressively dominant males that are assumed to be in good condition have well-built and decorated bowers. In comparisons involving 4 measures of bower quality and 9 different types of bower decorations, we could not find a consistent pattern that supported the predicted relationship with level of infection (Table 6). Male satin bowerbirds commonly destroy bowers of other males, and there is evidence that this is related to the relative dominance of males (Borgia 1985b). We could find no significant correlation between the number of parasites on a male and the number of times a male had his bower destroyed (1984: $r_s=0.027$, $N=17$, $P=0.14$; 1985: $r_s=-0.26$, $N=20$, $P>0.50$). Thus, the inverse correlation between number of parasites and mating success appears not to be due to a correlation of the former with other characters that have been shown to affect female choice in satin bowerbirds. Furthermore, we were not able to show a relationship between the number of parasites on birds and the condition of birds.

Plumage brightness

The bright male model predicts that endoparasitic infection leads to a lower level of condition that affects the brightness of male plumage. We closely inspected male satin bowerbirds and could not find any noticeable and consistent variation in the brightness of plumage of adult male satin bowerbirds. There were two males that had noticeably dull plumage, but these were rare and were not bower holders. Our inability to score plumage differences among adult males did not allow us to make comparisons with overall condition, mating success, and ectoparasitic infection.

Discussion

Plumage dimorphism is highly variable among bowerbird species (e.g., Marshall 1954), and its function in highly dimorphic species has never been understood. Gilliard (1956, 1963, 1969) noted that there appeared to be an inverse correlation in the brightness of male plumage and the degree of elaboration of bowers and their associated decorations. He suggested that elaborated bowers functioned in place of bright plumage; however, he never specified a functional role for plumage or bower elaboration.

The evidence reported here suggests a possible functional role for plumage dimorphism in satin bowerbirds. Specifically, our finding that male mating success is inversely correlated with numbers of ectoparasites supports predictions of the bright male, correlated infection, and parasite avoidance models. The overall consistency of age and sex patterns of infection across all 3 years suggests that parasitic infection is strongly sex- and age-related as might be expected when a cost to parasites exists. The finding that birds that return have fewer parasites provides additional support for the hypothesis that there is a cost to carrying ectoparasites. The between-year correlations in levels of infection are consistent with the hypothesis that resistance to *Myrsidea ptilonorhynchi* is heritable. Our findings that between-year correlations occurred within age and sex groups and that these patterns were maintained when uninfected birds were excluded from the analysis help reject several alternative hypotheses that might explain between-year correlations in levels of infection.

Several predictions of the bright male and correlated infection hypotheses were not supported. Both models predict an inverse correlation of male condition with infection, but we did not find this relationship. The bright male hypothesis alone predicts a correlation between individual male brightness and the number of parasites. We were unable to show any relationship between plumage brightness and parasitic infection. Our inability to separate males on the basis of plumage brightness does not mean that satin bowerbirds cannot make these determinations, but it suggests that if these differences exist they are quite subtle.

The bright male hypothesis assumes that it is the effect of parasites on the overall condition of birds that affects plumage brightness. The correlated infection model assumes that reduced condition from endoparasitic infection allows ectoparasites to become common. Thus, the absence of a relationship between condition and differences in parasite numbers is evidence against both the bright male and the correlated infection hypotheses. Parasite avoidance requires no such association in adults, if as is common with ectoparasitic infection, major costs of parasites are on nestlings (e.g., Rothschild and Clay 1952; Eveleigh and Threlfall 1976; Marshall 1981). Thus, it may be important for females to avoid infection in order to reduce the transmission of parasites to their offspring.

The parasite avoidance model thus emerges as the most consistent with the available data. Patterns of male plumage change and display behavior provide additional support for the suggestion that it is important for females to see parasites. As stated, we noted that the dark blue-black plumage of adult male satins makes the whitish lice easier to see on these adults than on females and juvenile males. Also significant is that the appearance of blue feathers in juvenile plumaged but sexually mature fifth and sixth year males starts most often around the males' eyes (Collis and Borgia, unpublished data). This is where the majority of parasites are located and is the closest part of the male's plumage to females during display. In display, a male satin bowerbird is close to the female and presents himself with his head turned so that one eye (and the surrounding feathers) is directed at her. This behavior allows the females to directly observe parasites, especially around the male's eyes, and is unique when compared with other species of bowerbirds with similar types of bowers. For example, the closely-related male spotted bowerbirds display much further from the female, have no sexually dimorphic plumage, and have no visible ectoparasites (Borgia, in preparation).

One difficulty with the parasite avoidance hypothesis is that females have a generally high overall level of infection; therefore, the benefits of choosing relatively parasite-free males as mates are not clear. It is possible that new infections of lice carry with them novel pathogens and females are selected to avoid these secondary infections. Also, it may be that uninfected females choosing parasite-free males are the cause of the inverse correlation of male mating success and infection. Because we could not capture females at the time they mated we cannot test this possibility. High levels of female infection does not lessen the value of choosing mates that might provide heritable disease resistance.

There has been some controversy over the plausibility of Hamilton and Zuk's bright male hypothesis. Kirpatrick (1986) claimed that this model could not work, but Pomiankowski (1987a, b) and Charlesworth (1988) have shown that the mechanism proposed by Hamilton and Zuk can work, although the conditions necessary for its operation are somewhat restrictive. Since the correlated infection model has requirements very similar to the bright male model, it is likely that these conclusions would apply to that model also. By contrast, the parasite avoidance model is based on immediate benefits to females and, as such, should require no complicated circumstances to evolve, e.g., being restricted to particular circumstances such as temporally varying natural selection.

A potential difficulty with all of these models is that we might expect that parasites evolve to match male plumage in order to avoid detection as an aid to their own transmission. Lice have higher reproductive rates and generation times than bowerbirds so it might be expected that they should be able to track changes in the color of their host. However, while such mimicry of male plumage is possible, it is not necessarily expected. Parasites are most abundant on females and young males that have a predominantly green and white speckled plumage. Any change to become blue-black to match the adult male plumage would probably make these lice more visible on these other classes of birds. If, however, crypsis is important for these parasites in avoiding detection (e.g., during preening by the host, or male rejection of heavily parasitized females), then the different colors of satin bowerbirds impose conflicting selection pressures on lice. Given that the great majority of lice occur on female plumage birds and because females are the most likely vectors to young birds, it is probably most important for lice to avoid detection on females. Thus, it is not obvious that lice should evolve to match adult male plumage.

Our data show that females favor relatively parasite-free males as mates and that these individuals tend to live longer. There is even evidence suggesting that disease resistance may be heritable. These results provide some support for all three of the mate choice models we consider. Our inability to obtain data supporting predicted inverse correlation between several independent measures of condition and level of infection and the absence of a correlation between parasitic infection and plumage quality causes us to favor the parasite avoidance hypothesis over the others. The parasite avoidance and correlated infection models have not been considered elsewhere, and our results suggest that they may be important in understanding the relationship between ectoparasitic infection and plumage dimorphisms.

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