Behav Ecol Sociobiol (1986) 19:355–358

Behavioral Ecology and Sociobiology
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Satin bowerbird parasites: a test of the bright male hypothesis

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Received October 23, 1985 / Accepted July 8, 1986

Summary. The number of a common parasite (*Cuclotogaster* sp.) on male satin bowerbirds was related to male mating success in a test of Hamilton and Zuk's (1982) bright male hypothesis. The data do not show the expected inverse correlation between female mating preferences and the level of parasitic infection of males predicted by that model. Nearly all matings are accomplished by bower-holding males (Borgia 1985a), but the vast majority of these males were uninfected. There were large differences in mating success among the uninfected bower holders, but this could not be explained by between male differences in the level of parasitic infection. From this I conclude that levels of parasitic infection are not now an important direct cause of intermale variation in mating success. The results are, however, consistent with a hypothesis that a low level of infection is indicative of the overall healthy condition of a male. If this is true, it supports the hypothesis that the ability to hold a bower may be an indicator of male condition to females.

Introduction

Hamilton and Zuk (1982) have proposed that bright male plumage can serve as an indicator of a male's relative resistance to parasites. They argued that by choosing bright males, females are able to enhance the viability of their offspring through increased disease resistance. Several models of female choice have been proposed which suggest that male display characters indicate male quality (Fisher 1930; Zahavi 1975; Borgia 1979; Andersson 1982), and that strong female choice should reduce heritable variation among males for these characters (Borgia 1979; Taylor and Williams 1982). Selection of males based on their resistance to disease might provide an exception to this pattern. Rapid coevolution of pathogens with their hosts makes it likely that there is a significant heritable variation in resistance traits that confer immunity. This "red queen" effect (Van Valen 1973) may provide heritable variation in traits that have important effects on offspring survival.

Hamilton and Zuk (1982) state that their model "...is contradicted if *within* a species preferred mates have most parasites... [and] ...is supported if *among* species those with the most evident sexual selection are most subject to attack by debilitating parasites." They evaluate only the second of these tests by showing a correlation between the degree of plumage brightness and the number of parasites found in a species. This result, however, does not provide convincing support for their "bright male" model. First, it is not a sufficient test because the bright male model could also predict the opposite result: species with bright males should be the least parasitized if female selection for male brightness has lowered the level of infection in the population. Second, a well established correlation of male brightness with polygyny (e.g., Darwin 1871) makes their result difficult to interpret. In polygynous populations external parasites should spread rapidly because of the high rate of contact of polygynous males with females in the population. External parasites are important vectors for internal parasites (Marshall 1981), hence, we expect a correlation between the degree of polygyny and the overall level of parasitic infection. A correlation of parasitic infection and male brightness is then an expected result given the association between male brightness and the type of mating system.

Here I describe the first intraspecific test of the bright male hypothesis based on a study of the satin bowerbird (*Ptilonorhynchus violaceus*). An intraspecific test of the bright male model is less ambiguous than interspecific comparisons because it leads to a very definite prediction: that female preference for mates should be inversely correlated with their level of infection. Satin bowerbirds are a highly polygynous species in which males are not involved in parental care. Males have a shiny blue-black plumage that is attained only after they are seven years old (Vellenga 1981), and differs from the mottled green plumage of females and young males. Males build twig structures called bowers on individually owned and widely separated display courts where matings occur. Individual male mating success was quantified by monitoring with cameras male activity at bowers. The results reported here are from captured, color-banded birds that were scored for numbers of parasites.

Methods

This study was carried out from September through October 1984 at Wallaby Creek, in the Beaury State Forest, 120 km NW of Lismore, New South Wales, Australia. Birds were captured in baited traps and removed immediately. External parasites were counted, the birds weighed, measured, and immediately released. Counts of parasites were initially made over the entire body of birds. However, we soon found that the only common external parasite (*Cuclotogaster* sp.) were restricted to the head, mostly in the areas immediately above and around the eyes. 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. When possible, these flies were captured and the parasites they carried were counted.

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. Behavior at bowers was monitored with specially designed super-8 camera system (see Borgia 1985a). Tukey's studentized range (HSD) test for multiple comparisons was used to test for differences among group means, and Student's *t*-test was used for pairwise comparisons.

Results

Among bowerbirds there was a low level of infection by most large external parasites. The only common large parasite was the louse *Cuclotogaster* sp. Using the relative abundance of this parasite I tested the bright male hypothesis by contrasting the number of parasites with the number of matings by each male. There was no significant inverse correlation between the level of parasitic infection and male mating success, as predicted by the bright male hypothesis. However, its should be noted that the level of infection among bower holding males was very low: only three of these males had any infection of lice. This contrasted sharply with other age and sex classes of bowerbirds. Bower holding males had significantly fewer lice than non-bower holding adult males ($P < 0.001$, and see Table 1). Moreover, older non-bower holding males had fewer parasites than young males and females (Table 1).

Table 1. Average number of lice (*Cuclotogaster* sp.) on sex and age classes of the satin bowerbird

Class	$\bar{X}$	SD	*n*	HSD[a]
Adult plumage males with bowers	2.8	6.6	20	a
Adult plumage males without bowers	15.6	22.7	37	b
Males with mixed adult and juvenile plumage	9.8	10.7	15	b
Yellow beak/juvenile plumage males	11.6	14.2	9	b
Juvenile plumage males	27.2	29.6	37	c
Females	30.2	29.3	159	c

[a] HSD: Rows with different letters are statistically significantly different (Tukey's range test, $P < 0.001$)

Other parasites that were found were ticks and hippoboscid flies. Both were found on all classes of satin bowerbirds and 31% of these flies carried lice.

Discussion

These results are relevant to considering the bright male model. The initial prediction of the model, an inverse correlation between parasite infestation and male mating success, was not supported. This negative result is mitigated to some extent, however, because the absence of a significant result could be accounted for by the low occurrence of infection among bower-holding males and the finding that the few infected males were males that did not mate. Even so, females did still show strong discrimination among bower holding males. Hence, females must be using factors other than the amount of parasitic infection on a male to discriminate among males. So while it is still possible that the "bright male" effect might be important in some cases, and perhaps was important in the past history of satin bowerbirds, that effect could not be demonstrated in the comparisons shown here.

Interclass differences in infection might occur for different reasons than suggested in the bright male model. If the accumulation of parasites is time dependent, and parasites are lost when feathers are lost, then late moulting by bower holders might explain the differences in infection among classes. Vellenga (1981) found that males and non-breeding females moult at the same time, with breeding females moulting somewhat later. This moulting pattern predicts that females should have the lowest level of infection, which is opposite to what was observed.

Interclass differences in levels of infection may be due to systematic differences in patterns of transmission. Lice may be transferred by direct contact (Matthysse 1944) or carried (phorosy) on hippoboscid flies (Corbet 1956; Bennet 1961; Keirans 1975a, b; see results above). None of the behavior of satin bowerbirds suggests that females or young males have more contact with infected individuals or are more susceptible to movements by hippoboscids. Both sexes form unisexual groups in the late winter and early spring. Males more often fight at feeding sites and bower-holding males have close contact with numerous females and young males that come to bowers. Young males court many visitors at temporary bowers and also use the bowers of established males. Thus each class of individuals has contact with the others and it is not clear that any one of the groups has a higher rate of exposure.

An alternative explanation for female preference for males with the fewest parasites is to minimize the number of external parasites they obtain when mating. This model predicts that females prefer males with the fewest parasites. It does not predict a lower level of infection on bower holders relative to other classes of males, unless perhaps bower holders devote more effort to grooming.

The near absence of parasites on bower-holding males is consistent with the hypothesis that the male ability to hold a bower is an indicator of overall physical superiority to other males (Borgia et al. 1985). Marshall (1981) notes that the level of external parasitic infection is less often a cause of differences in male vigor than an indication of differences in well-being. Weakened individuals commonly have more ectoparasites (Ash 1960; Overal and Wingate 1976) often resulting from their inability to remove parasites (Brown 1972; DeVaney 1976; Nelson and Murray 1971), and/or an increase in their susceptibility to infection. Nelson (1962) showed that acquired resistance can be lost through injections of stress-related pituitary-adrenal hormones such as ACTH and cortisone.

There is evidence for the physical superiority of bower-holders including their success in aggression against non-bower-holders at feeding sites (Borgia, in preparation) and their ability to prevent other males from building and decorating bowers near their own (Borgia 1985b; Borgia and Gore 1986). If the level of parasitic infection on males is only an indication of male physical condition, then there is additional support for the view that only males in good condition who can dominate other males can hold bowers. This interpretation of the results supports the view that bowers serve as indicators of male quality as sires. It is also supported by the observation that males of increasing rank and age tend to have fewer parasites, suggesting perhaps that weaker males die off or are unable to hold bowers. It does not, however, provide an explanation for the existence of plumage dimorphism in bowerbirds nor does it eliminate the possibility that plumage dimorphism evolved via a female preference of males with few parasites.

The complexity of field studies and the vagaries of evolutionary history suggest that no single test can be used to validate or falsify a hypothesis where the behavior of complex organisms is being observed. The results presented here must be considered as only one of many tests that will be needed to evaluate the bright male hypothesis.

Acknowledgements. This work was supported by funds from the American Philosophical Society, Harry Frank Guggenheim Foundation, the University of Maryland and the University Computer Center, and the National Science Foundation (BNS-81-13477, BNS-83-08154). Thanks for support goes to members of the University of Melbourne Zoology Department, especially M.J. Littlejohn and J. Hook. R. Condit, K. Collis, C. Loffredo, S. Lukert, E. Thompson, and L. Willimont were invaluable as assistants. The Hayes, Mulkay and Bell families provided many forms of assistance and, with the N.S.W. Forestry Commission, allowed access to their property. Richard Donaghey marked birds and provided me with bower locations at Wallaby Creek. Valuable criticisms of the manuscript were made by J. Allan, J. Coyne, D. Gill, A. Houde, D. Inouye, C. Loffredo, J. Sullivan and J. Lauridsen.

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