

Parasites and Bright Male Plumage in the Satin Bowerbird (*Ptilonorhynchus violaceus*)¹

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SYNOPSIS. Results from our field studies of the satin bowerbird (*Ptilonorhynchus violaceus*) suggest that females choose males as mates based on their level of infection with the ectoparasite (*Myrsidea ptilonorhynchi*; Menoponidae). We evaluated predictions from three hypotheses for why this pattern of choice might evolve. The bright male and correlated infection models both suggest that females choose parasite free males because these males are more likely to sire parasite resistant offspring. The bright male hypothesis suggests that females are able to gauge infection based on plumage brightness. The correlated infection hypothesis claims that females assess resistance to endoparasites through a correlated effect on ectoparasites. In the parasite avoidance model female choice is shaped by the proximate benefits of avoiding infection. Six predictions from these models were tested using information on patterns of infection in satin bowerbirds. Of these models the parasite avoidance model was best supported by the available data.

INTRODUCTION

Recent models suggest that mate choice decisions based on the level of parasitic infection of a prospective mate can have important fitness consequences and may be involved in the evolution of sexual dimorphisms (e.g., see Bradbury and Andersson, 1987; Pomiankowski, 1987a, b; but see Kirkpatrick, 1986). While there is some evidence that directly supports the occurrence of such choice (Borgia and Collis, 1989; Jaenike, 1988; Kennedy et al., 1987; Read, 1987; Stoumen, 1987; this symposium) the ultimate basis for this choice is not well understood (Partridge and Harvey, 1986; Read, 1988). Here we describe patterns of infection of the satin bowerbird (*Ptilonorhynchus violaceus*) by its most common ectoparasite (*Myrsidea ptilonorhynchi*) and then use this information to test different models that seek to explain why females choose to copulate with parasite-free males.

Among the most frequently discussed models for the evolution of mating preferences 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 parasites. Then, by choosing bright males as sires for their offspring, females are more likely to produce disease resistant offspring.

A key prediction of the bright male hypothesis made by Hamilton and Zuk was that females should prefer to mate with parasite-free males. Our studies of satin bowerbirds have provided evidence for such a preference. We were able to show an inverse correlation of male mating success with ectoparasitic infection (Borgia and Collis, 1989) and that male bower holders, the group in the population responsible for mating, have consistently lower overall levels of infection than other age and sex classes (Borgia, 1986; Borgia and Collis, 1989). Curiously, the apparent object of selection is an ectoparasite which is not the kind of parasite Hamilton and Zuk predicted should be important in shaping mating preferences. This raises the issue of whether the bright male hypothesis provides the best explanation for the evolution of this preference.

Here we review several predictions that can be developed from the Hamilton and Zuk model. In addition, we consider two alternative hypotheses that may explain the evolution of dimorphism in plumage and other display traits that results from females choosing parasite free males. The "correlated infection" model suggests that females are selected to avoid males with ectoparasitic infection because the pres-

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TABLE 1. Predictions from models.*

	Bright male hypothesis	Corre- lated infection	Para- site avoidance
1. Parasite numbers on males should be inversely correlated with male mating success.	yes	yes	yes
2. The level of infection in the host population should decrease with age of the host (at least up to breeding age).	yes	yes	yes
3. Male differences in plumage brightness should exist and this character should be correlated with male mating success.	yes	no	no
4. Male differences in disease resistance should be heritable.	yes	yes	no
5. Parasite numbers and male condition should be negatively correlated.	yes	yes	no
6. Parasites that vary in abundance on males because of environment should be less important in mate selection than those that differ because of heritable differences in male resistance.	yes	yes	no

* Predictions represent necessary conditions for models to operate.

ence of ectoparasites serves as an indicator of low overall male resistance to disease. It is hypothesized that dark plumage of male satin bowerbirds has evolved because it enhances female ability to see parasites on males. 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. Females who selectively choose among dark plumage males are better able to see ectoparasites and consequently avoid

infection. By this model females prefer males which have a low level of infection and dark plumage males are chosen over others only because their ectoparasite loads are easier to assess. Unlike the two other models, parasite avoidance produces an immediate payoff for females in lowering their own risk of infection. Differences in the predictions of these three models are summarized in Table 1.

Satin bowerbirds have a mating system well-suited to testing models for the evolution of sexual dimorphism. Males 7-yr and older have a shiny blue-black plumage that differs from the mottled green plumage of females and younger males (Vellenga, 1980). Males are polygynous and do not provide parental care or other material benefits to females or offspring. Males build and defend twig structures called bowers where matings occur and, in the present study, were monitored using cameras controlled by an infrared detection system (Borgia, 1985a).

The work described here was carried out from October through December in 1984-86 at Wallaby Creek, in the Beauray State Forest, 120 km NW of Lismore, New South Wales, Australia. Birds were captured in baited traps and removed immediately. The birds were scored for plumage characters and numbers of ectoparasites, weighed, measured for wing length, and immediately released. 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. Male behavior around traps was recorded and the number of interactions among males was recorded. Plumage characters and measurements of wing length allowed sexing and aging of birds (Vellenga, 1980). Plumage comparisons were made among adult males in an attempt to score for differences in plumage quality. A more detailed description of methods is supplied elsewhere (Borgia and Collis, 1989).

TESTS OF MODELS

In earlier papers (Borgia, 1986; Borgia and Collis, 1989) we presented data and tested several hypotheses derived from

TABLE 2. Number of lice (*Myrsidea ptilonorhynchi*) on males and females in 1984 and 1986.*

Class	1984	1986
Adult plumage males with bowers	2	2
Adult plumage males without bowers	15	15
Males with mixed adult and juvenile plumage	9	9
Juvenile plumage males	27	27
Females	30	30

* In an earlier paper (Borgia, 1986) this table was presented for 1984 and 1986.
** Classes with different letters have significant differences.

these models. Here we review the results of those tests and extend them by testing their suitability for explaining related differences in male infection. In all 3 years males had fewer parasites than females and older males had fewer parasites than younger males (Table 2). Overall, there was an inverse relationship between infection and age among males and among bower holders in 1984 and 1986 but not in 1986.

The age-related reduction in male infection could occur for several reasons: (1) parasite-related mortality among males, lower contact rate and a subsequent lower rate of infection among males with age, mortality among parasites after initial infection at birth, and increased preening and/or ability to remove parasites with age. Information about the nature of the age-related reduction in infection numbers can be used to evaluate hypotheses about how mate choice operates. We have been able to collect data that are useful in evaluating at least three hypotheses and they are considered below.

All of the above mate selection hypotheses predict that if there is some cost to infection there should be greater mortality among infected than non-infected males. The observed lowering of infection numbers to male age might then represent the result of selection for relatively immune males. We can support this hypothesis by the observation that returning males had a significantly lower rate of infection than nonreturning counterparts.

We note however, that there was

TABLE 2. Number of lice (*Myrsidea ptilonorhynchi*) for six sex- and age-classes of the satin bowerbird in 1984, 1985, and 1986.*

Class	Years											
	1984				1985				1986			
	\bar{x}	SE	n	Sig.**	\bar{x}	SE	n	Sig.**	\bar{x}	SE	n	Sig.**
Adult plumage males with bowers	2.8	1.5	20	a	7.6	2.4	22	a	5.7	1.7	21	a
Adult plumage males without bowers	15.6	3.7	37	b	11.4	1.9	63	a	16.6	4.5	25	ab
Males with mixed adult and juvenile plumage	9.8	2.8	15	b	18.1	3.6	28	ab	18.2	4.8	19	ab
Juvenile plumage males	27.2	4.9	37	c	24.0	4.0	31	b	25.1	4.0	39	b
Females	30.2	2.3	159	c	18.4	2.5	75	b	23.5	2.3	120	b

* In an earlier paper (Borgia, 1986) this parasite was misidentified as *Cuclotogaster* sp.

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

this model females prefer a low level of infection. Bright plumage males are chosen over dull plumage males because their ectoparasite loads are lower. Unlike the two other models, this model produces an offset for females in lowering the level of infection. Differences in the results of these three models are shown in Table 1.

Satin bowerbirds have a mating system that is being tested using models for the evolution of sexual dimorphism. Males 7-year old have a shiny blue-black plumage, while older males have the mottled green plumage. Younger males (Vellenga) are polygynous and do not provide parental care or other material benefits to their offspring. Males build large structures called bowers where courtship occurs and, in the present study, are monitored using cameras connected to an infrared detection system (Table 2).

The study described here was carried out from August through December in 1984-1986 at a creek in the Beaury State Park, 10 km NW of Lismore, New South Wales, Australia. Birds were captured in mist-nets and removed immediately. The study was aimed at determining the prevalence of ectoparasites, weighing, measuring wing length, and immediately removing the lice. The louse *Myrsidea ptilonorhynchi* is the only abundant ectoparasite of satin bowerbirds. It was restricted mostly to the areas immediately around the eyes. Male plumage and traps was recorded and the number of interactions among males was recorded. Plumage characters and measurements of wing length allowed sexing of birds (Vellenga, 1980). Comparisons were made among plumage characters in an attempt to score for display plumage quality. A more detailed description of methods is supplied in Borgia and Collis (1989).

TESTS OF MODELS

In previous papers (Borgia, 1986; Borgia and Collis, 1989) we presented data and tested several hypotheses derived from

these models. Here we review the results of those tests and extend them by considering their suitability for explaining age-related differences in male infection.

In all 3 years males had fewer parasites than females and older males had fewer parasites than younger males (Table 2). Overall, there was an inverse relationship between infection and age among all males and among bower holders in 1984 and 1985 but not in 1986.

The age-related reduction in male infection could occur for several reasons. These include: parasite-related mortality among males, lower contact rate and a subsequent lower rate of infection among males as they age, mortality among parasites after an initial infection at birth, and increased male preening and/or ability to remove parasites with age. Information about the causes of the age-related reduction in parasite numbers can be used to evaluate hypotheses about how mate choice operates. We have been able to collect data that are useful in evaluating at least three of these hypotheses and they are considered below.

All of the above mate selection models predict that if there is some cost to infection there should be greater mortality among infected than non-infected birds. The observed lowering of infection related to male age might then represent the results of selection for relatively immune males. We can support this hypothesis with the observation that returning males had a significantly lower rate of infection than their nonreturning counterparts.

We note however, that there were con-

sistent and quite dramatic changes in parasite numbers between age classes and it is important to determine what level of mortality must occur among males to account for the observed reductions in parasite numbers. The mean level of infection among males decreases by 2 parasites per year as they age. We can then ask what kind of mortality is necessary to shift the mean level of infection each year by this amount? If there is truncation selection so that only the most infected males die, males need suffer approximately 5% mortality per year to account for the observed shifts in level of infection. This is close to mortality estimates for satin bowerbirds (Borgia, in preparation). This test suggests that male mortality is a sufficient explanation for changes in parasite numbers, although for this to be true mortality from infection must represent the sole cause of male death, and this may be an unrealistic assumption.

Differences in the extent of social contact could account for age-class differences in patterns of infection. We hypothesized that males with a greater frequency of social interactions were more likely to become infected with parasites. Data from male interactions at feeding sites were used to provide an estimate of the tendency of individual males to become involved in social interactions that were likely to allow the transfer of parasites. A comparison involving all males showed no relationship of the level of male infection with either the total number of interactions of a male with other birds or the number of individuals interacted with (Table 3). Among green plum-

TABLE 3. 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	<i>n</i> = 103 <i>r_s</i> = -0.045 <i>P</i> > 0.50	<i>n</i> = 103 <i>r_s</i> = -0.075 <i>P</i> > 0.50
Females	<i>n</i> = 26 <i>r_s</i> = 0.140 <i>P</i> > 0.40	<i>n</i> = 26 <i>r_s</i> = 0.064 <i>P</i> > 0.50
All males	<i>n</i> = 77 <i>r_s</i> = 0.027 <i>P</i> > 0.50	<i>n</i> = 77 <i>r_s</i> = -0.010 <i>P</i> > 0.50
All juvenile plumage males (dark billed, yellow billed, and mixed plumage males)	<i>n</i> = 38 <i>r_s</i> = 0.300 <i>P</i> = 0.07	<i>n</i> = 38 <i>r_s</i> = 0.232 <i>P</i> = 0.17
Dark billed males	<i>n</i> = 23 <i>r_s</i> = 0.333 <i>P</i> = 0.13	<i>n</i> = 23 <i>r_s</i> = 0.234 <i>P</i> > 0.30
Transitional plumage males (yellow billed and mixed plumage males)	<i>n</i> = 15 <i>r_s</i> = 0.254 <i>P</i> > 0.30	<i>n</i> = 15 <i>r_s</i> = 0.204 <i>P</i> > 0.40
All adult plumage males	<i>n</i> = 39 <i>r_s</i> = -0.297 <i>P</i> = 0.07	<i>n</i> = 39 <i>r_s</i> = -0.296 <i>P</i> = 0.07
Adult plumage males with bowers	<i>n</i> = 23 <i>r_s</i> = -0.256 <i>P</i> > 0.20	<i>n</i> = 23 <i>r_s</i> = -0.265 <i>P</i> > 0.20
Adult plumage males without bowers	<i>n</i> = 16 <i>r_s</i> = -0.461 <i>P</i> = 0.08	<i>n</i> = 16 <i>r_s</i> = -0.385 <i>P</i> = 0.15

age males there was, however, a significant association between number of parasites and number of contacts (one-tailed test $P < 0.04$). An association of a similar magnitude but in the opposite direction occurred among blue males for the relationships of the number of parasites with both number of males contacted and total number of interactions. These conflicting results suggest no consistent pattern in how social contacts might influence the degree of ectoparasitic infection. Most importantly, however, they suggest that different rates of contact are not important in determining differences in levels of infection among blue males.

In another test of the hypothesis that age and sex classes differ in their exposure to parasites we examined patterns of infection of initially uninfected individuals in each group. Pooling data across years we could find no between-class differences in the probability of becoming infected.

The age-related decrease in infection could be due solely to extinctions of demes of parasites on individual birds after initial infection during the nestling stage. If parasites were lost from birds as a function of time, then the observed age-related reductions in the infection of males could be explained. This hypothesis is not supported by our data. Reinfection is relatively common and it is similar to rates of parasite loss. Consequently, the level of infection of individuals appears to be due to reinfections as well as parasite loss. We showed (Borgia and Collis, 1989) that more than half of the uninfected birds were infected the next year, and a similar proportion 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 both infection and loss of parasites is quite high.

Of the four hypotheses for exposure-related changes in male infection of those that we could test, time dependent extinction and male differences in infection and transmission, were not supported. The third hypothesis we found, however, that mortality rates necessary to cause observed age class differences in parasite infection were consistent for what is known from satin bowerbirds. One remaining hypothesis, enhanced male grooming could not be tested because of our inability to reliably estimate the occurrence of grooming. This hypothesis remains attractive because it could explain both related trends in male infection and differences in infection among bower holders.

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 100 satin bowerbirds and could not find any noticeable and consistent variation in the brightness of their plumage. There were a few males that had noticeably dull plumage but these were exceptional and were not bower holders. Our inability to detect plumage differences among adult males does not allow us to make comparisons between overall condition, mating success and endoparasitic infection.

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 could test the hypothesis that if there were a genetic component for disease resistance in the population then individual males should show consistent patterns of parasite infection across years. We were able to confirm this prediction both for males and for females.

We tested the hypothesis that male condition affects levels of infection by comparing the relative weights (weight/length) of birds to levels of infection. We found no correlation between relative weight and number of parasites. Elsewhere (Borgia, 1985a, b) we have shown that aggressively dominant males who were to be in good condition have well built and decorated bowers. In comparisons involving 4 measures of bower quality and

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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. Elsewhere (Borgia, 1985a, b) we have shown that aggressively dominant males who we take to be in good condition have well built and decorated bowers. In comparisons involving 4 measures of bower quality and num-

bers of 5 different types of decorations on bowers (yellow leaves, yellow straw, blue feathers, snail shells, blue blossoms, yellow blossoms, and the total number of decorations) we did not find the predicted inverse relationship with level of infection. In addition, 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 by competitors. 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 any measure of the condition of birds.

DISCUSSION

The evidence discussed 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 three years suggests that parasitic infection is strongly sex- and age-related as might be expected if there was a cost to parasites. This finding is further supported by results that show that mortality rates observed in natural populations are sufficient to account for age-related changes in levels of male infection.

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 satin bowerbird 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 allowed us to reject several alternative hypotheses that might explain between-year correlations in levels of infection.

Predictions of the bright male and correlated infection hypotheses were not supported in several tests. 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 found no noticeable relationship between plumage brightness and parasitic infection. Our inability to separate males based on plumage brightness does not preclude the possibility that satin bowerbirds can make these determinations, but it suggests that if these differences exist they are quite subtle. The absence of a relationship between condition and differences in parasite numbers, where we could measure differences among males, is evidence against the bright male and correlated infection hypotheses.

The parasite avoidance model thus emerges as the most consistent with our data. Patterns of male plumage change and display behavior provide additional support for the suggestion that it is important for females to see parasites. Above we noted that the dark blue-black plumage of adult male satins makes the whitish lice easier to see on these males than on females and young males. Also significant is that the appearance of blue feathers in the juvenile plumage of sexually mature fifth and sixth year males starts most often around the males' eyes (Collis and Borgia, manuscript). 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 patch of feathers) is directed at her. This display behavior allows females to directly observe parasites, especially around his eyes, and is unique when compared with other species of bowerbirds with similar types of bowers.

Unlike the other two models, the parasite avoidance model does not require a heritable basis for differences in parasite numbers. Thus, its operation could explain female preference for unparasitized males even if differences in levels of infection were

due, in part, to different levels of social contact among males. Our finding of such a result among green males but in a direction opposite to that among blue males is consistent with a scenario in which green males that are not courting females spend less effort removing parasites so that their infections are proportional to their level of contact. This is supported by the relatively high level of infection among green males. By contrast, blue males, and especially bower holders who have very low levels of infection, may spend more effort preening and are able to lower parasite counts. The patterns we have observed might then be a product of differences in male effort in removing parasites and female preference for parasite free males. Unfortunately, we have no reliable measures of male preening that might be used to test this model. However, differences in the quality of other display characters, such as the bower, can be related to differences in male effort (Borgia, in preparation), so it would not be unreasonable to expect that effort is important in this case as well.

An issue relevant to evaluating all of these models is the apparent asymmetry in concern about infection exhibited by the sexes. Females as a class carry a relatively large number of ectoparasites. Given this, why should they favor mating with parasite free males and why don't females make a greater effort in removing parasites already on them? One possibility is that current levels of infestation are less important than the cost of secondary infection by lice that serve as vectors for other harmful parasites. These secondary infections could be important in two ways. First, they might affect the female directly through effects on her survivorship or through her ability to invest in offspring. Second, young birds might be especially susceptible to infection from novel parasites carried by their mother's ectoparasites. It might then be important for females to limit the transfer of these parasites from their mates even though the parasites may have little or no direct effect on her viability. Female bowerbirds shake violently after copulation (personal observations) but males do not. It is possible that this behavior functions

to remove parasites transferred after copulation. Its expression only in females could be related to the absence of male copulation with offspring.

In summary, the model that is most strongly supported is the parasite avoidance model. It is the only one of the models that is consistent with all of the predictions needed for its operation (Table 1). If parasite avoidance produces direct benefits to females there is little question that such a mechanism could evolve. It is possible that there might be correlated benefits to offspring from choosing parasite free mates who might confer parasite resistance. Although we did not attempt to demonstrate such an effect we can show the conditions that would allow for the occurrence of such choice exist in satin bowerbirds and that several factors that might inhibit the operation of this type of choice do not occur.

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We thank the American Philosophical Society, Harry Frank Guggenheim Foundation, the University of Maryland at College Park, the University Computer Center, and the National Science Foundation for financial support. Members of the University of Melbourne Zoology Department, especially M. J. Littlejohn and J. Hook provided significant logistical support. We thank numerous field assistants and the National Science Foundation for many forms of assistance. The N.S.F. Office of Biological Resources and the University of Maryland System provided access to the property. Valuable criticisms of the manuscript were made by A. Houde, R. H. J. Ott, C. Loffredo, J. Lauridsen, C. Kinson. Additional helpful comments were provided by many participants in the Parasites and Sexual Selection Symposium.

different levels of social... Our finding of such... en males but in a direc... among blue males is... scenario in which green... courting females spend... parasites so that their... portional to their level of... ported by the relatively... on among green males... males, and especially... have very low levels of... and more effort preening... er parasite counts. The... bserved might then be... ences in male effort in... and female preference... ales. Unfortunately, we... asures of male preening... o test this model. How... the quality of other dis... h as the bower, can be... es in male effort (Bor...), so it would not be... expect that effort is... se as well.

o evaluating all of these... ent asymmetry in con... exhibited by the sexes... rry a relatively large... sites. Given this, why... ating with parasite free... females make a greater... parasites already on... y is that current levels... ss important than the... ection by lice that serve... er harmful parasites... infections could be... ys. First, they might... irectly through effects... or through her ability... r. Second, young birds... usceptible to infection... rried by their moth... might then be impor... limit the transfer of... m their mates even... may have little or no... viability. Female bow... ntly after copulation... ns) but males do not... is behavior functions

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We thank the American Philosophical Society, Harry Frank Guggenheim Foundation, the University of Maryland and the University Computer Center, and the National Science Foundation for financial support. Members of the University of Melbourne Zoology Department, especially M. J. Littlejohn and J. Hook provided significant logistical support. We thank numerous field assistants and the N. and J. Hayes, Mulkay and Bell families provided many forms of assistance. The N.S.W. Forestry Commission allowed access to their property. Valuable criticisms of the manuscript were made by A. Houde, R. Howard, J. Ott, C. Loffredo, J. Lauridsen, G. Wilkinson. Additional helpful comments were provided by many participants in the Parasites and Sexual Selection Symposium.

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