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Sexual selection, parasites and bower height skew in a bower-building cichlid fish

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ABSTRACT

The good genes mechanism of sexual selection predicts that secondary sexual ornaments may reliably reveal a male's resistance to parasites. We studied correlates of courtship and spawning success in a species of *Copadichromis*, a lekking cichlid fish from Lake Malawi, Africa, which builds sand bowers. We present the first evidence of a negative relationship between the structure of an extended phenotypic character (height skew of sand bowers) and male parasite load. Males that spawned had significantly fewer dilepipid cestodes in their livers than males that did not spawn, never before demonstrated in a lekking species of fish. Furthermore, males that spawned had significantly heavier gonads than unsuccessful males. We also found significant correlations between relative liver weight and some measures of reproductive success. This may indicate females are choosing to mate with males in better condition.

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Darwin (1859) first proposed the theory of sexual selection in an attempt to account for the extravagant characteristics found in the males of many species. Although our understanding of sexual selection has advanced considerably since then, several fundamental questions still remain unanswered. Are secondary sexual characteristics meaningful and honest indicators of viability, first suggested by Williams (1966), and later championed by Zahavi (1975, 1977), or the outcome of runaway sexual selection acting on arbitrary traits (Fisher 1930; Lande 1981)? By implicating parasites in the evolution and current maintenance of many sexually selected characteristics, Hamilton & Zuk (1982) provided a significant boost to advocates of indicator mechanisms of sexual selection. They suggested that the expression of secondary sexual characteristics such as long tails or bright plumage may reflect an individual's resistance to parasites. Assuming some heritability of parasite resistance, females may enhance the fitness of their offspring by mating with males that have the most elaborate traits. In addition, the cyclical coevolution of parasite virulence and host resistance may also help to maintain heritable additive fitness variation within a population. This simple hypothesis has led to an explosion in studies attempting to elucidate the effects of parasites on host reproductive behaviour and evolution (see Read 1988; Clayton 1991; Hamilton & Poulin 1997 for reviews).

The *Copadichromis eucinostomus* species complex consists of at least seven extremely closely related species of cichlid fish, all of which are endemic to Lake Malawi, Africa. All species are sexually dimorphic, lek-breeding, maternal mouthbrooders, with males reaching between 10 and 14 cm standard length. Like most other similar-sized Malawian haplochromines, females of this species probably produce around 10–20 eggs per clutch, but usually lay only a single egg, occasionally two, per spawning visit to a male's bower. The female picks up the egg in her mouth almost immediately and fertilization occurs within the buccal cavity. Males build and defend bowers, which vary from large constructions built from sand and shaped like upturned cones with their tops cut off, to small patches of scattered sand on top of tall boulders. The full range of bower types can be found on one lek. As with most lekking species, females spend most of their time away from the lek and visit only to mate (McKaye 1983). Previous studies on *Copadichromis* have revealed that males defending tall bowers may have a greater reproductive success than males defending short bowers (McKaye et al. 1990). Microsatellite DNA studies have indicated five or six fathers may sire the average brood (Kellogg et al. 1995). These fish are an ideal subject for the study of lek breeding as the eggs are large and

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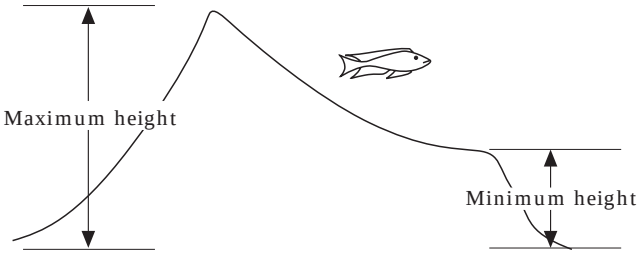

Figure 1. Cross-section of a sand bower showing maximum and minimum height measurements.

conspicuous, making it easy to count the number of eggs a female lays with each male.

In lekking species, reproductive success is often strongly skewed in favour of a few males. Much of the work so far conducted on lek systems has sought to clarify the factors responsible for this. In the present study we concentrate on testing some broad assumptions of the Hamilton & Zuk hypothesis, that is, parasites impose a cost on males in the breeding population, this cost is reflected by a reduction in male phenotypic quality (bower quality or male condition), and females use these cues to avoid mating with heavily parasitized males.

METHODS

Field Observations

We conducted the study at Harbour Island, just south of Monkey Bay, Lake Malawi, Africa, during February and early March 1995. The lek extended over sand scattered with boulders at approximately 6 m depth. We labelled bowers on the lek with numbers to facilitate identification. Individual females were followed by divers using SCUBA equipment between 0700 and 1000 hours, when spawning activity appeared to be at its peak, and the following behaviours noted.

(1) Visits: the female follows the male into his bower, but leaves without any further activity having occurred.

(2) Circling bouts: the female enters a male's bower and circles (a prelude to spawning which involves the male and female swimming in a tight circle, the male displaying his anal fin and genital region to the female) with the male, then leaves before spawning occurs.

(3) Spawning bouts: defined as the number of visits by females to a male's bower during which eggs were laid.

(4) The total number of eggs laid by females with each bower-defending male.

(5) Total courtship activity: number of visits+circling bouts+spawning bouts.

During the afternoons, we recorded maximum and minimum bower rim heights, and rim diameters of labelled bowers (see Fig. 1). Bower height skew was taken as the (maximum height − minimum height)/maximum height. At the end of the study period, we captured males from labelled bowers using monofilament nets, humanely killed them by anaesthetic (phenoxyethanol) overdose, and fixed them in formalin before preserving them in ethanol.

Laboratory Work

We weighed the gonads and livers and produced residuals by the linear regression of liver and gonad weight on eviscerated body weight. For preserved males, standard condition factors were calculated as residuals from the logarithmic regression of weight on standard length. The number of individual parasites found in the alimentary canal, liver and gills was then quantified. From this we calculated a measure of total parasite burden.

Ethical Note

Species of the *C. eucinostomus* complex are extremely common and widespread throughout Lake Malawi where millions are killed each year by artisanal fishermen. In this study we killed only 63 of the many hundreds of males present on the lek. We considered that 15 males defending each of the four bower types was the minimum sample size for the analysis. No female fish were killed. The low sample size and the fact that parental care is provided exclusively by females ensured the study had minimal impact on future population size.

RESULTS

Eight types of parasites were recorded from the preserved material. All specimens examined carried some parasite load (Table 1).

Over the study period, a strong skew in male reproductive success was found, with relatively few males achieving most of the matings (Fig. 2a,b).

Males could be divided into two main types: males that built sand bowers and those that defended bare rock. Sand bowers could be built directly on the substrate or constructed on top of a boulder. Males defending sand bowers had a significantly higher total courtship activity (Mann–Whitney *U* test: median values 3.0 and 1.0, ranges 0–19 and 0–18; $W=3844.0$, $N_1=76$, $N_2=17$, $P=0.006$), had more visits from females (median values 1 and 0, ranges 0–6 for both; $W=3782.5$, $N_1=76$, $N_2=17$, $P=0.030$) and circled with more females (median values 2 and 1, ranges 0–12 and 0–11; $W=3787.0$, $N_1=76$, $N_2=17$, $P=0.029$) than those defending bare rock. Males defending areas of bare rock were significantly less likely to spawn than males defending sand bowers (*G* test: $G_1=4.867$, $P<0.05$).

The number of liver cestodes was negatively correlated with all measures of reproductive success, although two of the correlations were not significant (Table 2). Furthermore, males that spawned had significantly fewer dilepipid cestode larvae in their livers than males that had not spawned (Mann–Whitney *U* test: median values 5 and 1.5, ranges 0–12 and 0–18; $W=304.0$, $N_1=14$, $N_2=49$, $P=0.017$; Fig. 3a,b).

Relative gonad weight was positively correlated with all but one measure of reproductive activity (Table 2). Males that had spawned had significantly heavier gonads than those that had not (Mann–Whitney *U* test: median values 0.10 and 0.08, ranges 0.06–0.16 and 0.04–0.15; $W=601.0$, $N_1=14$, $N_2=49$, $P=0.012$).

Table 1. Median number and range of parasite loads and prevalence in males observed to spawn or not seen to spawn during the study period

Parasite type	Median	Minimum	Maximum	Prevalence in nonspawning males (%)	Prevalence in spawning males (%)	Mann–Whitney test (*W*)	*P*
Intestinal trematode	0	0	2	38.8	21.4	401.5	0.361
Larval nematode (stomach wall)	1	0	7	61.2	64.3	1567.0	0.986
Intestinal encysted larvae	2	0	13	79.6	78.6	375.5	0.225
Dilepipid cestode larvae; probably *Paradilepis* (liver)	4	0	18	93.9	57.1	304.0	0.017
Encysted liver cestodes	3	0	14	85.7	92.9	1557.0	0.861
Encysted gill parasites	18	2	64	100	100	378.5	0.250
Poecilostomatoida: family Ergasilidae, *Ergasilus* sp. (gills)	5	0	31	91.8	100	1539.5	0.636
Cyclopiida: family Lernaeidae, *Lamproglene* sp. (gills)	0	0	9	16.3	14.3	1567.5	0.990

Mann–Whitney *U* test between median parasite loads of spawning ($N=14$) and nonspawning males ($N=49$).

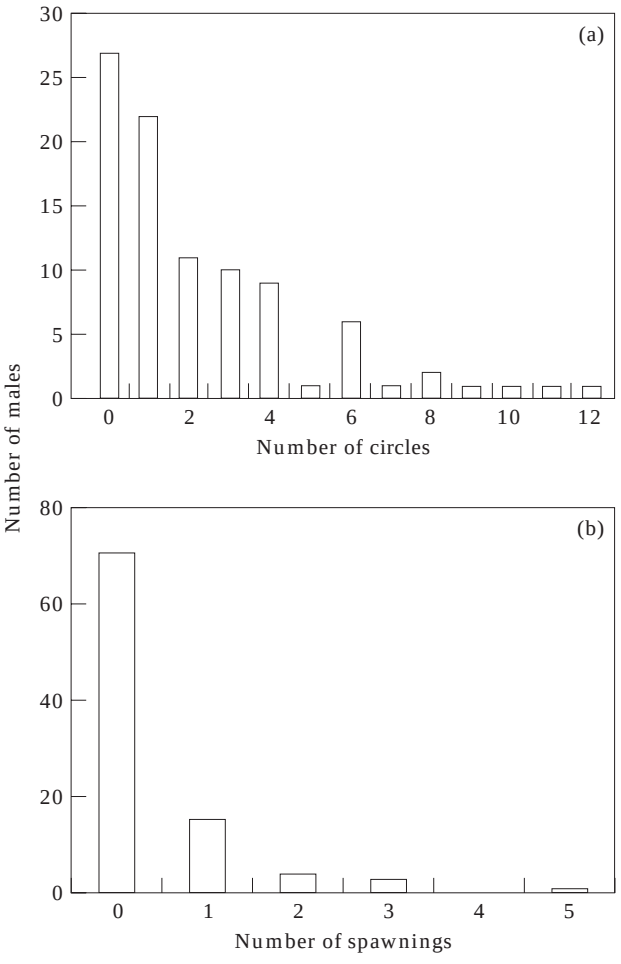

Figure 2. (a) Number of circling bouts (a prelude to spawning) with females and (b) number of spawnings with females by bower-defending males.

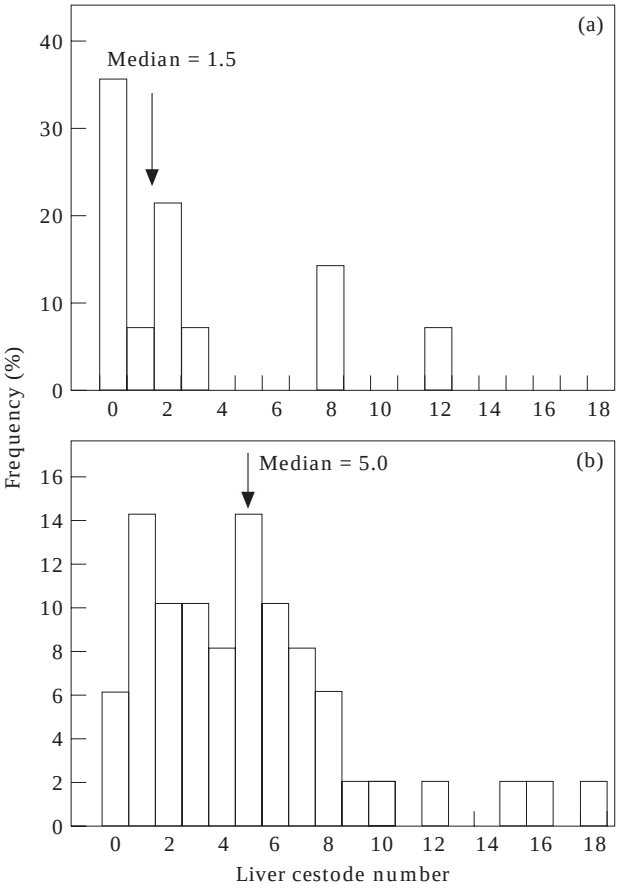

Figure 3. Number of dilepipid cestode larvae in the livers of (a) spawning and (b) nonspawning males. The median parasite burden is shown.

No significant difference was found in relative liver weight between spawning and nonspawning males (Mann–Whitney *U* test: median values 0.195 and 0.170, ranges 0.11–0.31 and 0.05–0.36; $W=491.0$, $N_1=14$, $N_2=49$, $P=0.482$).

The condition factor of males was not significantly correlated with any measure of reproductive activity (Table 2).

We found a significant correlation between the number of dilepipid cestode larvae in the liver and bower height skew (log–log regression: $r_S=0.527$, $N=32$, $P<0.002$; Fig. 4). Only bowers built directly on sand were used for this analysis. Differences in rim height in bowers built on boulders may be due to differences in boulder shape and not the individual's ability to construct a bower with a horizontal rim.

Bower height skew was not significantly correlated with any measure of reproductive success (Spearman rank correlation: total courtship activity: $r_S=-0.052$; visits: $r_S=-0.275$; circles: $r_S=0.051$; spawnings: $r_S=0.017$; eggs: $r_S=0.011$; $N=42$, NS for all).

For all bower types pooled, there was no significant correlation between bower height and male reproductive

Table 2. Spearman rank correlation coefficients of the morphological traits and measures of reproductive activity

	Liver cestode number	Relative gonad weight	Relative liver weight	Condition factor
Total courtship activity	−0.243 NS	0.361**	0.266*	−0.021 NS
Visits	−0.252*	0.140 NS	0.345**	−0.117 NS
Circles	−0.192 NS	0.356**	0.232 NS	0.040 NS
Eggs laid	−0.296*	0.340**	0.095 NS	0.061 NS
Spawnings	−0.322*	0.333**	0.102 NS	0.064 NS

$N=63$ for all comparisons.
*$P<0.05$; **$P<0.01$.

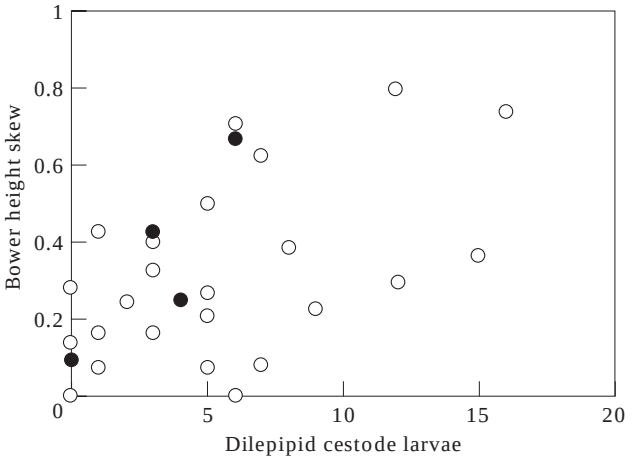

Figure 4. Relationship between the number of dilepipid cestode larvae in the livers of males defending bowers built directly on sand and bower height skew. Filled circles indicate two superimposed points.

success (Spearman rank correlation: total courtship activity: $r_S = -0.046$; visits: $r_S = 0.064$; circles: $r_S = 0.128$; spawnings: $r_S = 0.089$; eggs: $r_S = 0.117$; $N = 85$, NS for all). For males defending bowers built on sand, there was a significant correlation between bower height and total courtship activity ($r_S = 0.314$, $N = 42$, $P < 0.05$). Positive but nonsignificant relationships were found between bower height and numbers of visits ($r_S = 0.286$), circles ($r_S = 0.290$), spawnings ($r_S = 0.100$) and eggs laid ($r_S = 0.100$) with females ($N = 42$ for all).

DISCUSSION

Our results reveal associations between male reproductive success and parasite load, consistent with the predictions of Hamilton & Zuk's model of sexual selection. Furthermore, parasites may impose a cost on males, indicated by the increased bower height skew shown by more heavily parasitized males. This is the first study to suggest a relationship between the structure of an extended phenotypic trait (sand bowers) and level of parasite infestation. It is important to emphasize that bower height skew is not a bilateral morphological character, and cannot therefore show fluctuating asymmetry. However, we consider sand bower structure to be an analogous trait, which may be subject to similar selection pressures. Borgia (1985) found significant relationships between male reproductive success and the symmetry of the bower, quality of construction, stick size and stick density in the satin bowerbird, *Ptilonorhynchus violaceus*.

The present study also reveals that males with fewer dilepipid cestode larvae in their livers had a higher reproductive success. It appears that females may acquire information about male parasite load during the course of the courtship sequence. This may be through bower height skew, and/or other cues that may be affected by parasite load such as male colour or courtship vigour. Females may use these cues to make their final spawning decisions.

Why should parasitized males build skewed bowers? McKaye et al. (1990) demonstrated that males defending tall bowers did not desert them during afternoon periods to feed, whereas those defending short bowers often did. If males with a heavier parasite load are burdened with an increased metabolic cost, they may spend more time feeding away from the bower, resulting in less time available for bower building and maintenance.

Although many studies have indicated that females prefer less parasitized males in species where males provide parental care (Møller 1988, 1990; Milinski & Bakker 1990), this need not be interpreted as being due to the Hamilton & Zuk mechanism. It is more parsimonious to suppose that females get the immediate benefit of better care of offspring. Females may also gain direct benefits if parasites are directly transferred during courtship. Dilepipid cestodes are unlikely to be directly transferred between fish, as the definitive host stage is usually avian (Jarecka 1970, 1975). Evidence from lekking species, where the Hamilton & Zuk mechanism is most likely to be applicable, is scarce. Female preference for less parasitized males has been conclusively demonstrated only twice before in lekking species, both birds (Borgia & Collis 1989, 1990; Johnson & Boyce 1991; Spurrier et al. 1991). This study provides the first evidence of female choice for less parasitized males in a lekking species of fish.

Liver weight is a commonly used measure of condition in fish biology. Females preferred to court with males with larger livers; however, relative liver weight did not correlate with parasite load. The increased mating advantage of males with larger livers may be due to other factors such as increased courtship vigour, better coloration, or superior ability to exclude other conspecific males or heterospecific species from the territory.

A previous study indicated that females may prefer to court with males defending taller bowers (McKaye et al. 1990). Our results are consistent with this study: a positive correlation was found between number of visits and number of circling bouts with males defending bowers on sand. The sample size in McKaye et al.'s (1990) study was twice that of our sample size for males defending this type of bower. Although we found no significant correlation between bower height and visits and number of circling bouts, these were only just nonsignificant, and total courtship activity (visits+circles+spawnings) was significantly correlated with bower height. McKaye et al. (1990) implicated a Fisherian mechanism to explain the origin and current maintenance of bowers. Our study is not inconsistent with this, and although females appear to choose males in better reproductive condition and with lower parasite loads (implying a good-genes indicator mechanism), bower height may be a trait under simultaneous Fisherian selection (Møller & Pomiankowski 1993).

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