

A role for male bower size as an intrasexual signal in a Lake Malawi cichlid fish

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Summary

Disruptive sexual selection through female mate choice has been proposed as a key mechanism driving the evolution of haplochromine cichlid fish diversity. Here we investigated if male secondary sexual traits employed by females in direct mate choice have an additional function in male competition. We conducted a field experiment on aggression among males of a lekking Lake Malawi cichlid species that build volcano-shaped spawning craters, known as bowers, in their breeding territories. Males placed on a short artificial bower received significantly more aggression from adjacent resident males than when placed on a tall artificial bower. This supports the hypothesis that bower size provides information about male competitive ability, and suggests an additional function for this extended phenotypic trait besides a role in attracting females.

Keywords: armament–ornament model, bower, cichlid, lek, Malawi, male competition, pre-existing trait model, sexual selection.

Introduction

Sexual selection of male traits through direct female choice has been proposed as a key factor in the evolution of species-rich adaptive radiations. A prominent example in which sexual selection has been implicated is the large-scale and rapid speciation of haplochromine cichlid fishes in Lake

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Malawi, Africa (Dominey, 1984; Turner & Burrows, 1995). This lake contains up to 1000 species (Konings, 2007) that appear to have evolved from common ancestry within the last 2 to 4 million years (Genner et al., 2007). A role for sexual selection in the speciation of haplochromine cichlids is supported by evidence that females show directional intraspecific mating preferences for elaborate male traits such as breeding coloration (Pauers et al., 2004; Maan et al., 2006). Moreover, closely-related species often differ conspicuously in these male traits (van Oppen et al., 1998; Kidd et al., 2006), and it has been shown in experimental mate choice trials that females actively choose among heterospecific males based on these male traits (Seehausen & van Alphen, 1998; Knight et al., 1998; Knight & Turner, 2004).

Evaluating the role of sexual selection in speciation requires a detailed understanding of the origins and functions of traits preferred by females. It is notable that in many species females appear to receive no direct mating benefits, but still spend time and resources on mate choice. Such costly female preferences could arise via a 'runaway' process (Fisher, 1930), or they may initially have adaptive value if the preferred male secondary sexual traits are honest indicators of higher genetic fitness that can be inherited by the female's offspring ('good genes' models; Trivers, 1972; Hamilton & Zuk, 1982). Importantly, mate choice does not evolve in a vacuum; traits and preferences are often constrained and open to exploitation and co-option by the opposite sex. Ryan (1990) proposed that male sexual traits take advantage of pre-existing female preferences, a view now supported in multiple systems (Basolo, 1990; Rodd et al., 2002). Conversely, pre-existing male traits used for intrasexual competition (Berglund et al., 1996; Borgia & Coleman, 2000) or other functions (Borgia, 2006) may be subsequently also used by females as honest indicators of male quality. In support of this, numerous taxa utilize the same traits in male competition and female choice, since both sexes often seek the same information about male quality (Berglund et al., 1996; Borgia, 2006). Thus, in addition to determining which male traits are preferred by females, it is necessary to understand the complete spectrum of female preferences and potential multiple functions of male secondary sexual traits.

One of the most complex male secondary sexual traits is the bower, broadly defined as an elaborate structure built in a male's territory where courtship and mating takes place. The term was originally used to describe the constructions of bowerbirds and widowbirds in Australia and New Guinea. In these species male birds build 'avenue' or 'maypole' structures

from twigs or clear display areas of the forest floor and may decorate these with up to thousands of items (Borgia, 1995; Frith & Frith, 2004). Many lekking cichlid species also build elaborate spawning platforms from sand in their territories that have been termed 'bowers' by analogy (Karino, 1996; McKaye, 1991; McKaye et al., 2001). Bower shape shows considerable variability among species, and ranges from three metre wide pits to volcano-shaped mounds, rock platforms, and small depressions cleared of vegetation (McKaye, 1991; Kocher, 2004; Kidd et al., 2006; Konings, 2007). Observations show that females often visit and mate with multiple males within a lek (Kellogg et al., 1995; Taylor et al., 1998). Eggs are laid on the bower platform, collected in the female's buccal cavity, fertilized, and brooded away from the lek for approximately one month before release of free-swimming fry. Thus, males provide only their genes to females, and perhaps limited protection from egg-predators during spawning.

The functions of cichlid bowers are still not fully understood. Field observations and experiments have demonstrated that in some species males on taller bowers receive more female visits and fertilize more eggs (McKaye et al., 1990; Kellogg et al., 2000; Stauffer et al., 2005; Genner et al., 2008). Moreover, females appear to be mate more often with males guarding bowers located in the centre of the lek (Kellogg et al., 2000; Genner et al., 2008). It is, therefore, possible that bowers are honest indicators of male quality. Consistent with such 'good genes' models of sexual selection (Hamilton & Zuk, 1982), Taylor et al. (1998) found that males on more symmetrical bowers tended to have fewer parasites, and lower parasite load was related to greater spawning success. Together this evidence is largely consistent with females employing bowers in direct mate choice as honest signals for choosing mates.

The repeated convergence of bower shape (Kidd et al., 2006) suggests additional constraints on bower morphology beyond female preferences. The raised platform lip of some bowers might limit entry to the egg-stealing fishes that are common on leks (McKaye, 1983). Additionally, bowers may have a role as species-specific markers (Karino, 1997; Kidd et al., 2006), however manipulation of bower shape to that of a co-occurring species did not alter male success in one species of Lake Malawi cichlid (Genner et al., 2008). Another untested possibility is that bower size is an honest indicator of male competitive ability on the lek (Schaedelin & Taborsky, 2006). In support of this suggestion is evidence that access to females is not constant among all

males, and instead male success is most strongly influenced by courtship rate, which is in turn strongly related to bower height and position on the lek (Genner et al., 2008). If so, bower position and shape may form a signal that allows dominant males to establish territories in sites with more females, and in turn these male traits are selected through indirect female mate choice. Consistent with a role for bowers in male competition, McKaye et al. (1990) found in one lekking species that males defending taller bowers were more aggressive toward other males, and this was interpreted as evidence that taller bowers comprise a more valuable territory for attracting females.

Here we report a field experiment where the influence of bower form on male competition in a Lake Malawi cichlid was assessed by measuring the relative aggressive response of territorial males toward intruder males placed on short or tall artificial bowers. We also present observational data on associations between male aggression, bower size, standard length, body coloration and male reproductive success.

Methods

Study species and location

Our focal species, *Nyassachromis cf. microcephalus*, is a sand-dwelling zooplanktivore present in the Cape Maclear region of Lake Malawi where it is exploited by artisanal fisheries. Males aggregate in shallow waters (3–15 m) and construct volcano-shaped sand bowers (Konings, 2007). Males sometimes incorporate rocks into their bowers or defend bare patches of rock, but in this study only males defending sand bowers built on sand or rock substrate were sampled. Fieldwork was conducted on a lek at Thumbi West Island (14°01'22.7"S, 34°49'23.5"E) by one researcher (CHM) using SCUBA.

Field observations

Observations were made during morning hours (0700–1100) between August and October 2006. Focal territorial males defending bowers were observed for 10 min each, and the following behaviours were recorded: (1) aggressive charges to neighbouring territorial males guarding bowers, (2) aggressive charges to roaming non-territorial males, (3) aggression received from neighbouring males, (4) number of females courted and (5) number of females visiting the focal male's bower platform. Territorial males also made threats, but it was difficult to distinguish conspecific from het-

erospecific targets during field observations and this behavior was excluded. Territorial males were only observed performing lateral displays and lunges toward non-territorial males; biting and extended lip-locking between two territorial males was observed once outside of timed observations (C.H.M., pers. obs.). Following observations, bowers of focal males were individually marked. The bower height and top diameter were then measured twice (rotated by 90°), along with the distance to the nearest neighbouring bower.

Sixteen males guarding sand bowers on the lek were captured using a barrier net. Each male was anesthetized in MS-222 (0.2% solution; Argent Laboratories, Redmond, WA, USA), photographed on both sides alongside a standard orange color patch, and measured for standard length. Males were allowed to recover and then released on the lek. The bower dimensions of photographed males were measured as described above following capture. We measured normalized values of hue, saturation, and lightness from the average of three orange points on the image of each lateral surface of the male using image analysis software, as described in Martin & Johnsen (2007). Animals are unable to synthesize carotenoids (Goodwin, 1984), a major component of orange pigmentation and, thus, the saturation and lightness of this color may be a condition-dependent signal of male quality (Houde, 1997).

Field experiment

Observations were made between December 2006 and January 2007. Females were frequently present on the lek and were observed visiting males to spawn. Two artificial bowers (22.5 cm top diameter), one short (height 3.5 cm) and one tall (height 27 cm), were constructed by gluing sand from the lek onto an inverted plastic bucket (Figure 1). Building natural sand bowers in situ resulted in considerable substrate disturbance that attracted foraging fishes and distracted territorial males. By contrast artificial bowers caused minimal disturbance. Territorial males defend rocks in place of their original sand bowers (C.H.M. & M.J.G., pers. obs.), suggesting that a range of mound-like objects are acceptable as bower locations for this species.

For each trial an 'intruder' male was captured from a neighbouring lek using a barrier net. Only territorial males guarding bowers were captured, ensuring that male body sizes were not greatly mismatched (mean \pm 95% CI for standard length of territorial males = 9.8 ± 0.1 cm, $N = 43$). The male was placed inside a transparent cylindrical bottle with slits cut around the rim for water circulation (15 cm diameter \times 25.5 cm height, Figure 1)

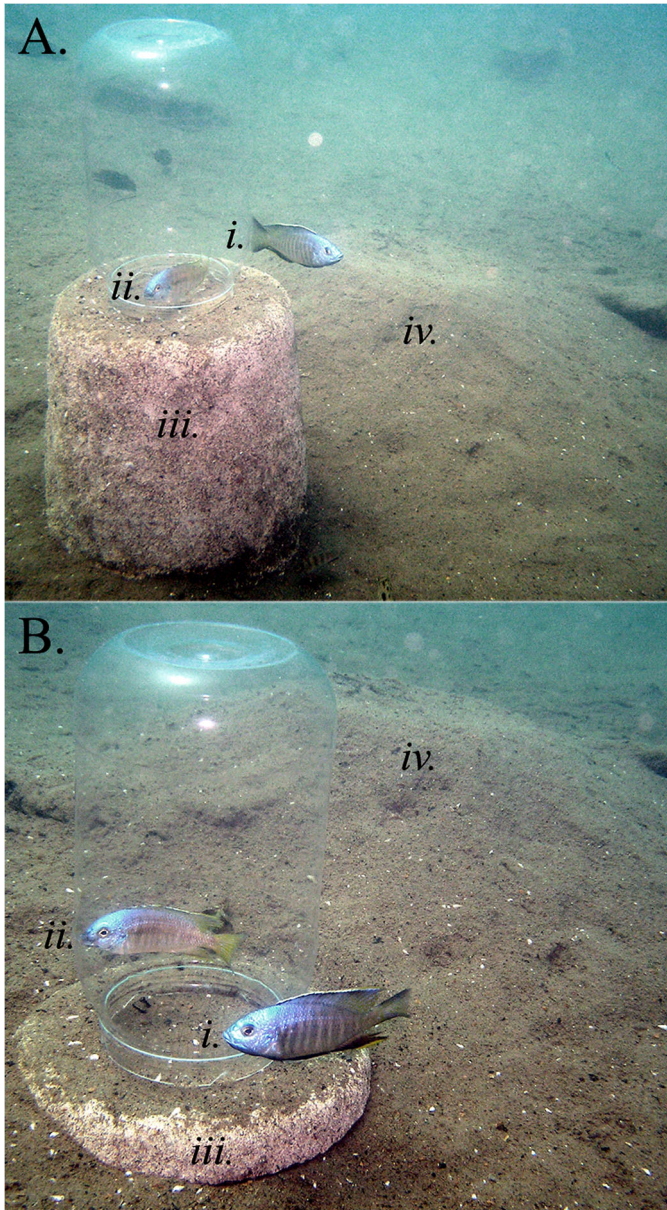


Figure 1. Example of experimental setup during trials with intruder males on (A) a tall artificial bower and (B) a short artificial bower. Images show (i) resident territorial male, (ii) intruder male confined to transparent bottle, (iii) artificial sand bower and (iv) resident male's natural sand bower. This figure is published in colour in the online edition that can be accessed via <http://www.brill.nl/beh>

and allowed to acclimate to the bottle for 10 min away from the lek before beginning the first aggression trial. Each intruder male was used for up to 5 aggression trials with no apparent behavioral changes.

Each aggression trial involved an intruder male being placed sequentially on artificial bowers for a 5-min observation period close to a resident focal male (Figure 1). First, one of the artificial bowers was placed near (mean \pm 95% CI = 72.5 \pm 4.02 cm) the resident male bower and the sediment was allowed to settle. This distance was greater than the minimum distance between natural sand bowers (50 cm). The tall (27 cm) artificial bower was taller than 98.6% of focal male bowers and the short (3.5 cm) artificial bower was shorter than 97.1% of focal male bowers.

The short artificial bower was presented first in 36 aggression trials and the tall bower first in 35 trials. Due to high bower density, two resident males were frequently observed simultaneously with one intruder male between them. Next, the acclimated intruder male was placed on the artificial bower for 5 min during which all aggressive behaviours by resident males toward the intruder male were recorded (Figure 2). Following this period, the intruder male and first artificial bower were removed from the lek and the sec-



Figure 2. Aggressive behaviours by resident males toward intruder males during experimental aggression trials: (a) threat, (b) lunge, (c) lateral display and (d) bite. See Table 1 for descriptions. This figure is published in colour in the online edition that can be accessed via <http://www.brill.nl/beh>

ond artificial bower was placed in the same spot. After a 15-min rest period the same intruder male was placed on the second artificial bower for another 5 min of observation. We did not observe any change in the intruder male's coloration when placed on the short or tall artificial bower (C.H.M., pers. obs.). All statistical tests were performed using JMP-IN 5 (SAS Institute, Cary, NC, USA).

Results

Field observations

Sand bowers on average measured 13.5 ± 5.5 cm in height (mean \pm SD; range 2.0–30.0, $N = 134$), 25.1 ± 3.5 cm in top platform diameter (range 18.0–35.0, $N = 118$), and the nearest neighbour distance was 1.1 ± 0.2 m (range 0.5–1.7, $N = 63$). On average focal males made 1.13 ± 2.03 (mean \pm SD, range 0–11, $N = 54$) aggressive charges toward neighbouring territorial conspecific males and received 1.65 ± 2.98 (mean \pm SD, range 0–13) aggressive charges per 10-min observation period.

Focal males initiated significantly more aggression towards non-territorial males roaming the lek than toward neighbouring territory-holders (Wilcoxon signed-rank test: $W = -101.0$, $p = 0.025$; $N = 34$). There were no significant correlations between the focal male's bower height, platform diameter or nearest neighbour distance and aggression received (multiple regression; \log_{10} transformed aggression: height $F_{1,49} = 0.068$, $p = 0.796$; diameter $F_{1,49} = 0.004$, $p = 0.947$; distance $F_{1,49} = 1.126$, $p = 0.294$) or aggression directed toward neighbouring males (height $F_{1,49} = 0.153$, $p = 0.698$; diameter $F_{1,49} = 0.001$, $p = 0.981$; distance $F_{1,49} = 1.121$, $p = 0.295$).

Male sand bower height was significantly associated with male reproductive success (female visits/courted females; $r^2 = 0.101$, $N = 51$, $p = 0.023$), but bower diameter was not associated with male reproductive success ($r^2 = 0.001$, $N = 51$, $p = 0.810$). There was no significant association between the height of a male's sand bower and orange body coloration (hue: $r^2 = 0.001$, $N = 16$, $p = 0.924$; saturation: $r^2 = 0.012$, $N = 16$, $p = 0.693$; lightness: $r^2 = 0.033$, $N = 16$, $p = 0.503$) or standard length ($r^2 = 0.023$, $N = 16$, $p = 0.576$).

Field experiment

Total male aggression was unaffected by which bower treatment came first, but territorial males were significantly more aggressive towards an intruder

Table 1. Aggressive behaviour by resident males toward intruder males during experimental trials and Wilcoxon paired signed-rank test statistics (Z) for differences in aggression toward intruder males on short and tall artificial bowers.

Aggressive behaviour	Description	Frequency per 5 min (mean \pm SD)	df	Z	P (two-tailed)
Threats	Forward lunges or circling greater than one body length away	4.51 \pm 5.82	70	663	<0.001
Lateral displays	Fully erect fins and sigmoid body curvature parallel to the intruder	1.82 \pm 3.72	70	53.5	0.228
Lunges	Deliberate, short-distance motion toward intruder	4.20 \pm 8.80	70	85.5	0.111
Charges	Rapid, long-distance motion toward intruder	0.71 \pm 2.54	70	50.0	0.014
Bites	Open mouth contacts bottle	1.32 \pm 4.08	70	13.0	0.587
Total aggression (a, b, c, d, e)		12.6 \pm 17.01	70	617.5	<0.001

male on a short artificial sand bower than the same male on a tall bower (two-way non-parametric ANOVA on ranks: order effect $F_{1,138} = 2.026$, $p = 0.157$; treatment effect $F_{1,138} = 5.680$, $p = 0.019$, order by treatment interaction $F_{1,138} = 1.954$, $p = 0.164$ (Table 1; Figure 3)). There was no significant difference in total aggression by resident males toward the 14 intruder males (Kruskal–Wallis ANOVA: short bower trials $\chi^2 = 17.076$, $p = 0.196$; tall bower trials $\chi^2 = 20.705$, $p = 0.079$).

When divided into specific aggressive behaviours (Table 1), territorial males made significantly more threats and charges toward intruder males on the short bower. Other aggressive behaviours were also more frequent toward males on the short bower, although not significantly (Table 1; Figure 3). The difference in height between the focal male and artificial bower was significantly correlated with total aggression toward the intruder male (2-way non-parametric ANOVA on ranks: difference in height $F_{1,137} = 4.506$, $p = 0.036$; treatment $F_{1,137} = 0.983$, $p = 0.323$; non-significant interaction term).

We initially speculated that reduced male aggression toward the taller artificial bower may be a xenophobic response to a large foreign object. To test this we conducted additional aggression trials with the intruder male

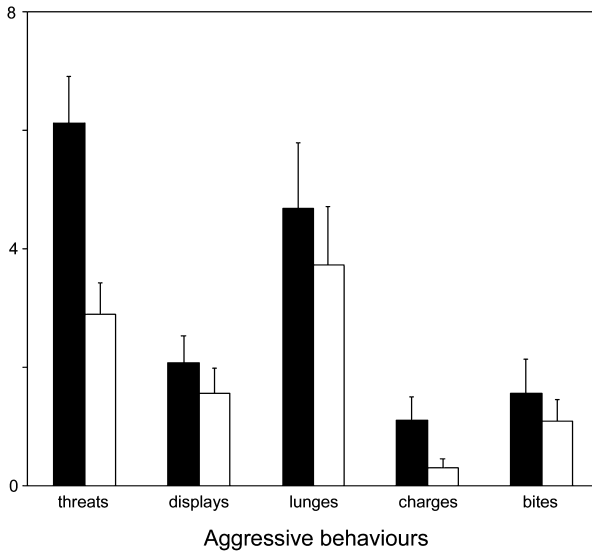


Figure 3. Mean (+1 SE) frequency of aggressive behaviours by resident males toward an intruder conspecific male on either a short (■, 3.5 cm) or tall (□, 27 cm) artificial bower during 5-min observation periods.

on a short artificial bower and an unoccupied tall artificial bower adjacent. Resident males showed no significant difference in aggression toward the intruder male on the short bower in the presence (9.4 ± 9.6 , mean \pm SD) or absence (12.3 ± 18.3) of the tall bower (Wilcoxon signed-rank test: $Z < 0.001$, $N = 7$, $p = 0.500$), indicating that resident males were not disturbed by an empty bower or a new object in their territory.

Discussion

We found that males of a Lake Malawi cichlid on short artificial bowers received more aggression from neighbouring territorial males than those on tall artificial bowers. By keeping the invader, defender, bower shape, and location constant in each aggression trial, these results are consistent with the hypothesis that bower height is used in competitive assessment among neighbouring males. Dominance hierarchies in haplochromine cichlid fishes are regulated by aggression, with the more dominant individuals typically the most aggressive (Clement et al., 2005), suggesting that bower size may be linked to hierarchical position on the lek. Previous observations of bower-

building cichlids found that males on taller bowers tend to be more aggressive toward conspecific males (McKaye et al., 1990), consistent with bower size as an indicator of male dominance.

We cannot rule out that males in our study were responding to cues other than bower height in experimental trials. Intruder males placed on the tall bower occupied a higher position in the water column and resident males may be responding to this elevation rather than the contrast in bower height. However, the difference in vertical position between artificial bowers in this study (23.5 cm) was much smaller than observed vertical movement in this species during bower defence, indeed territorial males often hover in the water column one metre or more above bowers (C.H.M. & M.J.G., pers. obs.). We speculate that male position in the water column should be a poor predictor of male competitive ability due to its low cost relative to the high production costs of maintaining and defending a tall bower. Selection should favour bower height, not water column position, as an honest indicator of male competitive ability. It is also possible that different positions of any conspecific or heterospecific fish in the water column solicit different levels of aggression from resident males. Heterospecific egg-stealing fishes were always observed to attack the bower platform from directly above during spawning, as the bower rim may prevent their horizontal entry (McKaye, 1983; C.H.M., pers. obs.). Thus, territorial males should be most aggressive toward heterospecific fishes higher in the water column and this bias may spill over to neighboring conspecific males. On the other hand, territorial males may have evolved less aggression toward any fishes high in the water column if territorial males guard taller bowers and are generally dominant. A final caveat is that we tested males on the same two artificial bower models in all trials, so differences in aggression may be linked to an unknown characteristic of these models.

Significant associations between bower height and male aggressive interactions were not observed during field observations. However, most neighbouring males on the lek were similar in bower size, in contrast to our field manipulations that were designed to replicate the largest differences in bower size observed across the lek. Moreover, only aggressive charges were recorded during field observations due to the difficulty of determining the intended receiver of male threats in the field. Finally, observations that males were more likely to chase invading non-territorial conspecifics, and not neighbouring territorial males, suggests that hierarchies among observed

territorial males may have stabilized, and aggression was, therefore, infrequent.

Bower height may be a signal of male tenure on the lek, rather than male competitive ability. Lake Malawi cichlid bowers gain approx. 1 cm in height per day, and building requires over two weeks to reach the average bower height in the lek (McKaye et al., 1990). Thus, short-term field observations cannot distinguish between males with short bowers due to their recent arrival on the lek, from low-quality males unable to build or maintain larger bowers. Several recent arrivals were observed starting bowers within an established group of taller bowers during the peak breeding season (C.H.M., pers. obs.). Our results suggest these new males would have solicited high levels of aggression and may be more likely to desert their small territorial investment. Such a process may explain why new males on a lek of the Lake Tanganyika cichlid *Cyathopharynx furcifer* deserted their bowers within four days (Karino, 1996). Variation in the duration that males have held bowers may also help to explain why male standard length and colour, two common measures of male dominance in cichlids, were not significantly correlated with bower height. Consistent with this overall pattern, young male bowerbirds establishing new bowers are frequently chased away by older males and their bowers are destroyed (Borgia, 1985). Thus, small bowers may be a signal of recent arrival and small territorial investment to other males. Resident males may concentrate their attacks during this early phase of construction when the new arrival is most likely to desert his bower, regardless of his competitive ability.

Schaedelin & Taborsky (2006) showed that bowers of Lake Tanganyika cichlids are individual-specific phenotypes and, thus, may serve as heritable indicators of overall male quality. However ours is the first study, to our knowledge, to provide direct evidence that bowers may function in male competition in addition to their well-documented role in female mate choice. The pre-existing trait hypothesis proposes that females have repeatedly incorporated intrasexual male aggressive displays into their own assessment of high quality males (reviewed in Berglund et al., 1996; Borgia, 2006), which is supported in bowerbirds (Borgia & Coleman, 2000). Our results suggest that it is possible that females only began using bower size to choose among males after an initial function of this signal in male competition. The reverse scenario or concurrent use of this signal by both sexes initially is also

possible, but these cases appear to be less common than the armament first, ornament second model (Berglund et al., 1996; Borgia, 2006).

The mechanism behind female preference for male cichlids with larger bowers is still relatively unclear, and may vary between species. There is evidence that females are attracted to taller bowers through direct mate choice (McKaye et al., 1990; Stauffer et al., 2005). Consistent with these results, we found a significant association between bower height and male reproductive success, after controlling for variation in female encounter rate among males. However, bower size may additionally be selected through indirect mate choice. Dominant males defending taller bowers may suffer fewer attacks from neighbouring males, in turn providing more opportunity for courtship display and mating. Similarly, dominant males may establish taller bowers in locations on the lek where they are likely to encounter more females (Genner et al., 2008).

In support of an indirect role for bowers in mate choice are observations that most bower building cichlids primarily initiate courtship to females at a distance away from their bowers prior to lead swims toward the bower platform (Genner et al., 2008). These males can be difficult to assign to their respective bowers during their initial courtship displays (C.H.M., pers. obs.). Thus, initial mate selection often occurs before females have assessed bower size, and only after assessment of colour, courtship vigour, and potential auditory (Amorim et al., 2004) and olfactory cues (Plenderleith et al., 2005). Bower size could then play a role in later stages of courtship as part of direct mate choice (Coleman et al., 2004). All previous studies demonstrating female cichlid preferences for taller bowers are consistent with both direct and indirect functions of bowers in mate choice since none, to our knowledge, have quantified the importance of bower dimensions in mate selection while simultaneously assessing the role of these signals in male competition.

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