

ORIGINAL ARTICLE

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Characteristics that influence male reproductive success on a lek of *Lethrinops c.f. parvidens* (Teleostei: Cichlidae)

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Abstract Sexual selection has long been proposed as a mechanism leading to the diverse cichlid (Teleostei: Cichlidae) fauna of Lake Malawi, Africa. Many of the shallow-water, sand-dwelling, bower-building cichlid species are particularly well suited for studies of sexual selection because they participate in leks. Since females in lekking systems appear to acquire only genetic material from their mates, it has been suggested that leks are ideal systems to study female mate choice. The objectives of the investigation were to examine *Lethrinops c.f. parvidens* male bower characteristics (i.e., bower size and location) as well as other male characteristics (i.e., length, gular color, and duration on the lek) for their influence on male mating success as measured by the number of visits, circles, and eggs laid by females. These measures are nested in that a visit by a female may or may not lead to circling, and circling by a female may or may not lead to egg-laying. We found increased bower height and higher numbers of conspecific neighbors (analogous to shallow-water, near-shore bower positions) to be positively, significantly associated with the number of visits by females. The only significant correlate with the number of circles was visits, and similarly circles was the only significant correlate with the number of eggs laid. The R^2 value for the egg-

laying regression was quite low (19.8%) compared with visits (54.3%) and circling (78.9%), suggesting that females may be using additional cues, that we failed to measure, when in close proximity to males or simply that a small proportion of the females were ready to spawn. Both indirect selection and direct selection pressure due to egg predation may have influenced female choice on the lek.

Key words Sexual selection · Bower · Cichlid · Lake Malawi · Sand-dwelling

Introduction

The cichlid fishes of the Great Lakes of Africa are the most extreme case of adaptive radiation among vertebrates. This astounding speciation is exemplified in Lake Malawi where 450+ species have arisen within the last 2 million years (e.g., Greenwood 1991). Numerous theories have been put forward to explain the rapid diversification of Lake Malawi cichlids. The consensus is that allopatric or micro-allopatric speciation has been frequent (Greenwood 1991). In addition, an increasingly frequent reference to sexual selection by female mate choice and its possible contribution to cichlid speciation can be found throughout the literature (e.g., Dominey 1984; McKaye 1991; Turner and Burrows 1995; Deutsch 1997).

The shallow-water, sand-dwelling cichlids of Lake Malawi are particularly well suited for studies of sexual selection and, subsequently, its role in speciation. Many of these species participate in true leks, that is, adult males form large aggregations and females visit these assemblies for the sole purpose of egg fertilization (Bradbury and Gibson 1983; Höglund and Alatalo 1995). Since females in lekking systems appear to acquire only genetic material from their mates, it has been proposed that leks are ideal systems to study female mate choice and indirect selection of preferences (i.e., selection that operates through differential success of the offspring without any effect on parental survival or fertility) (Bradbury and Gibson 1983; Balmford 1991).

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As male sand-dwelling cichlids aggregate, they construct and defend sand structures (termed bowers) (McKaye et al. 1990). Bowers serve as sites for courtship and spawning, but offer no additional resources to females or offspring. We consider bowers to be manifestations of male behaviors and hence a male characteristic (Stauffer et al. 1995). Females in this system visit many males, but only lay eggs with a subset of these males. A female lays her eggs on the open top of the bower, and then immediately picks them up in her mouth where they are subsequently fertilized by the resident male (Kellogg et al. 1995). After laying all of her eggs, the female leaves the lek and is solely responsible for parental care.

Bower shape appears to be species specific; however, bower size varies tremendously (McKaye et al. 1993; Stauffer et al. 1993). Previous studies have shown that increased bower size (McKaye et al. 1990) as well as central bower positions within the lek (McKaye 1991) are associated with elevated male mating success. To evaluate the generality of these previous findings, the first objective of this study was to examine relationships between male bower characteristics (i.e., bower size and location) and male mating success in an unstudied lek of *Lethrinops* c.f. *parvidens* Trewavas. Second, we explored the effects of other male morphological characteristics (e.g., coloration and body length) and behaviors (e.g., foraging, heterospecific encounters) on male mating success.

Methods

Study population and setup

The study lek was located between 3–4 m depth adjacent to a submerged rocky outcrop (0–3 m depth; Fig. 1). The lek spanned an area of approximately 15×25 m in the southeastern arm of Lake Malawi, Africa at Songwe Hill (34°56' E, 14°00' S). The lek consisted of approximately 100 *L. c.f. parvidens* males and overlapped with leks of two other cichlid species: *Otopharynx* sp. Regan and *Copadichromis* c.f. *thinos* Stauffer, LoVullo & McKaye. Using SCUBA, we observed the activities of *L. c.f. parvidens* for a 6-week period during their peak breeding season (February–March). Most of the breeding activity on this lek (personal observation) and many other leks (McKaye 1983) takes place between 0600 and 1000 hours, and therefore all observations were conducted during this time. All potentially disruptive activities (e.g., male tagging) were performed during the non-peak times.

A numbered plate mounted on a metal stake was secured next to each bower so that individual bowers could be identified. To map the lek, a string grid system, anchored with metal stakes, was installed on the arena at the onset of the breeding season (Fig. 1). The grid system was flush with the sand surface so as not to hinder fish movement. The position of each *L. c.f. parvidens* bower was plotted using the nearest grid line, and verified weekly.

From this map, we extracted two nearest-neighbor measures. We counted the number of conspecific and heterospecific neighbors within a 2-m radius of each bower center. We considered 2 m to be biologically relevant considering that most resident male-male interactions occurred within this distance. The number of conspecific neighbors not only described the nearest neighbors, but also appeared to indicate the position of a bower with respect to the rocky-outcropping (Fig. 1). We calculated the distance of each bower from the nearest point of the rocky-outcropping (Fig. 1) as a measure of bower position and this was highly correlated with the number of conspecific neighbors (Pearson correla-

Fig. 1 Map showing the string grid system and the layout of bowers on the study lek. Each solid circle represents what was originally a *Lethrinops* c.f. *parvidens* bower. Solid circles surrounded by a square represent bowers that were taken over by *Copadichromis* c.f. *thinos*, solid circles surrounded by a triangle represent bowers that were taken over by *Otopharynx* sp., and solid circles surrounded by an ellipse symbolize bowers that were initially taken over by *C. c.f. thinos*, but were eventually invaded by *Otopharynx* sp. The rocky-outcropping outline is shown

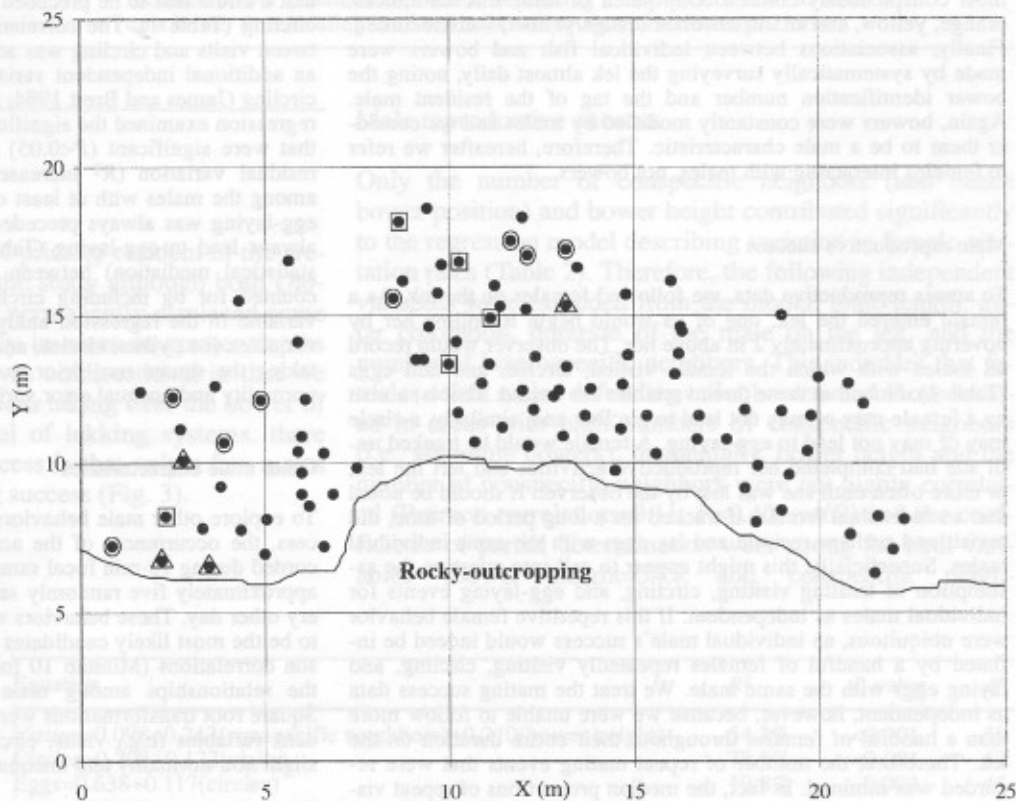
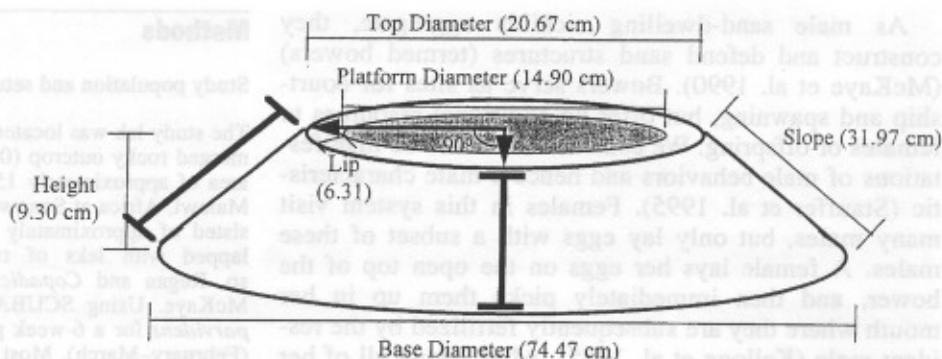


Fig. 2 A bower sketch illustrating the six dimensions taken during the first round of bower measurements. Averages of each dimension calculated from all bowers on the lek are shown in parentheses. An example (illustrated on the slope dimension) of how bower measurements were taken is shown in heavy lines. Note that measurements were taken at two points on the bower separated by 90° and subsequently averaged



tion -0.55 , $n=98$, $P<0.001$). Therefore, high conspecific neighbor density was characteristic of bowers located in the shallow-water, shore-side of the lek, whereas low densities were indicative of deeper-water, peripheral positions. The dual interpretation of this variable (number of neighbors and bower position) is valuable for the discussion of the study results.

To measure bower size, six dimensions were recorded for every bower (Fig. 2). Due to bower asymmetry, two measurements for each dimension, taken at points on the bower separated by 90° (see Fig. 2 for example), were recorded to the nearest 0.5 cm and averaged. Bower size changed constantly, so bower measurements were repeated every 2 weeks. We found all major bower dimensions from the first round of measurements to be highly correlated (Pearson correlations ranged from 0.50 to 0.80, $n=98$), and in an attempt to reduce disturbance of the lek, all subsequent bower measurements were restricted to only height.

To identify individual males throughout the course of the study, males were captured using monofilament nets and tagged underwater using Floy-T tags with individual identification markings. Approximately two-thirds of the tagged fish returned to their bowers within 24 h. Because male turnover on the lek occurred quite frequently, tagging was repeated periodically so that the majority of males on the lek at any given time could be identified. During tagging, male standard length (mm) and gular color (the most conspicuously colored body patch of three discrete colors: orange, yellow, and an intermediate orange/yellow) were recorded. Finally, associations between individual fish and bowers were made by systematically surveying the lek almost daily, noting the bower identification number and the tag of the resident male. Again, bowers were constantly modified by males and we consider them to be a male characteristic. Therefore, hereafter we refer to females interacting with males, not bowers.

Male reproductive success

To amass reproductive data, we followed females on the lek. As a female entered the lek, one of us would begin to follow her by hovering approximately 2 m above her. The observer would record all males with which the female visited, circled, and laid eggs (Table 1). Note that these three variables are nested. That is, a visit by a female may or may not lead to circling and, similarly, a circle may or may not lead to egg-laying. A female would be tracked until she had completed her reproductive activities and left the lek, or more often until she was lost by the observer. It should be noted that an individual female, if tracked for a long period of time, did revisit and perhaps recircle and lay eggs with the same individual males. Superficially, this might appear to call into question the assumption of treating visiting, circling, and egg-laying events for individual males as independent. If this repetitive female behavior were ubiquitous, an individual male's success would indeed be inflated by a handful of females repeatedly visiting, circling, and laying eggs with the same male. We treat the mating success data as independent, however, because we were unable to follow more than a handful of females throughout their entire duration on the lek. Therefore, the number of repeat mating events that were recorded was minimal. In fact, the median proportions of repeat vis-

its, circles, and egg-laying recorded while following individual females were all zero.

To evaluate the most appropriate model to describe the variation observed in the dependent variables (i.e., visiting, circling, and egg-laying; Table 1), a series of three nested, multiple linear regressions, in conjunction with best-subsets analyses (Minitab 10 for Windows), were used. The independent variables considered for all three models were male length, gular coloration, duration of the male on the lek (measured as the number of days post-tagging), bower height, number of conspecific neighbors, and number of heterospecific neighbors. Gular coloration was a categorical variable and therefore was coded as such for the regression analyses. All independent variables were considered for each of the three models because it was possible that some characteristics (e.g., bower size) were important in getting females to visit, but other male characteristics (e.g., body coloration) were important in getting a visiting female to lay an egg. The first regression examined the significant correlates [i.e., those variables that were significant ($P<0.05$) and explained at least 3% of the residual variation (R^2 increase of at least 3%)] of visits among all males. The second regression examined the significant correlates [i.e., those variables that were significant ($P<0.05$) and explained at least 3% of the residual variation (R^2 increase of at least 3%)] of circling among males that were visited by at least one female, considering that a circle had to be preceded by a visit, but not all visits led to circling (Table 1). The correlation (i.e., statistical mediation) between visits and circling was accounted for by including visits as an additional independent variable in the regression analysis for circling (James and Brett 1984; Baron and Kenny 1986). The third regression examined the significant correlates [i.e., those variables that were significant ($P<0.05$) and explained at least 3% of the residual variation (R^2 increase of at least 3%)] of egg-laying among the males with at least one female circle, considering that egg-laying was always preceded by circling, but circling did not always lead to egg-laying (Table 1). Again, the correlation (i.e., statistical mediation) between circling and egg-laying was accounted for by including circling as an additional independent variable in the regression analysis for egg-laying. All dependent variables (i.e., visits, circles, and egg-laying) were transformed by taking the square root prior to analyses to adjust for slight non-normality and unequal error variances.

Other male characteristics

To explore other male behaviors that might influence mating success, the occurrences of the activities listed in Table 1 were recorded during 10-min focal samples (Martin and Bateson 1986) of approximately five randomly selected *L. c.f. parvidens* males every other day. These behaviors were selected because they seemed to be the most likely candidates to influence mating success. Pearson correlations (Minitab 10 for Windows) were used to explore the relationships among male behaviors and mating success. Square root transformations were again necessary for some dependent variables (e.g., visits, circles, and egg-laying) to adjust for slight non-normality and unequal variances.

Table 1 Male behaviors recorded during 10-min male focal samples. Asterisks indicate those behaviors that were also recorded while following females

Behavior	Description
Behaviors directed toward females	
Courting	Display of a male to a female, but the female never entered the bower. Male displays included body quivers and fast turns.
Visit	*Female entered the bower of a displaying male, followed by female departure or circling behavior.
Circling	*Female and male made contact by touching nose to tail and swimming in tight circles. This activity was followed by female departure or egg-laying.
Egg laid	*Female laid an egg on the bower platform, quickly turned, and picked it up in her mouth.
Behaviors directed toward other males	
Threats toward heterospecifics	Erect fin displays and body quivering directed primarily at pedophages. Pedophages (literally baby-eaters) ram brooding females to dislodge fry for consumption or interact with mating pairs to consume the eggs that are being laid.
Attacks on heterospecifics	Fin nipping and other forms of male-male contact directed toward heterospecifics, again primarily pedophages.
Threats toward territorial conspecifics	Defined as above, but directed at conspecific males that had been previously associated with a bower.
Attacks on territorial conspecifics	Defined as above, but directed at conspecific males that had been previously associated with a bower.
Threats toward non-territorial conspecifics	Defined as above, but directed at either conspecific males in breeding coloration that were attempting to take over existing bowers or sneaky males, which have been documented on many cichlid leks (McKaye 1983).
Attacks toward non-territorial conspecifics	Defined as above, but directed at either conspecific males in breeding coloration that were attempting to take over existing bowers or sneaky males, which have been documented on many cichlid leks (McKaye 1983).
Miscellaneous behaviors	
Foraging	Males either sifted through sand or picked at the sand surface.
Sand movement	Included bower maintenance such as depositing a mouthful of sand to build up a bower or relocating sand on the bower to clean the bower platform.

Results

Study population

L. c. f. parvidens remained the primary resident of the arena throughout the course of the study although both *Otopharynx* sp. and *C. c.f. thinos* permanently displaced some *L. parvidens* males, especially in areas at greater depths (Fig. 1). This displacement was unidirectional in that we never witnessed *L. c.f. parvidens* taking over the bower of another species. As is typical of lekking systems, there was skewed male mating success in that only a few males attained high levels of mating success (Fig. 3).

Male reproductive success

Only the number of conspecific neighbors (and hence bower position) and bower height contributed significantly to the regression model describing variation in female visitation rates (Table 2). Therefore, the following independent variables were excluded from the model: male length, gular coloration, duration of the male on the lek, and the number of heterospecific neighbors. This indicates that females select males defending taller bowers and those located in areas with high numbers of conspecific neighbors (i.e., shoreline bowers). Incidentally, bower height and the number of conspecific neighbors were not highly correlated (Pearson correlation=0.11, $P=0.40$, $n=60$) and the coefficients of partial determination were strong for both variables (bower height=34.8 and conspecific neigh-

Table 2 Regression of male reproductive success as measured while following females

Equation	R ²	P-value	df
Visits=-0.098+0.243(conspecific neighbors)+0.210(bower height)	54.3%	<0.001	59
Circles=0.705+0.127(visits)	78.9%	<0.001	52
Eggs=0.638+0.117(circles)	19.8%	0.002	45

bors=19.5). Only the number of visits contributed significantly ($P<0.05$) to the regression model describing variation in female circling (Table 2). Similarly, only the number of circles contributed significantly ($P<0.05$) to the regression model describing variation in female egg-laying (Table 2). This indicates that in terms of the variables that we measured, getting a female to visit was the only significant correlate of circling and, subsequently, circling was the only significant correlate of egg-laying.

Other male characteristics

In general, the three most frequently occurring male behaviors were bower maintenance (sand movement), heterospecific attacks, and courting females during the 107 total 10-min focal samples that were collected (Table 3). Many males were observed for more than one focal sample, so the behavioral means of all focal samples for each male were used for the correlational analyses. We observed a total of 51 different males during the focal samples, and therefore, the degrees of freedom for the correlations was 50 (Table 4). Sand movements were significantly, negatively associated with visits, circles, and egg-laying (Table 4). Foraging was significantly, negatively associated with circles (Table 4). Finally, threats on heterospecifics was significantly, positively associated with both circles and eggs laid (Table 4).

Table 3 Means and standard deviations of the occurrences of male behaviors recorded per 10-min male focal sample ($n=107$)

Behavior	Mean	Standard deviation
Courting	4.65	3.10
Visit	1.25	1.13
Circling	0.80	1.06
Number of eggs laid	0.98	3.26
Attacks on heterospecifics	22.00	15.50
Threats toward heterospecifics	0.04	0.20
Attacks on territorial conspecifics	1.20	1.85
Threats toward territorial conspecifics	1.18	1.11
Attacks on non-territorial conspecifics	0.04	0.20
Threats toward non-territorial conspecifics	0.04	0.20
Foraging	0.49	1.35
Sand movement	31.43	19.09

Table 4 Correlation coefficients ($df=50$ for each; $*P<0.05$, $**P<0.01$) for behaviors recorded during male focal samples and mating success

	Courting	Visiting	Circling	Egg-laying
Threats toward heterospecifics	-0.076	0.225	0.327*	0.345*
Attacks on heterospecifics	-0.181	0.124	0.232	0.031
Threats toward territorial conspecifics	-0.054	0.032	0.045	0.011
Attacks on territorial conspecifics	-0.248	0.218	0.161	-0.014
Threats toward non-territorial conspecifics	0.089	0.225	0.124	-0.030
Attacks on non-territorial conspecifics	0.023	0.044	0.134	-0.061
Foraging	-0.242	-0.210	-0.335*	-0.130
Sand movement	0.071	-0.318*	-0.479**	-0.346*

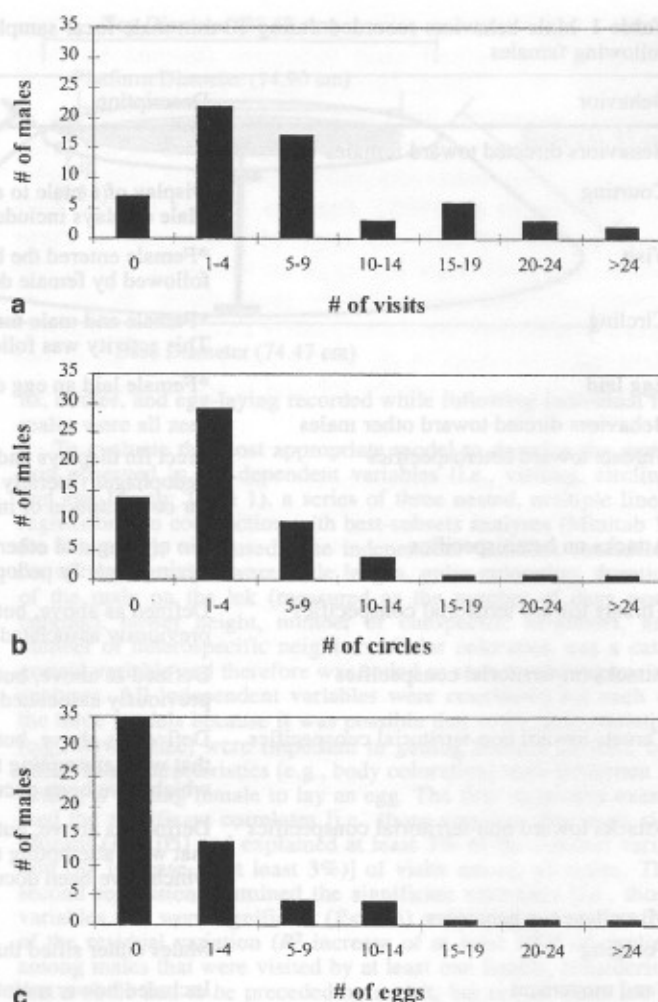


Fig. 3 The skewed distribution of mating success on the lek as shown by the number of males that attained different levels of visits (a), circles (b), and egg-laying (c) from females

Discussion

Our results are congruent with previous studies of other cichlid leks in that both bower size and position strongly influence the number of females that visit a male (McKaye et al. 1990; McKaye 1991). Exaggerated visual cues have also been found to influence female mate choice in many other lekking organisms (see

Höglund and Alatalo 1995 for a review). In addition, the importance of position and density within a lek has been demonstrated in many other organisms (again see Höglund and Alatalo 1995 for a review). On this *L. c.f. parvidens* lek, visits was the only significant correlate with circling and, likewise, circling was the only significant correlate with egg-laying. None of the other male characteristics that we measured (e.g., gular color, standard length) were significant in explaining variation in male mating success as measured by visits, circling, or egg-laying. However, given the reduction in our ability to explain the variation in egg-laying ($R^2=19.8\%$, as compared to $R^2=54.3\%$ for visits and $R^2=78.9\%$ for circles; Table 2), it seems plausible that females are using additional cues (e.g., courtship vigor, overall body coloration) that we failed to measure, when in close proximity to the males. Dual sets of mating criteria have been demonstrated in many lekking organisms (e.g., Andersson 1989; McDonald 1989; Gibson and Langen 1996). Alternatively, there may be no additional female selection after visiting and circling with a male, but simply that a small proportion of females were ready to spawn.

We found several interesting relationships between the male behaviors and mating success recorded during the male focal samples. The negative correlations between visits/circles/egg-laying and sand movements as well as foraging (Table 3) imply that during times of reduced female attention, males engage in other maintenance activities. The positive correlation between circling/egg-laying and heterospecific threats can be interpreted as the final stages of reproductive activity drawing the attention of heterospecifics (which were primarily pedophages; Table 1).

Based on these study results, we can speculate about the explanation for females' selection of males defending tall, shoreline bowers. Bower height explained the largest portion of the variation in female visits (coefficient of partial determination was 34.8). Taller bowers may simply catch the attention of more females because they are more conspicuous. However, bower maintenance was the most frequent male behavior (some males engaged in more than 50 sand movements per observation period), and it therefore seems plausible that females may be using bower size as an indicator mechanism, assuming of course that the ability to maintain large bowers indicates heritable condition and viability (Andersson 1994). Bower position also strongly influenced the number of female visits (coefficient of partial determination was 19.5). High density, shoreline locations may be advantageous from a reduced egg predation standpoint. Pedophages are a threat to females on this lek, and the final stages of reproductive activity drew the attention of heterospecifics (based on the significant, positive correlation between heterospecific threats and circling/egg-laying discussed above). It may be that choosing mates in an area of dense breeding activity reduces the probability of any individual female's eggs being eaten (i.e., a dilution effect). This implies that direct selective forces, such

as reduced egg predation, may influence mating preferences. Multiple selection forces are evidently influencing the dynamics of this system, as is the case on many leks (Höglund and Alatalo 1995).

The leks of Lake Malawi are an ideal forum for the study of sexual selection. The results of this study, in conjunction with previous work, provide the baseline data necessary for this line of investigation. Further studies isolating additional male characteristics (e.g., courtship vigor, body coloration) might be particularly telling in terms of which models of sexual selection might be most relevant. Furthermore, a closer examination of predation pressure will be critical to differentiate the relative importance of the selection forces acting on this system.

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