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Hotshots, hot spots, and female preference: exploring lek formation models with a bower-building cichlid fish

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In many animals, males congregate in leks that females visit for the sole purpose of mating. We observed male and female behavior on 3 different-sized leks of the bower-building cichlid fish *Nyassachromis* cf. *microcephalus* to test predictions of 3 prominent lek models: the "hotshot," "hot spot," and "female preference" models. In this system, we were able to refine these predictions by distinguishing between indirect mate choice, by which females restrict their set of potential mates in the absence of individual male assessment, and direct mate choice, by which females assess males and their territories through dyadic behavioral interactions. On no lek were males holding central territories favored by indirect or direct mate choice, contrary to the prediction of the hotshot model that leks form because inferior males establish territories surrounding hotshot males preferred by females. Average female encounter rate of males increased with lek size, a pattern typically interpreted as evidence that leks form through female preference for lekking males, rather than because males congregate in hot spots of high female density. Female propensity to engage in premating behavior once courted did not increase with lek size, suggesting female preference for males on larger leks operated through indirect choice rather than direct choice based on individual assessment. The frequency of male–male competitive interactions increased with lek size, whereas their foraging rate decreased, implying a cost to males maintaining territories on larger leks. Together these data most strongly support the female preference model, where females may benefit through indirect mate choice for males able to meet the competitive cost of occupying larger leks. *Key words:* bowers, cichlids, direct mate choice, indirect mate choice, lek formation models. *[Behav Ecol 20:609–615 (2009)]*

Lekking animals are model systems for studying sexual selection because females often display strong preference for certain males and/or locations within a lek, despite receiving no obvious material benefit from doing so (Höglund and Alatalo 1995). Research on lek systems has focused on 2 related issues: reconciling the relationship between female mate choice, male mating skew, and the maintenance of genetic variance, that is, the lek paradox (Reynolds and Gross 1990; Kirkpatrick and Ryan 1991; Mackenzie et al. 1995; Rowe and Houle 1996; Tomkins et al. 2004; Hamilton et al. 2006), and developing and testing models to explain why leks form (Gibson et al. 1990; Höglund and Alatalo 1995; Isvaran and St Mary 2003; Jiguet and Bretagnolle 2006). One successful approach for assessing such models is to test their mechanistic predictions by comparing male and female behavior within and between leks of varying size (Shelly 1990, 2001; Alatalo et al. 1992; Apollonio et al. 1992; Aspi and Hoffman 1998; Höglund et al. 1998; Widemo 1998; Jones and Quinnell 2002; Isvaran 2005). Here we apply this approach to a bower-building cichlid fish from Lake Malawi, Africa, to test predictions of 3 prominent lek formation models (Höglund and Alatalo 1995): the female preference, hotshot, and hot-spot models.

The female preference model was formalized by Bradbury (1981) and posits that males aggregate on leks because females prefer to mate with clustered males. Such preference may benefit females by reducing predation risk, reducing the cost of comparing potential mates, or because only "better" males can meet the cost of attending larger leks (Bradbury 1981; Reynolds and Gross 1990). Males form leks when the costs associated with clustering (e.g., increased territoriality or reduced foraging rate) are outweighed by the benefits of female preference. The hotshot model (Beehler and Foster 1988) invokes female preference for particular males rather than clustered males in general. Leks form when inferior males establish territories surrounding competitively dominant "hotshot" males, which increases their chance of intercepting females seeking such males. The hot-spot model differs in that it does not invoke female preference for clustered males in general or dominant males in particular but instead proposes that males form leks in hot spots with high concentrations of females (Bradbury and Gibson 1983).

The predictions of the 3 models can be refined by distinguishing between direct and indirect female mate choice (Wiley and Poston 1996; Sæther et al. 2005). Defining mate choice as any behavior that reduces a female's pool of potential mates, direct mate choice, the focus of most sexual selection research, involves direct assessment and discrimination among males based on phenotypic traits such as feather length, call volume, or color. By contrast, indirect female choice results from behaviors that reduce the set of potential mates without discrimination among individual males by the

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female. Such mate choice can occur if females prefer to mate in a certain location or at a certain time, and the outcome of indirect female choice is typically governed by male–male competition. Importantly, direct and indirect mate choice may act in concert or opposition, and when females prefer competitively dominant males through direct choice, distinguishing between the 2 can be difficult (Wiley and Poston 1996; Sæther et al. 2005; Wong and Candolin 2005; Genner et al. 2008).

The distinguishing predictions of the hot-spot model arise because it does not invoke female preference, through indirect or direct mate choice, for males in different-sized leks or for different males within leks. If males have accurate information about the distribution of females and the cost of occupying different-sized leks is constant, the distribution of males should match that of females (Bradbury and Gibson 1983). As a result, the average female encounter rate of males should not vary with lek size. Furthermore, because direct female choice should not vary across leks, the willingness of females to mate once encountered should not vary with lek size. The hot-spot model does not make explicit predictions about variation in male mating success within leks.

The key general prediction of the female preference model is that male reproductive success increases with lek size, a pattern which can arise through indirect and/or direct mate choice (Bradbury 1981). If female preference for larger leks results from indirect choice, the model predicts that males in larger leks should enjoy a reproductive advantage because females prefer to visit larger leks. If females prefer males on larger leks through direct choice, the model predicts that females, once they have visited a lek, will be more likely to mate with males on larger leks. Average male mating success can increase with lek size through either mechanism, and the relative importance of each may vary between and within species. Like the hot-spot model, the female preference model makes no explicit predictions about variation in male mating success within leks.

The hotshot model explicitly predicts how male mating success should vary within leks. In introducing the model, Beehler and Foster (1988) invoked male–male competition and "default" female choice for dominant males able to defend favored territories. Whether females prefer hotshot males through indirect and/or direct choice clarifies the model's 2 key predictions (Hovi et al. 1994). Within a lek, the most successful males should occupy central/high-quality territories around which inferior males congregate. Females may prefer to visit such males through indirect choice if, for example, more central males happen to encounter a greater number of receptive females. Alternatively, females may prefer to mate with such males through direct choice after assessment of a range of males across the lek. The second prediction, that the most successful males should occupy the largest leks, can be met through either form of mate choice; the hotter the shot the more females and males it should attract and the larger lek it should support (Beehler and Foster 1988).

Here we test these predictions using male and female behavior from 3 different-sized leks of *Nyassachromis* cf. *microcephalus*, a bower-building cichlid fish endemic to Lake Malawi, Africa. Three features of the system make it well suited for a comparative study of lek formation models. First, males occupy easily quantified territories (bower size and location) and engage in a range of behaviors with obvious energetic/reproductive costs and benefits. Second, unlike many systems, males do not actively search for females but instead reliably court those swimming past their territory. As a result, within and between lek variation in male courtship rate is primarily a consequence of indirect female choice. Finally, after male courtship initiation, a predictable series of discrete interactions takes place. During this series, females decide whether to proceed to the next step of the series, and each of these decisions involves direct female choice based on assessment of individual males and their territories.

MATERIALS AND METHODS

Study system

We studied 3 *N.* cf. *microcephalus* leks in the Cape Maclear area of southern Lake Malawi (Table 1; Figure 1). The species is a small (maximum total length 10–13 cm) planktivore that breeds in near-shore sand habitats between 3 and 20 m depth (Konings 2007). Males defend territories centered on volcano-shaped bowers from which they court passing females. Prior research on lekking cichlids suggests female encounter rate and mating success increases with territory quality (bower size) and position (centrality) (McKaye et al. 1990; Kellogg et al. 2000; Genner et al. 2008). Only recently, however, have there been attempts to distinguish between the roles of indirect and direct mate choice in bower-building cichlids (Stauffer et al. 2005; Genner et al. 2008), and to our knowledge, this is the first study to use the system to test predictions of lek formation models.

Behavioral observations

Observations were conducted using SCUBA between 2 and 8 September 2005 during 1 of the peak breeding seasons (McKaye 1983). Prior to collecting behavioral data, we conducted preliminary surveys of the size and shape of each lek and used rope to establish 2 orthogonal axes for orientation and subsequent mapping (Figure 1). We collected behavioral data during the daily period of peak breeding activity, between 0800 and 1100. Prior to formal observations, observers calibrated behavioral classifications by watching the same individual focal males. During dives, each observer selected males haphazardly while moving inward or outward along an axis to ensure that we observed males from throughout the lek. Each male was observed once for a single 10 min period (Kellogg et al. 2000), after which the bower was marked with numbered flag.

During each observation period, we recorded the number of times the focal male engaged in the following behaviors: initiation of courtship with a passing female, aggression toward conspecific male, aggression toward a heterospecific male, bower-building activity (picking up and moving sand by mouth), and foraging in the water column. Courtship follows a predictable sequence that females can terminate at any stage. After courtship initiation by a male, females follow the male to

Table 1

Characteristics of the 3 study leks. Numbers in parentheses are one standard deviation of the mean.

	Lek		
Date	Domwe	Thumbi West	Msaka
Lek area (m^2)	2760	1335	278
Total bowers on lek	26	318	77
Average depth of lek (m)	6.8 (2.1)	7.9 (1.2)	3.0 (0.1)
Bower density ($\#/m^2$)	0.009	0.24	0.28
Focal males observed	14	50	34
Average number of behaviors	28.1 (15.8)	31.0 (12.5)	24.1 (13.7)

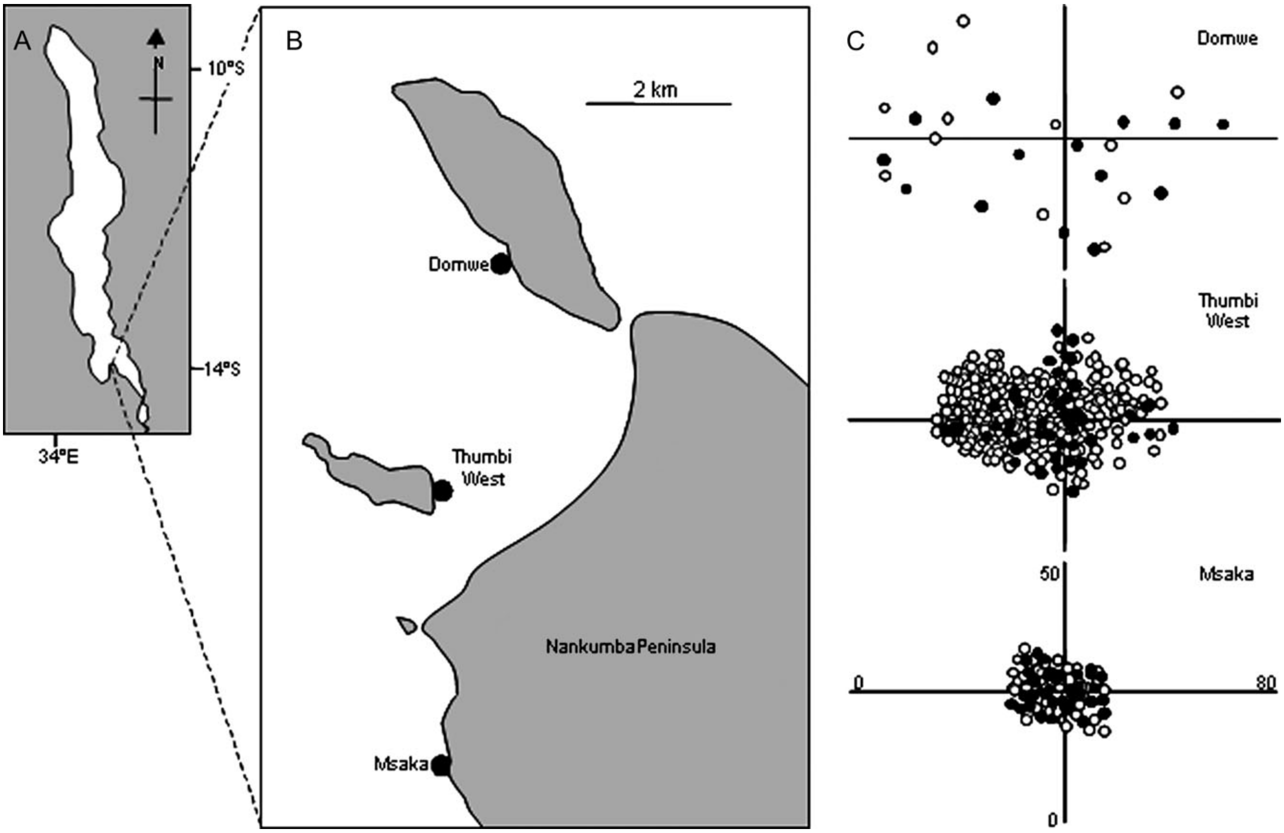

Figure 1
The study site: (a) Lake Malawi, (b) the 3 study leks in Lake Malawi National Park, and (c) the distribution of bowers within each lek. Closed circles represent locations of bowers from which observational data were collected. Leks are shown at the same scale (80 × 50 m) to highlight differences in area and the number and density of bowers. See Table 1 for a description of the leks.

the bower, visit the bower platform, engage in circling bouts with male on the bower platform, and finally lay one or more eggs that are collected in the mouth of the female as they are fertilized by the male.

We make 2 assumptions in our analyses and interpretation of the behavioral data. The first is that the number of male courtship initiation events accurately reflects female visitation rate. This requires that males reliably court females passing their territory. We confirmed this by following 21 females as they entered and traveled through one of the leks (Thumbi West). The females passed 162 males, 142 of which courted. Of the 20 males that did not court, 9 were engaged with other females; thus, females were courted by 93% of the available males whose territories they passed. Because egg laying is rarely observed during focal male observations (we observed only 4 spawning events in 16.3 h of observations), the second assumption is that the number of courtships, follows, bower visits, and circling events provide increasingly accurate proxies of male reproductive success. This assumption has been convincingly confirmed in previous studies of Lake Malawi bower-building cichlids (Kellogg et al. 2000; Genner et al. 2008).

Male territory: bower size and location

After behavioral observations, we recorded the coordinates of every bower. For bowers associated with male observations, we measured twice (at 90° angles) the same 6 bower dimensions as Kellogg et al. (2000). Variation in bower size and shape within each lek (3 independent analyses) was summarized using principal components analysis on the covariance matrix of the 12 measurements (Supplementary material). Scores along the first principal component axis (PC1), which explained between 68% and 75% of total variation within leks, were used as measures of bower size. We calculated 2 positions (scaled 0–1) for each male's bower: the distance from the "geographical center" of the lek, where the origin (0,0) is defined as half the difference between the maximum and minimum *x*–*y* coordinates and the distance from the "density center" of the lek, where the origin is defined as the mean value of all *x*–*y* coordinates. The 2 distance measures were highly correlated in all 3 leks ($r = 0.82$–0.99), and results did not depend on the measure used, so we present results using geographical distance throughout.

Analyses

For each lek, we constructed a Spearman rank correlation matrix of the relationships between bower position, bower size, the 5 male behaviors, and female follows, enters and circles (Supplementary material). The total number of behaviors varied widely among males ($n = 98$, mean $= 28.2$, range: 4–62) but did not differ across the 3 leks ($F_{2,95} = 2.73$, $P = 0.07$; Table 1). Because testing the predictions of the models requires considering the absolute rather than relative number of behaviors, we analyzed variation in the frequency of each male behavior (number per minute) independently. For example, a male for which 50% (5/10) of behaviors are courtships could encounter more, not less, females than a male for which 80% (4/5) of behaviors are courtships.

To distinguish between the main predictions of the hot-spot and female preference models, we first tested whether female encounter rate increased with lek size using single factor analysis of variance (ANOVA). To determine if an increase in female encounter rate with lek size came at a cost, we used the same model to test whether the cost of territory defense and maintenance increased, while feeding rate decreased, with lek size. Recognizing that different behavioral events falling under the same category may vary in their cost/benefit, we estimate these costs and benefits using the frequency of intraspecific and heterospecific aggression (territory defense), bower-building activity (territory maintenance), and foraging.

The first ANOVA model above distinguishes between the principal prediction of the hot-spot model and the first prediction of the female preference model that per capita male mating success increases through indirect choice because females prefer to visit larger leks. To investigate the second prediction, that courted females prefer through direct choice to mate with males on larger leks, we tested for lek effects using analyses of covariance (ANCOVAs) with follows, enters, and circles as response variables and courtship as a covariate. For these models, we use only males that courted at least one female. If courted females prefer to mate with males on larger leks through direct choice, we expect significant lek effects after controlling for variation in courtship rate among males. At each stage of the behavioral sequence, a proportion of females abandon the male. As a result, uninformative zeros accumulate in the response variables of these models (e.g., if no females followed a particular male, it is meaningless to use that male to analyze females' choice to enter a bower). We thus repeated the ANCOVAs on enters and circles using the preceding behavior as the covariate and including only those males that engaged in at least one such behavior. These models have smaller sample sizes but provide more specific tests of whether direct female mate choice during different stages of the mating sequence varies with lek size.

Before testing the specific predictions of the hotshot model, we first tested the possibility that females prefer to visit males based on aggressiveness, territory location, and quality, for each lek individually using multiple regression on courtship rate with conspecific attack rate, bower location, and bower size as predictor variables. To test the prediction that courted females prefer hotshot males through direct choice, we repeated the analyses using only males that courted at least once with follows, enters, and circles as response variables and courtship number as an additional predictor variable. If hotshot males are preferred based on aggressiveness and/or territory location/size, then these variables should explain variation in the response after controlling for encounter rate. As above, we repeated these analyses with the previous behavior as the covariate using only those males with at least one such behavior (this sequence of models loses power rapidly for the Domwe lek; Table 1).

We tested the second prediction of the hotshot model, that the most successful males should be on the largest leks, by selecting from each lek the 5 males with the most follows, enters, and circles (these were generally, but not always, the same males). For each of these increasingly accurate predictors of mating success, we used Kruskal–Wallis (K-W) non-parametric ANOVA to test whether estimates of mating success increased with lek size.

RESULTS

We begin by describing the accumulation of male mating skew from courtship through circling on the 3 leks (Figure 2). Whereas 90% of males courted at least one female on the 2 larger leks, just over half of observed males courted females on the Domwe lek. On all 3 leks, females ignored approximately 70% of courtship events. Once they followed a male, the majority of females (67–83%) visited the bower. Approximately half the females (40–58%) that visited bowers engaged in pre–egg-laying circling. In total, direct female choice resulted in only 8–14% courtship events leading to circling, a percentage that appeared unrelated to lek size.

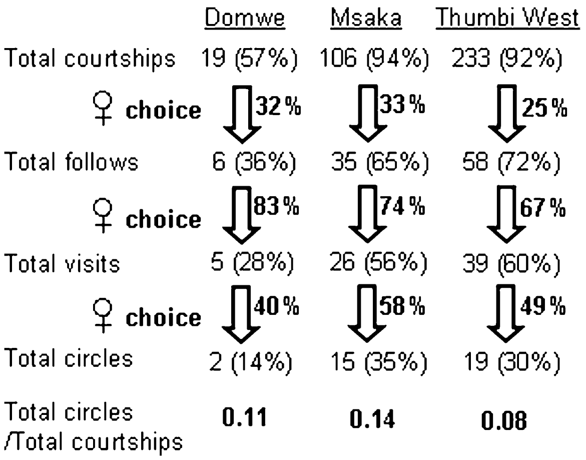

Figure 2
Ethogram summarizing accumulation of mating skew through the courtship sequence on the 3 study leks. For each behavior, we present the total number of behaviors observed and in parentheses the percentage of males accounting for all such behaviors. Bold arrows between behaviors indicate stages of direct female choice, with the percentage of positive responses shown. The bottom line shows the cumulative effect of post-courtship direct female choice on the accumulation of mating skew in each lek.

Contrary to the prediction of the hot-spot model and in support of the first prediction of the female preference model, male courtship rate increased markedly with lek size (ANOVA, $F_{2,95} = 11.99$, $P < 0.001$; Figure 3). The cost of defending territories against conspecific intruders also increased with lek size ($F_{2,95} = 11.54$, $P < 0.001$), whereas heterospecific attack rate did not vary with lek size ($F_{2,95} = 1.22$, $P = 0.3$). The cost of territory maintenance (bower building) did not vary with lek size (ANOVA, $F_{2,95} = 1.49$, $P = 0.07$); however, males on the Domwe lek foraged nearly 10 times more often than males on the 2 larger leks (ANOVA, $F_{2,95} = 7.42$, $P = 0.001$).

Though females prefer males on larger leks through indirect choice, contrary to the second prediction of the female preference model, courted females showed no tendency to prefer males on larger leks through direct mate choice. After controlling for courtship rate and including only those males that courted at least 1 female, females were not more likely to follow, enter, or circle with males on larger leks (ANCOVAs: all lek effects $F_{2,82} < 0.39$, $P > 0.68$). Sequential ANCOVAs using the preceding behavior instead of courtship rate as the controlling covariate confirmed these results. Across the leks, courtship predicted follows ($F_{1,82} = 21.22$, $P < 0.001$), follows predicted visits ($F_{1,59} = 46.52$, $P < 0.001$), and visits predicted circles ($F_{1,49} = 50.07$, $P < 0.001$). In no model was lek significant ($P > 0.6$). The absence of female preference through direct choice resulted in the relative encounter rate advantage enjoyed by males on larger leks decreasing through the courtship sequence (Figure 4).

We found little support for the prediction of the hotshot model that females prefer males based on territory location, quality, or aggressiveness. Bower location was negatively correlated to conspecific attack rate on the 2 large leks (Thumbi

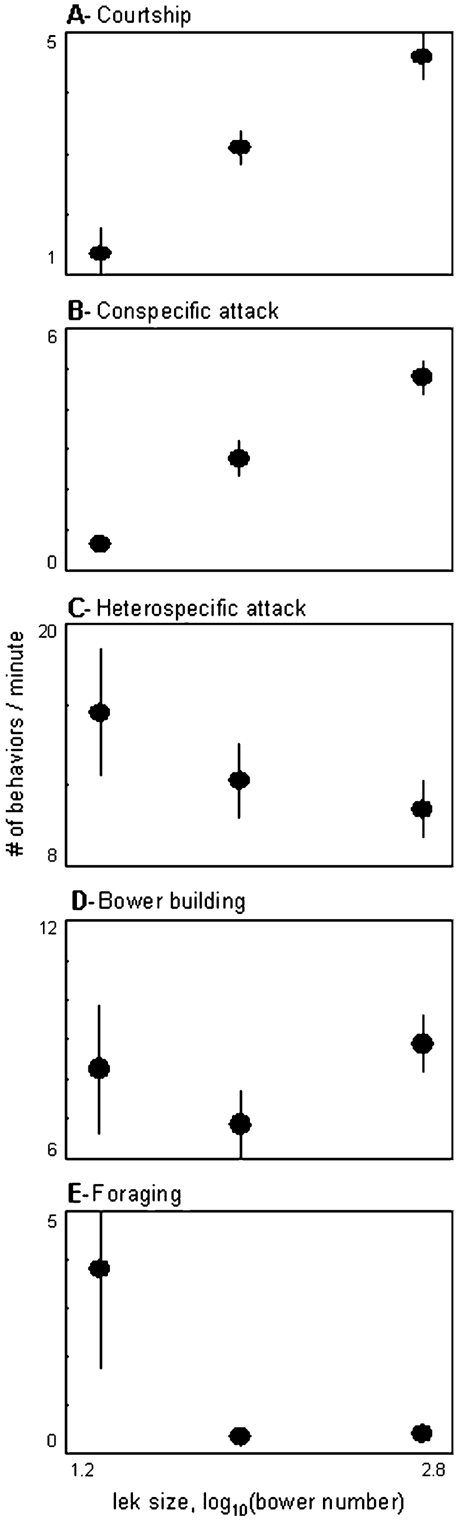

Figure 3
Average frequencies (±standard error) of behaviors of observed males in the 3 study leks.

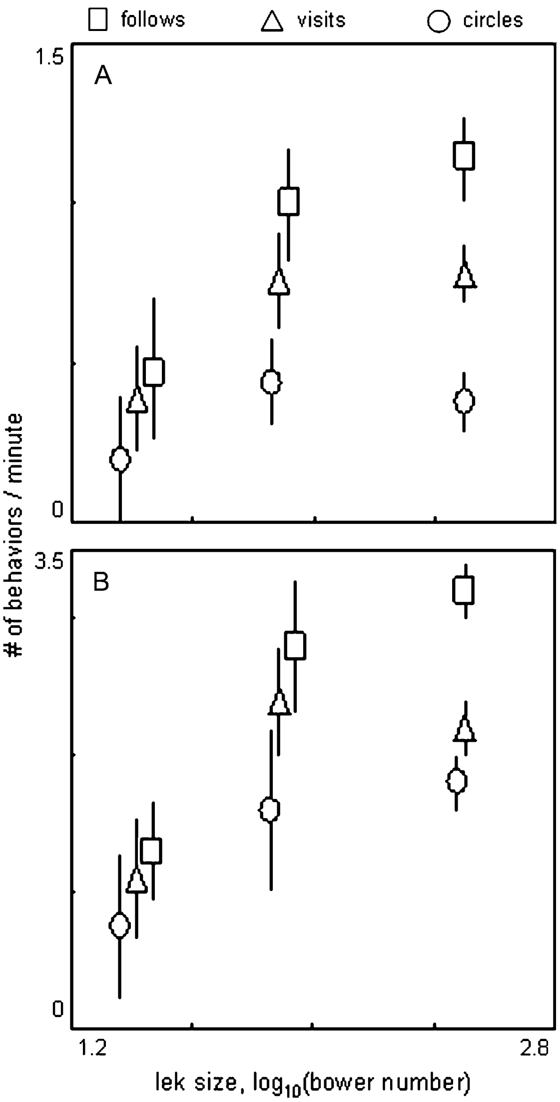

Figure 4
Average frequencies (±standard error) of estimates of reproductive success among (A) all observed males and (B) the 5 top ranking males in the 3 study leks. The points have been jogged along the *x* axis to make the error bars visible.

West: $r_s = -0.32$, $P < 0.05$; Msaka: $r_s = -0.34$, $P = 0.05$), consistent with there being a cost to holding a central territory that hotshots must bear (Supplementary material). However, within leks, bower position, bower size, and intraspecific attack rate were unrelated to male courtship initiation rate (all multiple regression coefficients, $P > 0.26$), suggesting neither territory position/quality nor male aggressive activity affected variation in encounter rate through altering female search patterns. Furthermore, none of these variables was significantly correlated with any subsequent proxy of male reproductive success (Supplementary material). Stepwise regression revealed that after controlling for courtship rate, females preferred to follow males holding territories with large bowers on only the Thumbi West lek (partial coefficient for PC1: $t = 2.2$, $P < 0.05$; Supplementary material). Multiple regression models on visits and circling using the previous behavior as the controlling variable provided no evidence for direct female choice based on bower location, bower size, or male aggressiveness.

We found consistent but statistically variable support for the second prediction of the hotshot model, that the most successful males occupy the largest leks (Figure 4). Considering only the 5 males with the highest counts from each lek, female encounter rate (K-W = 12.2, $P < 0.01$), female follows

(K-W = 8.1, $P < 0.05$), visits (K-W = 5.1, $P = 0.08$), and circles (K-W = 3.7, $P = 0.16$) all increased with lek size.

DISCUSSION

We found strong evidence that the per capita female encounter rate of males increased with lek size. This pattern is common (Shelly 1990; Alatalo et al. 1992; Apollonio et al. 1992; Balmford et al. 1992; Aspi and Hoffman 1998; Höglund et al. 1998), but not ubiquitous in lekking species (e.g., Deutsch 1994; Shelly 2001; Jones and Quinnell 2002). A positive relationship between female encounter rate and lek size is traditionally interpreted as support for the female preference model (e.g., Alatalo et al. 1992; Aspi and Hoffman 1998; Shelly 2001). Our analysis refines this interpretation by showing that variation in per capita female encounter rate varies with lek size as a result of indirect choice; females may prefer to visit larger leks, but once courted, they do not prefer through direct mate choice to mate with males on larger leks. In systems like ours, where repeated female harassment by the same males is uncommon, it is logical that female preference for larger leks arises through indirect rather than direct mate choice. Larger leks provide females more males from which to choose and shorter travel times between males, increasing the chance and reducing the cost, respectively, of finding acceptable mates (Figure 1; Reynolds and Gross 1990). It is important to appreciate, however, that none of these potential advantages that explain female preference for larger leks through indirect choice requires that direct female mate choice acts to increase average male mating success on larger leks (Kokko et al. 1998).

Our results did not support the prediction of the hot-spot model that males should arrange themselves such that per capita female encounter rate is constant across leks (Bradbury and Gibson 1983). One simple explanation is that males may not have sufficient information to make comparisons because of the distances between leks in our study system (Figure 1). If males do not have knowledge about the distribution of females and relative sizes of different leks, the size of each lek will be determined independently and the hot-spot model cannot apply. Another possibility is that males have such knowledge, but weigh the potential benefits (access to females) against the costs (increase in competition and reduction in foraging) of larger leks and make age or condition-dependent attendance decisions that maximize seasonal or lifetime fitness. Such trade-offs appear common and likely help explain variation in lek size in many systems (Apollonio et al. 1992; Höglund and Alatalo 1995; Aspi and Hoffman 1998; Shorey 2002). Finally, competitive asymmetries may reconcile the hot-spot model with the commonly observed positive correlation between lek size and measures of average male reproductive success. If the increased cost of competitive interactions on larger leks reduces the male density below that predicted by female distribution, average female encounter rate will increase with lek size, even if lek formation is primarily driven by female distribution (Parker and Sutherland 1986; Höglund et al. 1998).

We found only weak support for the predictions of the hotshot model (Beehler and Foster 1988). In both of the larger leks, conspecific attack rate was higher for males with centrally located and large bowers, suggesting a competitive cost to holding such territories (Supplementary material; McKaye et al. 1990; Martin and Genner forthcoming). However, female encounter rate was decoupled from bower position or size, suggesting that males able to secure and defend such territories did not benefit through indirect mate choice during our observation periods. Nor did courted females display a preference through direct mate choice for males holding centrally located territories. We did, however, find evidence on the largest lek that males defending territories with large bowers were favored by the direct choice of females to follow once courted, a pattern consistent with 2 previous studies suggesting that females prefer large bowers through direct choice (McKaye et al. 1990; Stauffer et al. 2005). Considering only the most successful males from each lek, the different proxies of reproductive success were consistently higher for the 2 larger leks. Although consistent with the hotshot model, experimental manipulations will be required to determine whether the most successful males actually attract the larger leks or whether the relative reproductive success of dominant males increases with lek size (Beehler and Foster 1988).

That males holding central bowers did not enjoy a reproductive advantage is contrary to the pattern observed on leks in general (Fiske et al. 1998) and studies of bower-building cichlids in particular. Kellogg et al. (2000) found that in *Lethrinops parvidens* males holding tall bowers and those in high-density areas (in their lek along the shoreline rather than in the middle) had higher female encounter rates. Using a similar analytical framework as here to study a lek of *Hemitilapia oxyrhynchus*, Genner et al. (2008) found that males occupying central bowers benefited through higher visitation rates and thus indirect choice, but not direct choice.

The apparent decoupling of bower location, bower size, and female encounter rate in this study underscores the broader issue of how the relationships between lek size, male behavior, and (in)direct female choice may depend on the sizes of leks studied. We studied leks varying in size by more than 2 orders of magnitude and found that average female encounter and conspecific attack rates increased with lek size but that within leks female encounter rate did not depend on territory position. Because the relationship between the frequency of a behavior and lek size may not be linear across all lek sizes, had we studied 3 different-sized leks at one end of the range observed in nature, we may have failed to detect the strong relationship between female encounter rate and lek size. Additionally, it is possible that territory position may affect female encounter rate on "average" leks but not on small/low density leks where different males are rarely in visual contact or on large/dense leks where females must pass the territories of many males before reaching the lek center. More generally, sexual selection and lek research stands to benefit from more empirical and theoretical work investigating how lek size, lek shape, and male density affects the relationships between territory position and quality, female search behavior, indirect mate choice, and direct mate choice.

To conclude, our data suggest that female preference to visit larger groups of males may drive lekking in this system. However, experimental manipulations across multiple leks will be required to unequivocally identify the mechanisms responsible for lekking in this and other bower-building cichlids. Because it is unlikely that any single model provides a general explanation for the formation and maintenance of leks (Widemo and Owens 1995; Fiske et al. 1998; Jiguet and Bretagnolle 2006), the goal of empirical studies should not be to credit lekking to any one model but rather to weigh the relative importance of the mechanisms each invokes. Here we have enhanced the ability of the comparative approach to meet this goal by highlighting the distinction between indirect and direct mate choice. Future theoretical and empirical work aimed at understanding the formation and maintenance of leks will benefit from distinguishing between these different mechanisms of female choice (Sæther et al. 2005).

SUPPLEMENTARY MATERIAL

Supplementary appendices can be found at http://www.beheco.oxfordjournals.org/

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