Unexploited females and unreliable signals of male quality in a Malawi cichlid bower polymorphism

Christopher H. Martin
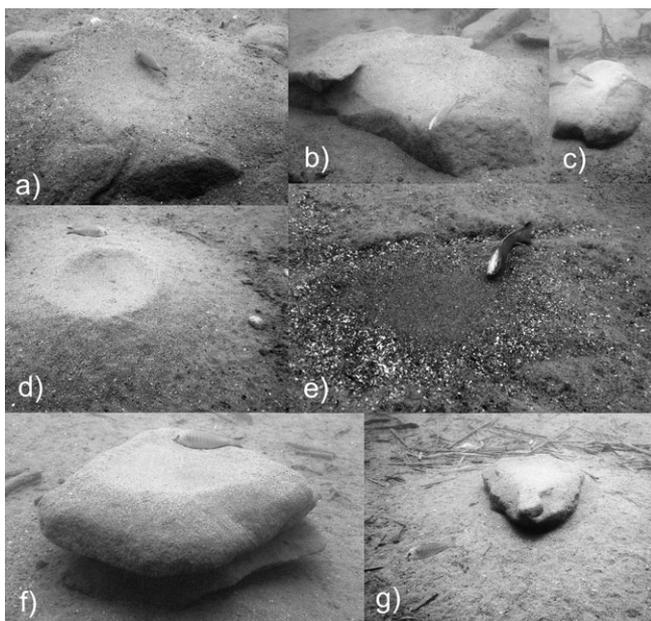Department of Evolution and Ecology, University of California, One Shields Avenue, Davis, CA 95616, USA

Complex signals present 2 outstanding questions: why do they exist and how are they interpreted? Multiple signals can be beneficial for the increased diversity or redundancy of information they convey; however, it is not clear how receivers use this additional information. I investigated a lekking Malawi cichlid fish that builds polymorphic bowers; some males build their sand spawning craters on rock platforms, rather than the sand floor, resulting in increased overall height and reduced construction, maintenance, and competition costs. This suggests that rock bowers are an unreliable signal of male investment. Using field observations and in situ bower manipulations I tested fitness costs, female preferences for bower type, bower height, and male displays, and mechanisms for the maintenance of bower polymorphism. In contrast to predictions, observational and experimental data confirmed that females were more likely to visit rock bowers but did not ultimately lay more eggs there. This indicates that females responded to potentially deceptive rock bower males by advancing to the next stage of courtship but were not ultimately fooled by these deceptive signals. Assessing additional signals during the next courtship stage may allow females to counteract initial sensory exploitation or females may be intentionally increasing their investment in mate assessment in response to deceptive signals. Male bower polymorphism may be maintained by the limited availability of rock platforms; there was no evidence for significant variation in individual female preferences or male bower-building strategies. *Key words:* African cichlid, dishonest signaling, "good genes" models, lek, *Nyassachromis microcephalus*, sexual selection. *[Behav Ecol 21:1195–1202 (2010)]*

Most animal communication involves multiple signals, often in sequential stages or across multiple sensory modalities (Candolin 2003). Complex signals increase display costs for the sender, but they can also more effectively elicit a response from the receiver (Rowe 1999). Numerous efficacy-based hypotheses can explain complex signaling, such as effective signaling across multiple sensory environments or receivers' sensory abilities (reviewed in Candolin 2003; Hebets and Papaj 2005), sensory exploitation of multiple preexisting sensory biases (Ryan et al. 1990), or synergistic effects among signals within a complex display (Patricelli et al. 2003; Byers et al. 2010). Female preferences for multiple signals can also increase offspring fitness by preserving adaptive complexes of male traits that would otherwise be unlinked (Lancaster et al. 2009).

If multiple signals contain information about signaler quality, they can also convey "multiple messages" about different aspects of signaler quality or provide "redundant signals" of overall quality (e.g., Bro-Jørgensen and Dabelsteen 2008; Gibson and Uetz 2008; reviewed in Møller and Pomiankowski 1993; Iwasa and Pomiankowski 1994; Johnstone 1996). These 2 strategies are stable, even with significant costs to mate choice, provided that the costs of displaying individual signals increase at an accelerating rate (Johnstone 1996) or that multiple signals provide independent information about male quality (van Doorn and Weissing 2004).

Females often use multicomponent sexual signals to choose among males, even among species in which the male does not provide direct benefits to the female or offspring (Andersson 1994). In particular, multicomponent signals should be most common in lekking species where male variance in mating success is high and the costs of mate choice are very low (Moller and Pomiankowski 1993). The honesty of sexual signals conveying multiple or redundant messages can be maintained by fitness costs on their expression so that only high-quality males can afford to express them (Zahavi 1975, 1987). Alternatively, Fisherian runaway sexual selection can result in extravagant male sexual traits with no connection to male quality (Fisher 1930). Such unreliable signals of male quality should also proliferate in lekking species because the costs of female choice are low and males can devote all their reproductive effort to extravagant displays (Moller and Pomiankowski 1993). Thus, complex displays and unreliable signals should be common in lekking species, but the dynamics of these signals and their interpretation by females is poorly understood (e.g., Coleman et al. 2004; van Doorn and Weissing 2006).

One benefit of complex displays is that females can improve their mate assessment by discounting unreliable signals in their overall picture of male quality (Candolin 2003; Hebets and Papaj 2005). For example, in red jungle fowl experimental exaggeration of the primary traits that females use to assess males, such as comb length, comb color, and tail size, caused females to switch to alternate sexual signals (Zuk et al. 1992). Similarly, female guppies did not respond to male display rate if it was not supported by orange coloration, an indicator of long-term male quality (Kodric-Brown and Nicoletto 2001). However, these studies were conducted in controlled laboratory trials; in a field setting females have more options than trait switching in response to a deceptive male signal. Females can avoid males displaying conflicting signals entirely (Schluter and Price 1993), or they could invest more time assessing these males using additional criteria in order to determine

their true quality. For example, one intriguing study found that older female satin bowerbirds ultimately based their mating preferences on male display intensity, whereas younger birds responded only to an initial ornament manipulation (Coleman et al. 2004).

Bower-building cichlids in Lake Malawi are an excellent system for studying complex sexual signals. A group of more than 200 species contains males that gather on leks and build elaborate spawning platforms, ranging from volcano-shaped sand mounds to 3 m craters, cleared patches of rock, or sand piles surrounded by numerous satellite mounds (McKaye 1991; Kidd et al. 2006; Konings 2007). These structures are analogous to bowers, the elaborate constructions of bowerbirds that are used to attract mates but do not provide a nest for eggs (McKaye 1991; Borgia 1995; Frith and Frith 2004). In cichlids, bowers provide a site for courtship and spawning in maternal mouthbrooding species (McKaye et al. 1990; McKaye 1991; Karino 1996).

Cichlid bowers play multiple roles in sexual signaling. In most 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; Martin and Genner 2009). Bower height may also signal dominance to other males. Males guarding taller bowers were more aggressive toward other males (McKaye et al. 1990), and field experiments indicated that males placed on shorter bowers were more frequently attacked by neighboring males (Martin and Genner 2009). In some species, males may also compete for the best position in the lek that can result in greater reproductive success (Kellogg et al. 2000; Genner et al. 2008). However, the signaling context of cichlid bowers is still poorly understood. Taller bowers may simply be more detectable to females over longer distances. Bowers may also provide additional functions, such as markers in male–male territorial disputes or protection from egg predators.

Here, I report on a population of Lake Malawi cichlids that build volcano-shaped sand spawning craters on the sand floor (sand bowers) and on raised rock platforms (rock bowers) interspersed throughout the lek (Figure 1). Males may also guard cleared patches on large flat rock slabs (slab bowers) where sand is not readily available for bower building (Figure 1). Thus, 3 discrete bower types occur in a single lek within one interbreeding population (Konings 2007). The high production and competition costs of sand bowers suggest that rock bowers may be less reliable indicators of male investment in bower construction, despite attaining similar heights. Building a new bower on the sand floor requires 2 weeks to reach the average height of bowers on the lek (McKaye et al. 1990). During this construction phase, field experiments have demonstrated that males on shorter bowers experience increased aggression from neighboring males (Martin and Genner 2009) and males guarding shorter bowers have less reproductive success (McKaye et al. 1990; Stauffer et al. 2005; Martin and Genner 2009). Alternatively, initiating a new bower on a rock platform requires less investment in bower construction to reach the average height of bowers in the lek. If there are unequal costs to constructing and defending different bower types, it is unclear what maintains bower polymorphism in this population.

In this study, I tested the following predictions of signaling theory in the context of polymorphic bower construction: 1) the reliability of bower height as a signal of male investment depends on bower type; 2) females should switch to alternate signals of male quality when assessing males on different bower types; and 3) females should prefer bower types which provide more reliable signals of male quality.

Female responses to multicomponent signals are rarely investigated in the field (but see Backwell et al. 2000). In this study, all hypotheses were tested in a natural field setting. I used in situ bower manipulations in addition to male and female focal observations to measure female preferences and the costs of maintenance, territoriality, and egg predation among bower types. Throughout, I recorded 3 components of male courtship (bower type, bower height, and display rate) and male reproductive success during 3 sequential stages of courtship (bower visits, circling bouts, and egg laying).

I also examined hypotheses for the maintenance of male bower polymorphism in this population: 4) polymorphic female preferences for bower type; 5) alternative male bower-building strategies; and 6) limited microhabitat availability. I followed individual females while they assessed males, manipulated substrates to measure male preferences for different bower types, and surveyed rock platform availability.

MATERIALS AND METHODS

Study species and site

Nyassachromis cf. *microcephalus* is a sand-dwelling zooplanktivore with a lake-wide distribution that is heavily exploited by local fishermen in the Cape Maclear region of southern Lake Malawi (Konings 2007). Males gather in leks and build volcano-shaped sand bowers, often defending the same bower for many months (CHM pers. obs.). Females cruise the lek in search of mates and often mate with multiple males. Courtship occurs in 3 stages, each of which may be terminated at any time by the female. First, while a female is being courted by many males, she may choose to follow one of these displaying males to his bower and rest on his spawning platform (female bower visit). Next, the male quivers rapidly in front of the female and the pair, positioned head to tail, swim tight circles around the spawning platform (circling bouts). Finally, during these circling bouts, the female lays one or more eggs on the spawning platform, which are fertilized by the male and collected in her buccal cavity. The pair may continue spawning at this point or the female may leave and visit additional bowers.

Figure 1
Examples of (a)–(c) rock bowers, (d) sand bowers, (e) slab bowers, and (f)–(g) bowers rebuilt in situ on movable rock platforms for field manipulations of bower type.

The study lek (lat 14°01′22.7″S, long 34°49′23.5″E) was located east of Mitande Rocks at Thumbi West Island, Cape Maclear, Malawi (Supplementary Figure S1). All fieldwork was completed by the author while scuba diving between August and October 2006 during the annual peak breeding season (McKaye et al. 1990). All male and female focal observations were conducted between 700 and 1200 h during the period of highest reproductive activity on the lek and recorded in waterproof notebooks (J.L. Darling Corporation, Tacoma, WA).

Male focal observations

Males guarding bowers (territorial males) were observed for 10 min each ($n = 127$). During that time, I recorded the frequency of the following behaviors: 1) bower building (transporting one mouthful of sand to the bower or removing one mouthful of sand from the bower platform), 2) aggression between neighboring territorial males (rapid long-distance charges that may result in contact), 3) male courtship displays (alternating quivering lateral displays to female), 4) total number of females courted, and 5) total number of female bower visits. If courtship proceeded to the next stage during a bower visit, I recorded the frequency of circling bouts, the number of eggs laid, and whether the pair was interrupted by specialist egg-stealing cichlids invading the bower platform (e.g., *Protomelas insignis*, *Otopharynx ovatus*; Konings 2007; see additional details in Supplementary Material). Bower type was recorded as sand, rock, or slab, and bower height was determined from the average of 2 measurements at 90° from one another.

Female focal observations

Females were followed individually as they searched the lek for mates ($n = 167$). Observations were made from approximately 1.5 m above the focal female while scuba diving. Female focal observations were sampled in the same time period as male focal observations during morning hours from the months of September–October during the peak annual breeding season. Focal females were chosen by following the first female actively inspecting or visiting bowers on the lek while swimming transects within the lek. An observation ended when the female left the lek, ceased actively searching for mates, or if the identity of the focal female became uncertain. Females were not marked in any way but repeated observation of the same female was unlikely due to the large population size (thousands of females aggregated around this lek) and high turnover of females actively visiting the lek.

For each courting male in the female's search path, I recorded his bower type, number of displays, and whether the female chose to visit his bower. Males that did not make at least one display toward the female were excluded. During bower visits, circling bouts, eggs laid, and egg-predation attempts were recorded as described above. A subset of bowers ($n = 160$, partially overlapping with the labeled bowers from male focal observations) was individually labeled, and their bower dimensions were measured (as described above) at least twice during the 2-month period of female focal observations. Bower labels were also recorded during female observations in order to tally the reproductive success of these males.

Field manipulation of bower type

Bower type was experimentally manipulated in the field while holding the territorial male, bower height, and location constant. Following an initial focal observation of a male guarding an unmanipulated sand bower, I rebuilt his bower in situ as either a rock or a sand bower (Supplementary Material). Each male ($n = 32$) was observed once on his original sand bower, at least twice on a rebuilt sand bower, and at least twice on a rebuilt rock bower. Treatment order was alternated between males and had no effect on female bower visits (2-way analysis of variance [ANOVA], $F_{1,61} = 0.149$, $P = 0.701$).

Reliability of bower height as a signal of male investment among bower types

To measure the relationship between bower height and male investment, I compared the benefits and costs of guarding different bower types. First, I compared the average height of sand spawning platforms and rock platforms; the overall height of sand, rock, and slab bowers; and the frequency of bower-building behaviors using Welch's ANOVA for unequal variances. I compared bower-building behaviors between manipulated bowers using a paired t test. Second, I compared the frequency of territorial male aggression among males on each bower type using the Kruskal–Wallis test or the Wilcoxon sign-rank test. Third, I estimated egg predation rates among bower types by comparing the frequency of invasion by egg predators during spawning using a likelihood ratio test. All statistical tests were performed using JMP 8.0 (SAS Inc., Cary, NC).

Female trait switching while assessing males on different bower types

I used an analysis of covariance (ANCOVA) model to test the association of the explanatory variables of bower height, male displays per female, and bower type (rock or sand) with the dependent variable, the proportion of female visits. Interaction terms between bower type and bower height or male displays were also included in the model. Female trait switching would be supported by significant interactions between bower type and bower height and bower type and male displays in the model. Data from male and female focal observations were pooled for this analysis (See additional details in Supplementary Material).

Overall female preference for bower type

I compared female preferences for rebuilt rock or sand bowers using the Wilcoxon sign-rank test. To compare female preferences for bower type during field observations, I calculated the difference between the observed number of visits to each bower type and the expected number for each female focal observation. The expected number was equal to the proportion of each bower type encountered multiplied by the total number of bower visits made by each female. Male displays, circling bouts, and eggs laid were compared with the expectation in the same way based on bower encounter rates for each female. For each comparison, the difference between observed and expected frequency was compared among bower types using Welch's ANOVA for unequal variances.

Female preference polymorphism for bower type

I performed simulations in R (R Development Core Team 2010) to test for significant variation in individual female preferences for bower type (Supplementary Materials).

Alternative male bower-building strategies

To determine if males exhibited substrate preferences for initiating their bowers, I presented rock and sand substrates simultaneously to territorial males in the field and recorded on which substrate the territorial males chose to rebuild their spawning platforms (Supplementary Material).

To determine if males preferred to build on raised rock platforms or the sand floor, I leveled 4 sand bowers in an entirely sandy region of the lek and placed 4 new rock platforms throughout the same region. The following day I recorded whether new territorial males built their bowers on these rock
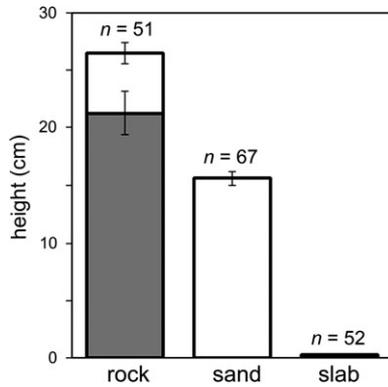
Figure 2
Mean (±standard error) height of sand spawning crater (□) among bower types and rock platform height of rock bowers (■).

platforms or on the sand floor. This manipulation was repeated twice in the same region to avoid disturbing large areas of the lek. This leaves open the possibility of pseudoreplication if the same males returned to this region twice ($n = 4$ instead of $n = 8$); however, this was unlikely due to the large number of mature males without bowers roaming the lek (1.9 ± 0.23 [mean ± standard error] males observed per 10-min focal period).

Microhabitat availability
The occupancy of rock platforms suitable for bowers was compared between sandy regions of the lek and adjacent rocky regions at similar depth (Supplementary Figure S1).

RESULTS

Reliability of bower height as a signal of male investment

There were clear benefits for males to initiate their bowers on rock platforms. First, the rock platforms supporting bowers were significantly taller than sand bowers (Figure 2; Welch's $t = 2.895$, $n = 118$, $P = 0.0053$), and the sand piles transported to the top of these rocks were also significantly shorter than sand bowers (Figure 2; Welch's $t = 9.457$, $n = 118$, $P < 0.0001$), indicating a lower investment in constructing taller bowers. Second, rock bowers required significantly less maintenance than sand bowers (Figure 3; field observations: Welch's ANOVA, $F_{1,87} = 4.097$, $P = 0.046$; in situ bower manipulations: paired $t_{31} = 2.333$, $P = 0.026$).

I found no strong evidence of increased competition or predation costs for males guarding rock platforms. During field observations, rock bower males were not significantly more aggressive toward neighboring territorial males (Figure 3d; Kruskal–Wallis test, $\chi^2 = 0.736$, degrees of freedom [df] = 2, $P = 0.692$). There was a nonsignificant trend of neighboring territorial males displaying more aggression toward rock bower males (Figure 3d; Kruskal–Wallis test, $\chi^2 = 5.784$, df = 2, $P = 0.056$). However, after bower manipulation, neighboring territorial males did not change their level of aggression toward the same male guarding a rebuilt rock or sand bower (Figure 3b; Wilcoxon sign-rank test, $Z_{31} = 53$, $P = 0.175$). Finally, the frequency of bower invasion by egg-stealing fishes during courtship was not significantly different among rock (4.2%, $n = 270$), sand (6.4%, $n = 217$), or slab (2.6%, $n = 391$) bowers (likelihood ratio test, $\chi^2 = 3.55$, $P = 0.170$).
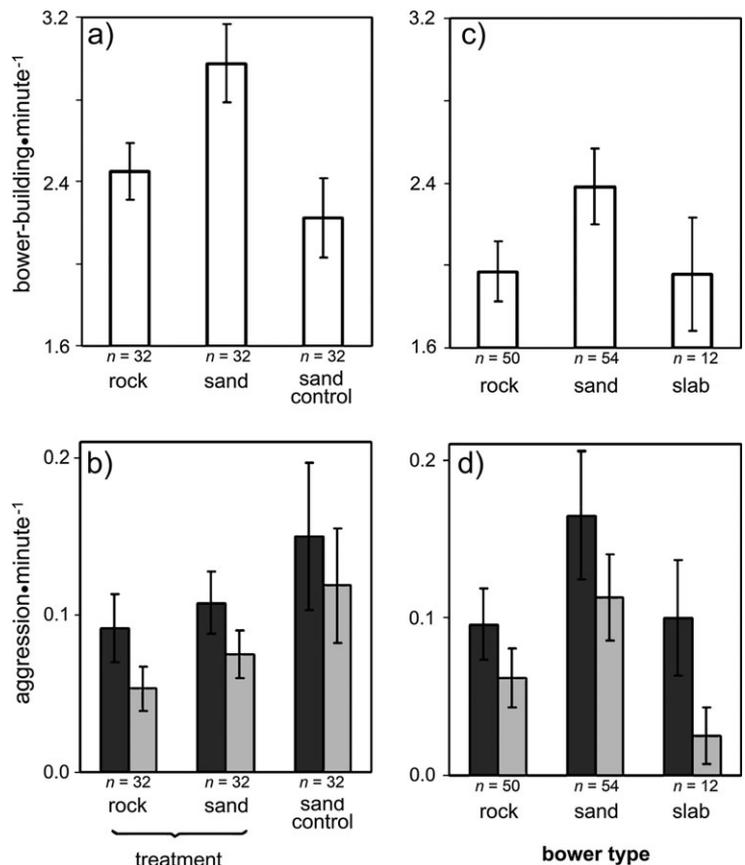
Figure 3
Mean (±standard error) frequency of bower-building behaviors (□), aggression toward territorial males (■), and aggression received from territorial males (▨) per minute among different bower types. In field manipulations (a, b), focal males were observed initially on sand bowers (sand control) and following in situ construction of rock bowers and sand bowers. Males on all 3 bower types were observed during field observations (c, d).

Female trait switching while assessing males on different bower types

There was equivocal support for the hypothesis that females assess different signals of male quality (bower height or male display rate) depending on the male's bower type (sand or rock). In an ANCOVA model, bower height was significantly correlated with an increased rate of female bower visits only among males guarding sand bowers (bower type by bower height interaction, $F_{1,119} = 11.100$, $P = 0.0012$). This supports the hypothesis that females preferred taller bowers only when evaluating sand bowers; however, bower height only explained 9% of the variation in female visits to sand bowers (sand bowers: $r^2 = 0.094$, $n = 58$, $P = 0.019$; rock bowers: $r^2 = 0.001$, $n = 51$, $P = 0.817$).

Furthermore, the effect of male displays on female visits did not significantly vary between rock and sand bowers (bower type by male displays interaction, $F_{1,119} = 0.009$, $P = 0.926$). Thus, there is no evidence that females switched to primarily assessing the number of male displays when evaluating rock bower males.

Across all bower types, there was no correlation between total bower height and male displays per female ($r^2 = 0.0003$, $n = 161$, $P = 0.831$). However, males on rock bowers performed a greater number of displays per female (Figure 4e; 1-way ANOVA, $F_{2,305} = 3.768$, $P = 0.024$).

### Overall female preference for bower type

Males were visited by a significantly greater proportion of the females they courted while guarding rebuilt rock bowers than while guarding rebuilt sand bowers (Figure 4b; Wilcoxon sign-rank, $Z_{31} = -92$, $P = 0.045$; additional results in Supplementary Material). However, circling bouts per female were not significantly different between rock and sand bowers (Figure 4c; Wilcoxon sign-rank, $Z_{19} = -35.5$, $P = 0.098$) nor was the number of eggs laid per female (Figure 4d; Wilcoxon sign-rank, $Z_{19} = -9$, $P = 0.25$).

Similarly, during field observations, rock bower males received a larger proportion of female visits (Figure 4f) and circling bouts (Figure 4g) relative to their frequency in a given female's search path (observed–expected visits: 1-way ANOVA, $F_{2,337} = 17.479$, $P < 0.0001$; observed–expected circling: Welch's ANOVA, $F_{2,130.94} = 7.112$, $P = 0.0021$). Ultimately, however, males on sand bowers fertilized more eggs than males on other bower types (Figure 4h; observed–expected eggs laid: Welch's ANOVA, $F_{2,60.12} = 4.646$, $P = 0.013$).

Female preference polymorphism for bower type

Individual females were frequently observed visiting and spawning with males on all 3 bower types during a single focal observation. Individual females encountered up to 135 courting males, laid up to 13 eggs, and spawned with up to 3 different males during a single focal observation. Females visited the bowers of 37.4% of all males encountered, engaged in circling bouts with 11.5% of all males, and ultimately spawned with 1.8% of all males ($n = 167$ female focal observations).

Individual females were variable in the sign and magnitude of their preferences for visiting different bower types (Supplementary Figure S2), but the observed variance in female preferences was not significantly greater than expected by chance ($P > 0.16$; Supplementary Material). Two females significantly preferred visiting sand bower males (Supplementary Figure S2); however, this number was not larger than expected by chance in the overall data set ($P = 0.578$; Supplementary Material).
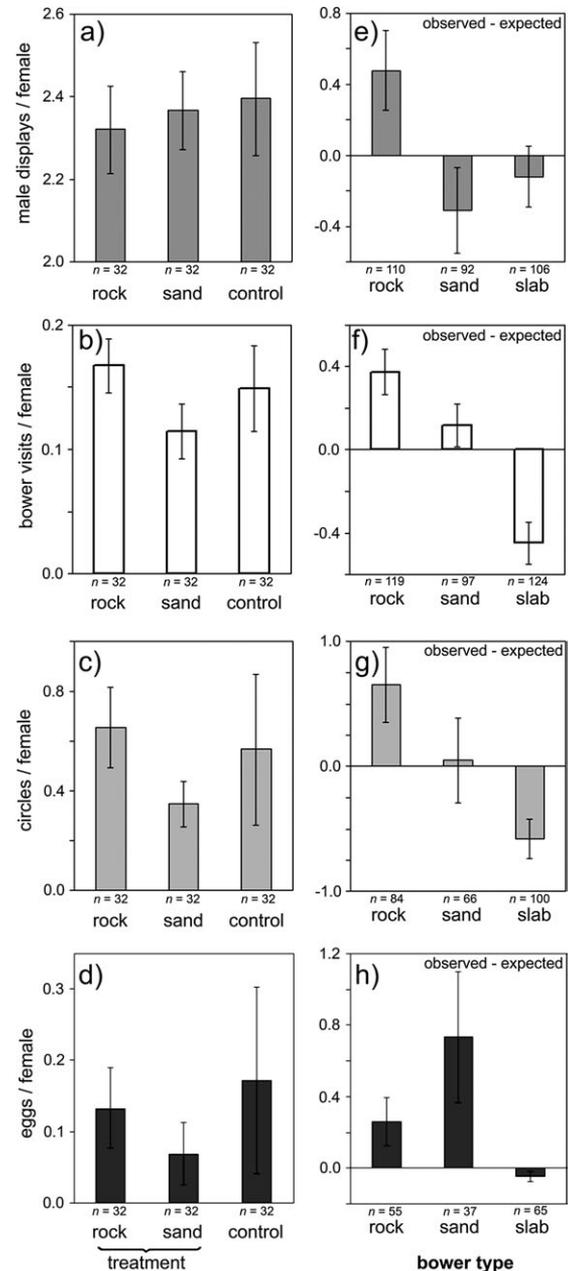
Figure 4
Mean (±standard error) frequency of male displays (■), bower visits (□), circling bouts (■), and eggs laid (■) per courted female among different bower types. In field manipulations (a–d), focal males were observed initially on sand bowers (control) and following in situ construction of rock bowers and sand bowers. Field observations of individual females (e–h) compared the observed number of each behavior with the expected number based on each female's encounter rate with each bower type.

Alternative male bower-building strategies

I found no evidence that individual males preferred to build on rock substrates; when given a choice between adjacent sand or rock platforms of equal height, 53% of males originally guarding sand bowers rebuilt on a rock platform ($n = 19$; binomial test, $P = 0.676$). However, after leveling sand bowers in a sandy region of the lek and placing new rock platforms in the area, males always chose to rebuild on the rock platform rather than the sand floor ($n = 8$; binomial test, $P = 0.004$).

Microhabitat availability

The availability of rock platforms was limited in sandy regions of the lekking arena; 74% of rock platforms surveyed were occupied by territorial males. In adjacent rocky regions, only 18% of rock platforms were occupied (Supplementary Figure S1).

DISCUSSION

Female responses to unreliable male signals

Here, I document male polymorphism in bower construction within a population of Lake Malawi cichlid fish. Males that built their bowers on rock platforms, rather than the sand floor, had taller bowers which required less maintenance and no increased conspecific aggression or egg-predation costs (Figures 2 and 3). This extra height should provide a more attractive signal to females and may be an advantage in male–male competition (McKaye et al. 1990; Martin and Genner 2009). Rock bower males also displayed at a higher rate, possibly due to their reduced bower investment costs (Figure 4). These data support the prediction 1) that rock bower height is an unreliable signal of male investment in bower construction.

Thus, 2) females should switch to an alternate signal when assessing rock bower males (Møller and Pomiankowski 1993; Hebets and Papaj 2005). In partial support of this prediction, females were more likely to visit taller sand bowers, but not taller rock bowers, suggesting that females ignored the height of rock bowers as a sexual signal. I found no evidence that females switched to assessing male displays on rock bowers, but there are numerous other components of the male courtship display, including conspicuous blue and yellow coloration (Figure 1), high frequency quivering of the anal fin, and male courtship sounds (Lobel 1998).

In addition to trait switching, females may also simply avoid males displaying unreliable signals. I predicted that 3) females would avoid visiting rock bower males displaying unreliable signals of their investment and instead visit sand bower males displaying more honest signals, as suggested by theory (Schluter and Price 1993; van Doorn and Weissing 2006). Instead, females were more likely to visit rock bowers, even after controlling for male identity, bower height, and location (Figure 4). Thus, the presence of a rock platform alone increased the rate of female bower visits. This may reflect sensory exploitation if females have a preexisting sensory bias for the higher contrast of a rock bower outlined against sand (Endler and Basolo 1998).

Despite receiving more visits, rock bower males ultimately did not fertilize more eggs than males on other bower types (Figure 4). In contrast to many studies of sensory bias (e.g., Ryan et al. 1990; Bro-Jørgensen and Pangle 2010), this suggests that females were able to avoid initial sensory exploitation by assessing additional male signals during the next stage of courtship before any eggs were laid. Similarly, a study of mate preferences in satin bowerbirds found that older, presumably more experienced, females based their ultimate mate choice on the intensity of male displays during the second courtship stage, whereas younger birds based their choice only on relative bower ornamentation during their initial inspection (Coleman et al. 2004; see also Robson et al. 2005). Bower ornaments were manipulated randomly by the researchers and so were unreliable signals of male quality, although natural bower ornaments are honest signals of male bowerbird guarding ability (Borgia 1985; Wojcieszek et al. 2007; Doerr 2010). This study of cichlid bowers provides a natural example of unreliable signaling in which females used multiple courtship stages to avoid sensory exploitation. Alternatively, if females do not have preexisting sensory biases for

rock bowers, they may be actively increasing their assessment of rock bower males displaying unreliable signals. Rather than rejecting males based on a single unreliable signal, this strategy could be beneficial for increasing the range of males sampled in a lek, where unreliable signals should proliferate (Møller and Pomiankowski 1993).

Maintenance of bower polymorphism

If males can reduce production and competition costs by building their bowers on rock platforms, why do males still build bowers on the sand floor or guard bare patches on rock slabs (see Supplementary Figure S1 for approximate relative abundance)? I found no evidence for 4) significant variation in individual female preferences that might contribute to bower polymorphism (Supplementary Figure S2). However, this was a conservative test of female preference polymorphism because it was restricted to females that encountered at least 2 bower types (Supplementary Material). I also found no support that 5) alternative male bower-building strategies contribute to bower polymorphism. Territorial males guarding sand bowers did not prefer to build on sand substrates rather than rock substrates during field choice trials. If these sand males were somehow better at building a bower on the sand floor or attracting females with a sand bower, they should have exhibited a preference for building on sand relative to rock.

Instead, 6) suitable rock platforms on the lekking arena appear limited. Field surveys indicated that only 1 in 4 rock platforms on or adjacent to sandy regions of the lek were unoccupied by territorial males. These unoccupied platforms may have been too close to neighboring males or unfit due to some unmeasured aspect of their slope or shape. Furthermore, new rock platforms placed on the sand floor were always occupied after a disturbance. There was an abundance of empty rock platforms adjacent to the main lekking arena on rock substrate (see Supplementary Figure S1), but these platforms were not close enough to sand to allow males to build sand spawning craters. Males defending territories in these regions were constrained to building slab bowers and had much lower reproductive success than males on either rock or sand bowers (Figure 4h). Thus, the ideal locations for bowers, rock platforms with access to sand, appear to be in very short supply.

Are rock bowers dishonest signals?

I found that males on rock bowers did not engage in greater territorial aggression nor were they better at preventing egg stealing. Furthermore, building on a rock platform avoids the higher initial production costs of starting on the sand floor (McKaye et al. 1990), the higher maintenance costs of sand bowers revealed in this study (Figure 3), and the higher competition costs of building at a lower height relative to neighboring territory holders (Martin and Genner 2009). In this way, rock bower males may have found a way to exaggerate their investment in bower construction to conspecifics. This type of signal dishonesty can occur when male signalers exploit female preferences for one component of a complex signal. For example, female fiddler crabs did not discriminate against males with regenerated claws, even though regenerated claws are less powerful and less effective in male combat (Backwell et al. 2000; Lailvaux et al. 2009). Females appear to be visually assessing males based only on claw length, rather than claw regeneration (Backwell et al. 2000; also see Wilson et al. 2007). A similar bias may have allowed male swordtail fishes to deceive females about their actual size by exaggerating their body length with tail extensions (Rosenthal and

Evans 1998). Similar to rock bower males, males in other species are also known to exaggerate their sexual signals by exploiting aspects of their environment, such as amplifying their mating calls by modifying leaves into sound baffles (Prozesky-Schulze et al. 1975) or matching their calls to the resonance frequency of tree-holes for amplification (Lardner and bin Lakim 2002). These amplified signals exaggerate the fitness costs of the male callers to females and thus may be examples of dishonest signaling. However, the complete fitness costs of building on a rock bower are still unknown.

Summary

Substrate heterogeneity in a lek of Lake Malawi cichlids allows some males to increase the height of their bowers without increased construction costs by building on rock platforms. Females more frequently advanced to the next stage of courtship when assessing these males. Ultimately, however, females were not fooled by these deceptive signals and rock bower males did not achieve higher reproductive success. This study provides manipulative field data on the costs, benefits, and maintenance of unreliable male signals and suggests that females can successfully combat initially deceptive signals by using additional information during later stages of courtship in a system with very low cost to mate assessment.

SUPPLEMENTARY MATERIAL

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

FUNDING

REFERENCES

Andersson M. 1994. Sexual selection. Princeton (NJ): Princeton University Press.

Backwell PRY, Christy JH, Telford SR, Jennions MD, Passmore NI. 2000. Dishonest signalling in a fiddler crab. Proc R Soc Lond B Biol Sci. 267:719–724.

Borgia G. 1985. Bower destruction and sexual competition in the satin bowerbird (*Ptilonorhynchus-violaceus*). Behav Ecol Soc. 18:91–100.

Borgia G. 1995. Complex male display and female choice in the spotted bowerbird—specialized functions for different bower decorations. Anim Behav. 49:1291–1301.

Bro-Jørgensen J, Dabelsteen T. 2008. Knee-clicks and visual traits indicate fighting ability in eland antelopes: multiple messages and back-up signals. BMC Biol. 6:47.

Bro-Jørgensen J, Pangle WM. 2010. Male topi antelopes alarm snort deceptively to retain females for mating. Am Nat. 176:E33–E39.

Byers J, Hebets E, Podos J. 2010. Female mate choice based upon male motor performance. Anim Behav. 79:771–778.

Candolin U. 2003. The use of multiple cues in mate choice. Biol Rev. 78:575–595.

Coleman SW, Patricelli GL, Borgia G. 2004. Variable female preferences drive complex male displays. Nature. 428:742–745.

Doerr NR. 2010. Does decoration theft lead to an honest relationship between male quality and signal size in great bowerbirds? Anim Behav. 79:747–755.

van Doorn GS, Weissing FJ. 2004. The evolution of female preferences for multiple indicators of quality. Am Nat. 164:173–186.

van Doorn GS, Weissing FJ. 2006. Sexual conflict and the evolution of female preferences for indicators of male quality. Am Nat. 168:742–757.

Endler JA, Basolo AL. 1998. Sensory ecology, receiver biases and sexual selection. TREE. 13:415–420.

Fisher RA. 1930. The genetical theory of natural selection. Oxford: Clarendon Press.

Frith CB, Frith DW. 2004. The bowerbirds. New York: Oxford University Press.

Genner MJ, Young KA, Haesler MP, Joyce DA. 2008. Indirect mate choice, direct mate choice and species recognition in a bower-building cichlid fish lek. J Evol Biol. 21:1387–1396.

Gibson JS, Uetz GW. 2008. Seismic communication and mate choice in wolf spiders: components of male seismic signals and mating success. Anim Behav. 75:1253–1262.

Hebets EA, Papaj DR. 2005. Complex signal function: developing a framework of testable hypotheses. Behav Ecol Soc. 57:197–214.

Iwasa Y, Pomiankowski A. 1994. The evolution of mate preferences for multiple sexual ornaments. Evolution. 48:853–867.

Johnstone RA. 1996. Multiple displays in animal communication: 'backup signals' and 'multiple messages'. Philos Trans Biol Sci. 351:329–338.

Karino K. 1996. Tactic for bower acquisition by male cichlids, *Cyathopharynx furcifer*, in Lake Tanganyika. Ichthyol Res. 43:125–132.

Kellogg KA, Stauffer JR, McKaye KR. 2000. Characteristics that influence male reproductive success on a lek of *Lethrinops* c.f. *parvidens* (Teleostei:Cichlidae). Behav Ecol Soc. 47:164–170.

Kidd MR, Kidd CE, Kocher TD. 2006. Axes of differentiation in the bower-building cichlids of Lake Malawi. Mol Ecol. 15:459–478.

Kodric-Brown A, Nicoletto PF. 2001. Female choice in the guppy (*Poecilia reticulata*): the interaction between male color and display. Behav Ecol Soc. 50:346–351.

Konings A. 2007. Malawi cichlids in their natural habitat. 4th ed. El Paso (TX): Cichlid Press.

Lailvaux SP, Reaney LT, Backwell PRY. 2009. Dishonest signalling of fighting ability and multiple performance traits in the fiddler crab *Uca mjoebergi*. Funct Ecol. 23:359–366.

Lancaster LT, Hipsley CA, Sinervo B. 2009. Female choice for optimal combinations of multiple male display traits increases offspring survival. Behav Ecol. 20:993–999.

Lardner B, bin Lakim M. 2002. Tree-hole frogs exploit resonance effects. Nature. 420:475.

Lobel PS. 1998. Possible species specific courtship sounds by two sympatric cichlid fishes in Lake Malawi, Africa. Environ Biol Fish. 52:443–452.

Martin CH, Genner MJ. 2009. A role for sand bowers in male competition in a Lake Malawi cichlid fish. Behaviour. 146:963–978.

McKaye KR. 1991. Sexual selection and the evolution of the cichlid fishes of Lake Malawi, Africa. In: Keenleyside MHA, editor. Cichlid fishes: behaviour, ecology, and evolution. London: Chapman & Hall. p. 241–257.

McKaye KR, Louda SM, Stauffer JR. 1990. Bower size and male reproductive success in a cichlid fish lek. Am Nat. 135:597–613.

Møller AP, Pomiankowski A. 1993. Why have birds got multiple sexual ornaments. Behav Ecol Soc. 32:167–176.

Patricelli GL, Uy JAC, Borgia G. 2003. Multiple male traits interact: attractive bower decorations facilitate attractive behavioral displays in satin bowerbirds. Proc R Soc Lond B Biol Sci. 270:2389–2395.

Prozesky-Schulze L, Prozesky OPM, Anderson F, Van der Merwe GJJ. 1975. Use of a self-made sound baffle by a tree cricket. Nature. 255:142–143.

R Development Core Team. 2010. R: a language and environment for statistical computing [Internet]. Vienna (Austria): R Foundation for Statistical Computing. Available from: http://www.R-project.org.

Robson TE, Goldizen AW, Green DJ. 2005. The multiple signals assessed by female satin bowerbirds: could they be used to narrow down females' choices of mates? Biol Lett. 1:264–267.

Rosenthal GG, Evans CS. 1998. Female preference for swords in *Xiphophorus helleri* reflects a bias for large apparent size. Proc Natl Acad Sci. 95:4431–4436.

Rowe C. 1999. Receiver psychology and the evolution of multicomponent signals. Anim Behav. 58:921–931.

Ryan MJ, Fox JH, Wilczynski W, Rand SA. 1990. Sexual selection for sensory exploitation in the frog *Physalaemus pustulosus*. Nature. 343:66–67.

Schluter D, Price T. 1993. Honesty, perception and population divergence in sexually selected traits. Proc R Soc Lond B Biol Sci. 253:117–122.

Stauffer JR, Kellogg KA, McKaye KR. 2005. Experimental evidence of female choice in Lake Malawi cichlids. Copeia. 2005:657–660.

Wilson RS, Angilletta MJ, James RS, Navas C, Seebacher F. 2007. Dishonest signals of strength in male slender crayfish (*Cherax dispar*) during agonistic encounters. Am Nat. 170:284–291.

Wojcieszek JM, Nicholls JA, Goldizen AW. 2007. Stealing behavior and the maintenance of a visual display in the satin bowerbird. Behav Ecol. 18:689–695.

Zahavi A. 1975. Mate selection—selection for a handicap. J Theor Biol. 53:205–214.

Zahavi A. 1987. The theory of signal selection and some of its implications. In: Delfino VP, editor. Proceedings of the International Symposium of Biology and Evolution. Bari (Italy): Adriatic Editrica. p. 305–327.

Zuk M, Ligon JD, Thornhill R. 1992. Effects of experimental manipulation of male secondary sex characters on female mate preference in red jungle fowl. Anim Behav. 44:999–1006.