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Female choice of a non-bodily ornament: an experimental study of cichlid sand craters in *Cyathopharynx furcifer*

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Abstract In many species of East African cichlids, males build sand craters or "bowers" to attract females for spawning. It is commonly assumed that these exaggerated sexual traits have a function similar to bodily ornaments. In non-bodily ornaments, however, the behaviour creating the structure may serve as an additional source of information to potential partners, providing multiple signals for mate choice. We tested whether and to what extent females use these signals for choosing males by observing the individual sampling behaviour of female *Cyathopharynx furcifer* in the field. In addition, we experimentally manipulated crater characteristics in the field and laboratory. We found that females spawn preferably with owners of large and well-maintained craters, but when crater size was enlarged or reduced, the resulting building activity of crater owners affected female choice more strongly than the manipulated crater size *per se*. We discuss the importance of multiple signals in species constructing extended phenotypes.

Keywords Extended phenotype · Mate choice · Bower · Multiple signals · Lake Tanganyika

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Introduction

Complex displays by multiple signals involving different modalities are widespread in animals (Candolin 2003; Hebets and Papaj 2005). Several studies have focused on the interrelationship between different bodily ornaments or the combination of bodily ornaments and behaviour (Johnstone 1995; Künzler and Bakker 2001; Fawcett and Johnstone 2003; Scheuber et al. 2003; Candolin 2004).

In contrast, the multiple signalling opportunities provided by non-bodily ornaments and their construction have been little considered (Madden 2006). Non-bodily ornaments are extraordinary research subjects as they allow an experimental manipulation without direct physical or physiological constraints on behaviour. Subsequent changes in behaviour of the signal constructor (sender) and of potential receivers may reflect the significance of the signalling value of a construction. In bowerbirds (*Chlamydera maculata*), for example, males were found to modulate their courtship behaviour according to the transparency of the bower walls, as a too vigorous display can scare off females (Borgia and Presgraves 1998).

Non-bodily ornaments like bowers of bowerbirds (e.g. *Amblyornis*, *Chlamydera*, *Prionodura*, *Ptilonorhynchus*, *Sericulus*), mating craters of African cichlids (e.g. *Cyathopharynx*, *Cyrtocara*, *Hemitilapia*, *Lethrinops*, *Nyassachromis*, *Oreochromis*, *Trematocranus*) and stone piles of wheatears, *Oenanthe leucura*, probably signal mate quality more reliably than an instantaneous behaviour, because they provide information about a high investment of the constructor integrated over a prolonged time period (Schaedelin and Taborsky 2009). Mating craters of the sand-dwelling cichlids, for example, reflect male construction and maintenance effort lasting several days. Additionally, such non-bodily signals may be more reliable than

morphological ornaments developed over a longer time span during ontogeny: the construction is performed in the same environment where the ornament will be inspected, independently of the environment constructors experienced during ontogeny (Schaedelin and Taborsky 2009). This facilitates the comparison between the qualities of different constructors.

Non-bodily ornaments are often combined with bodily ornaments or with display behaviour. Female satin bowerbirds, *Ptilonorhynchus violaceus*, for example, can extract information on ectoparasite load of bower owners from their bowers, while the UV-plumage coloration of males correlates with their infection intensity with blood parasites (Doucet and Montgomerie 2003). In three-spined sticklebacks, *Gasterosteus aculeatus*, females prefer nests that have been decorated by their male owners, but they also use male coloration in mate choice (Milinski and Bakker 1990; Östlund-Nilsson and Holmlund 2003). These non-bodily and bodily ornaments may reveal different male qualities, such as parasite resistance and paternal skills.

Cyathopharynx furcifer (Vaillent, 1899) is a crater-building cichlid endemic to Lake Tanganyika (Karino 1997; Rossiter 1997; Schaedelin and Taborsky 2006). Here we evaluate the significance of their crater as a non-bodily sexual ornament in female choice, and its relationship with courtship behaviour. In crater-building African cichlids, males construct mating craters in close aggregations, and females visit the craters on these leks and spawn with multiple males on the bottom of their sand craters. Females take up the eggs in their mouth and care for the offspring by mouth-brooding. Studies of crater-building cichlids from Lake Malawi suggest that males with larger craters enjoy higher reproductive success (McKaye et al. 1990). However, no relationship between male reproductive success and crater characteristics was observed in *C. furcifer* (Karino 1997), and experimental evidence is missing (Rossiter 1997). In this study, we observed female sampling behaviour of males and craters in the field to unravel potential preferences for crater characteristics. Then we experimentally manipulated crater qualities in the field and laboratory to investigate the influence of crater characteristics on female choice. If crater size is an important criterion for female choice, we expected females to visit artificially enlarged craters quicker and spawn there more often than in smaller craters.

Materials and methods

Study species

C. furcifer (Ectodini, Cichlidae) is a lekking, maternal mouth-brooder endemic to Lake Tanganyika. In this study,

we investigated *Cyathopharynx* "c.f. *furcifer*" or "dark" (Vaillent, 1899). At Kasakalawe Bay near Mpulungu, Zambia, in the south of Lake Tanganyika, both colour morphs or subspecies "dark" and "light" occur syntopically. No morphological, behavioural and genetic differences between these two colour morphs of *C. furcifer* have been identified so far, despite extensive scrutiny (Mitsuto Aibara, personal communication). Sexually mature males show conspicuous secondary sexual traits: extremely elongated pelvic fins and a gaudy nuptial coloration. Additionally, sexually active males of *C. furcifer* construct large mating craters. Males pick up sand with their mouth from the crater surroundings, swim to the crater and spit the sand on the crater rim, creating a sand structure several times the male's body length in diameter (Rossiter 1997). Above these craters, males court females with vigorous displays.

In contrast to these sexually active, crater-owning males, inconspicuous females and subadults form large aggregations in the water column from where individual females occasionally visit the lek to spawn with crater owners.

General methods

We conducted the field study by scuba diving at Kasakalawe Point, Zambia, 4 km west of Mpulungu at the southern tip of Lake Tanganyika, from February to April 2003. Observations were performed throughout the daylight period, but an initial survey showed reduced activities after 15:00. Therefore, the main observation period was set between 7:00 and 14:00. We investigated two different leks of *C. furcifer* located about 100 m apart from each other at depths of 4.5 to 6 m, each hosting up to 150 males in mating craters (for details see Schaedelin and Taborsky 2006). On both leks, the ground was sandy and partly covered with stones (diameter ca. 10–20 cm).

Mating craters were measured to the nearest half centimetre with a folding ruler. Quantitative crater measurements included inner diameter (diameter of the rim of the crater), outer diameter (diameter of the base of the crater), rim height from the ground, depth of crater bottom in the centre against the rim and water depth at the crater base. In addition, crater neatness was estimated on an arbitrary ordinal scale to consider effects of small water movements, sand density and sand collection effort that do not change quantitative crater measurements. It was shown in bowerbirds that human aesthetic judgments correlate with mating success of bower owners (Madden 2006; Joah Robert Madden, personal communication). Six criteria were used for which each crater was assigned to a category between one for the best and four for the worst class. These criteria were (1) relative impressiveness of the crater at first sight (see Gladwell 2007) compared to the craters in its vicinity; (2) roundness of the crater (1=circular, 2=circular but with

small imperfection, 3=circular with large imperfection, 4= not circular but polygonal); (3) stones incorporated in the crater (incorporating stones into the crater would save time and energy, which may devaluate its signalling value) (1= none, $1.5 = 0 - 1/3$, $2 = 1/3 - 1/2$, $2.5 = 1/2 - 2/3$, $3 = 2/3 - 3/4$, $4 \geq 3/4$ of the crater rim consisting of stones); (4) substrate used to construct the crater (1=mostly fine sand, $2 \geq 1/2$ fine sand, $3 \geq 1/2$ gravel, 4=only gravel; where gravel is small pieces of broken shells and stones above a diameter of 3 mm); (5) substrate on which the crater was located (1=90–100% sand, 2=~75% sand, 3=~50% sand, 4=~25% sand only); (6) rim sharpness of the crater (1=very sharp, 2=edge slightly blurred, 3= rounded, 4=rim very rounded, hard to see).

Focal female observations

One lek was selected for focal observations. All 80 craters were marked with a numbered stone put adjacent to it. We located mate-searching females by slowly swimming transects over the lek, and chose the first female observed to visit a crater as focal animal. We followed her continuously about 2 m above ground until she left the lek, grouped with other females or was lost from sight. We noted all courtship behaviours of males that the focal female passed or visited, and the respective crater number. We recorded the frequencies of the following courtship and spawning behaviours (Table 1, Fig. 1): male courtship initiation, female following, female visiting, male and female circling, number of circling bouts, egg-laying and number of eggs laid. These behaviours are not independent from each other: A visit is

always preceded by a male leading a female into the crater, and a circling bout starts only when the female visits the crater. Egg-laying was never observed without previous circling, whereas not all circlings lead to egg-laying. The frequencies of courtship stage "female following" were almost identical with "visits", i.e. nearly all females visited the crater if they followed a leading male. Therefore, female following was not separately considered in the analysis. All behaviour frequencies and the sequence of behaviours were noted with pencil on a PVC board.

Crater size manipulation experiment

This experiment was done on the other lek to not interfere with the focal female observations. Each day, four craters of similar size were haphazardly chosen and assigned to one of four treatments: (1) enlargement by 1/4 of the original inner crater diameter; (2) reduction by 1/4 of the original inner crater diameter; (3) destruction and rebuilding to the original size of the crater; (4) the crater itself stayed untouched, but the surroundings was disturbed by putting up a camera, moving stones and sometimes moving sand outside of the crater; this latter control served to estimate the influence of any crater manipulation independent of human disturbance. The control treatments 3 and 4 allowed us to assess direct effects of crater manipulation on the behaviour of the owner. Crater diameters were measured twice on the day of manipulation and once on the following day. All focal craters were monitored with an underwater video camera on a tripod placed ca. 1.5 m from them. On a given day, we recorded one replicate of the experiment,

Table 1 Sequence of male and female courtship and spawning, and other recorded behaviours shown by male crater owners

Behaviour	Description	Next in sequence
Courtship sequence		
Male courtship initiation	Vigorous male display towards a female with maximally splayed pelvic fins, by body quivering with head turned down and towards his crater, sometimes followed by swimming towards the crater	Female following
Following the male	Female follows the male to the crater	Crater visit
Crater visit	Female enters the crater and drops to its bottom	Circling
Circling	Female and male turn around each other snout to tail; *circling*: one completed circle; *circling bout*: all circling before interruption (usually when one partner leaves the crater)	Egg-laying
Egg-laying	Female lays an egg in the crater, turns around quickly and picks it up	Circling
Crater building		
Sand transport	Male picks up sand outside the crater, passes through crater centre and spits sand on crater rim	
Rearranging	Male picks up sand from crater (inside or from outside face of crater) and spits it on the crater rim	
Aggression		
Threat display	When another male approaches the crater, the owner tilts and spreads his fins	Chasing opponent out of territory

Male behaviours: courtship initiation, crater building and aggression. Female behaviours: following the male, crater visit, circling (shown by both partners simultaneously), egg-laying
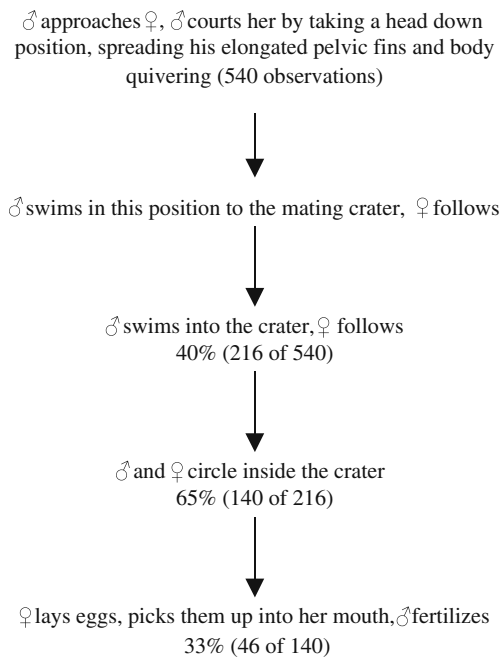
♂ approaches ♀, ♂ courts her by taking a head down position, spreading his elongated pelvic fins and body quivering (540 observations)

↓

♂ swims in this position to the mating crater, ♀ follows

↓

♂ swims into the crater, ♀ follows
40% (216 of 540)

↓

♂ and ♀ circle inside the crater
65% (140 of 216)

↓

♀ lays eggs, picks them up into her mouth, ♂ fertilizes
33% (46 of 140)

Fig. 1 Ethogram of the course of the courtship sequence of *Cyathopharynx furcifer*. *Numbers* indicate positive female responses

consisting of four craters monitored with four cameras (two treatments and two controls). Each camera recorded the respective focal crater and its surroundings continuously for up to 9 h in time-lapse mode. The following behaviours were recorded from the video tapes for the first 6 h after the manipulation: (1) frequency of relocating sand within the crater (rearranging) and carrying sand into the crater, (2) duration of rearranging sand, (3) number of female followings, (4) number and duration of female visits, and (5) number of circling bouts. The quality of the recordings varied due to water turbidity and some technical failures. To cope with this variation, the quality of all video recordings was rated with a number between 1 (perfect) and 4 (very bad), which sometimes changed within a recording. Only videos of an average quality between 1 and 3.5 were analysed. At the end of the experiment, we caught the crater owners and measured their standard length (tip of the mouth to the base of the tail fin) and fork length (tip of the mouth to the sinus of the forked tail fin).

Female preference experiment

In the laboratory at the Ethologische Station Hasli of the University of Bern, *C. furcifer* were kept in mixed-sex groups in 1,000-l tanks, at a water temperature of 27°C and a light/dark cycle of 13 h/11 h supplied by fluorescent tubes. Fish were fed 6 days per week (4× dry food, 2× frozen food) and additionally supplied with chopped spinach (2× per week). All aquaria were equipped with a layer of fine river sand, two biological filters and two air stones.

For the experiment, four 1,000-l tanks were separated into three equal compartments with transparent partitions. Each compartment was equipped with a biological air filter and an air stone. We introduced one male together with two females in both edge compartments. Males in a tank were matched for body size (fork length) and weight. After both males had built a crater, we removed the partitions. Whenever both males continued actively to maintain and defend their crater for at least 2 days, we started the experiment. This was achieved for nine male pairs. All females of the experimental tank were removed before a single, new female was released in the middle of the tank.

To ensure that females were ready to mate, experimental females were kept in all-female groups for at least 2 weeks. After the experimental female had acclimatised to the new tank for 1 h, both craters were measured and manipulated: One crater was changed to an inner crater diameter of 20 cm and the other one to 40 cm. The courtship behaviour of males and the female's behaviour were recorded for 3 h by time-lapse video with two separate cameras positioned in front of each crater. On the following day, the experiment was repeated with the same female but opposite crater manipulation. The following behaviours were analysed using the software program "The Observer" (Noldus): frequency and time of building activity (rearranging sand inside the crater and transporting sand into the crater from outside); threat towards the inspecting neighbour (or, very rarely, the female); defending; male attempt to lead; female following; female crater visit; and male and female circling. We analysed both the latency, until a certain behaviour was first observed, and its frequency.

Statistical analyses

We used backward logistic regressions to analyse the relationship between crater dimensions and male success for the female focal observation data. To investigate the significance of crater characteristics for female choice throughout the whole courtship sequence, we created three separate models, each one with another measurement of male reproductive success as a dichotomous dependent variable: whether females visited the crater, whether males and females circled or whether females laid eggs or not. We started with the full models including all crater measurements as continuous variables: inner and outer diameter, depth and height of crater, percentage of stones integrated into the crater rim, neatness, roundness, proportion of sand surrounding the crater and rim sharpness. Further, the courtship behaviour preceding a target behaviour in the model was also included as a covariate (female visits—male courtship initiation; female and male circling—female following; egg-laying—number of circling rounds and number of circling bouts). The final models were generated

by excluding in a stepwise procedure in each run the covariate showing the least significant P value in the Wald statistic.

If data distributions did not differ from normality (Kolmogorov–Smirnov test, $P>0.1$), relationships were tested with Pearson's correlation analyses; otherwise, a Spearman rank correlation analysis was used. For two independent sample comparisons, we used t tests for normally distributed data and Mann–Whitney U tests for non-normally distributed data. To analyse the size manipulation experiment, counts were log-transformed and we used a univariate ANOVA if data were normally distributed ($P>0.1$) and the homogeneity test of variances did not reveal significant differences ($P>0.1$). If data were not normally distributed, a Wilcoxon signed-ranks test for matched pairs was used to identify differences between the treatments.

In the female preference experiment in the laboratory, we analysed the differences between the behaviours of both males in the tank depending on treatment. For each behaviour, we subtracted the frequency of behaviour of one male from that of the other. Similarly, we subtracted the time until a certain behaviour occurred for the first time, thus its latency, of one male from that of the other. Afterwards, the two treatments were compared with a pairwise t test for frequencies and a nested ANOVA for latencies. Due to the experimental design, which included up to three females tested with the same male pair, preferences of different females choosing between males of the same pair constitute non-independent measurements. Therefore, females were nested in male pairs in the female preference experiment in the laboratory. All statistical analyses were two-tailed and performed with SPSS 11.0.

Results

Focal observations

Mating behaviour

On average, females entering the lek ($n=57$) were courted 9.5 times by some crater owner, they visited 3.8 craters, started circling bouts 2.5 times and laid 2.1 eggs during their stay on the lek. Forty percent (216 out of 540) of male courtship displays resulted in a female visit, 26% in circling ($n=140$; i.e. 65% of nest visits) and 8.5% in egg-laying ($n=46$; i.e. 21.3% of nest visits). Females spawned 1–15 eggs with the same male ($n=34$ spawnings, median=1.5). A comparison of frequently visited males (median=4) with rarely visited males (median=1) showed that the former succeeded to spawn significantly more often than the latter (Mann–Whitney U test—$Z=244.5$, $n=67$, $P<0.001$).

Female sampling behaviour

Nineteen of 45 (42%) spawning events occurred at a female's first visit of a particular male. Of all 15 egg-laying females, most (12) had visited several males on the lek before they started to lay eggs. Then seven of them spawned with one, four with two and four with three or more different males. Eight females (53%) returned to a male for spawning again with whom they had already spawned, and seven (47%) females returned to visit a male with whom they had spawned before, but without spawning with him again ($n=15$). Only four females (27%) left the lek immediately after the last egg was laid and two were courted by another male but did not respond, whereas nine females (60%) visited at least one other crater after their last egg was laid, presumably to collect further ejaculates (cf. Immler and Taborsky 2009).

Male reproductive success

As expected for a lekking species, the reproductive success was highly skewed among males, with most males having only few successful courtships (Fig. 2). Only "male courtship initiation" and the inner diameter of his crater contributed significantly to the logistic regression model describing the variation in female visits (Table 2). Thus, females visited larger craters and those with frequently courting males more often than smaller craters and less actively courting crater owners. No effects of outer crater diameter, inner crater depth, crater height or amount of stones integrated in the crater rim were observed, nor was there any influence of the quality characteristics of craters on female visitation rate. Circling, which follows visiting, was only significantly dependent on the number of visits (Table 2). Egg-laying was significantly related to the preceding circling activity, and to the impressiveness and roundness of craters (Table 2). Surprisingly, the effects of the two quality characteristics of craters showed up in opposite directions: females appear to prefer more impressive, but less round craters.
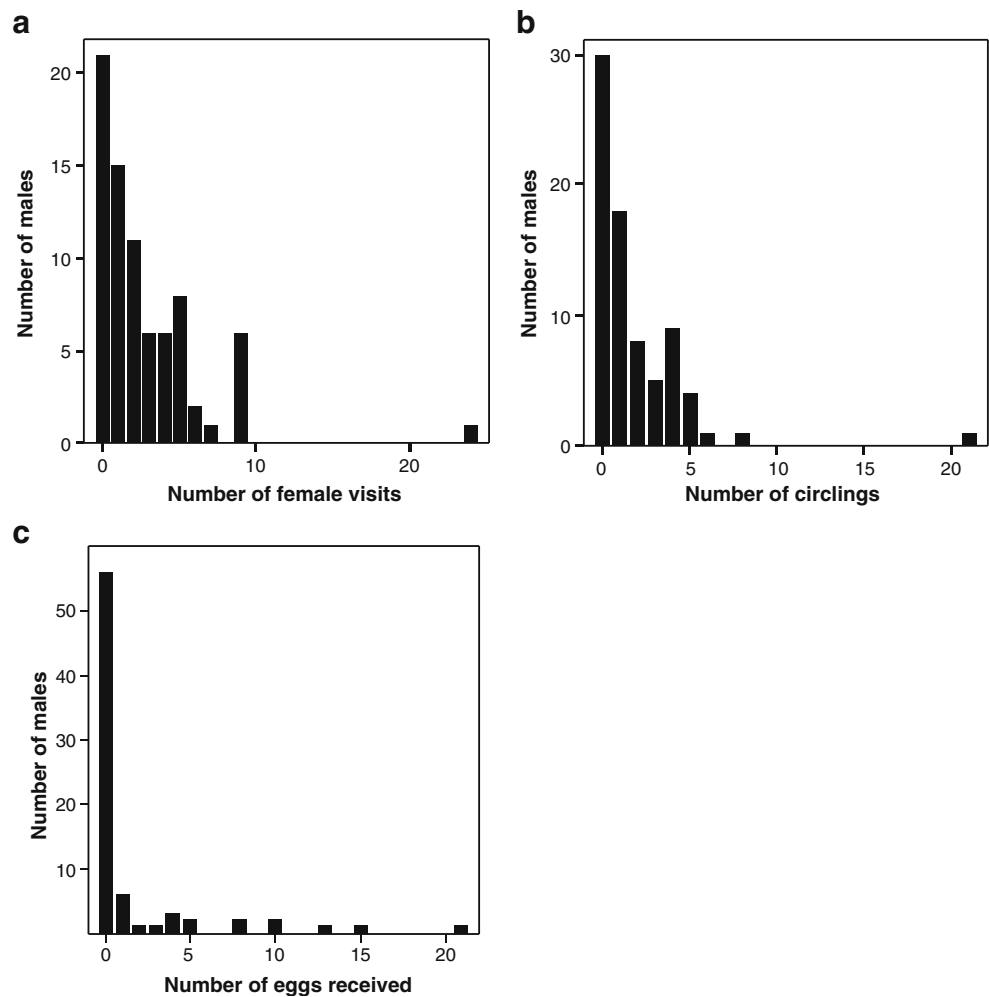
When the analyses was repeated after excluding one very poor crater in which only one female spawned, however, no significant negative effect of roundness was detected.

Crater size manipulation experiment

Does manipulated crater size influence female choice?

The number of females following the male and the number of female visits were not affected by the treatment (Fig. 3a; univariate GLM—$F_{3,39}=0.342$, $P=0.795$; $F_{3,39}=0.090$, $P=0.965$), nor was the number of circlings (Kruskal–Wallis

test—$\chi^2=1.749$, $P=0.626$). The treatment affected female visit duration significantly, and longer visits resulted more often in circling (Fig. 3b; univariate GLM—visit duration, $F_{1,121}=17.836$, $P<0.001$; crater size, $F_{26,121}=2.801$, $P<$

0.001; circling, $F_{11,121}=31.884$, $P<0.001$). Female visit duration did not differ between the two controls (treatments 3 and 4; t test—$t=0.594$, $df=130$, $P=0.554$) and between the two test treatments (treatments 1 and 2; t test—$t=0.018$,

Table 2 Logistic regressions of three female behaviours recorded during the female focal observations

$df=1$	Female visits				Circling				Egg-laying			
Variable	Wald $\chi 2$	P	Coeff.	±SE	Wald $\chi 2$	P	Coeff.	±SE	Wald $\chi 2$	P	Coeff.	±SE
Constant	**9.675**	**0.002**	**−3.233**	**1.039**	3.600	0.058	−0.920	0.485	0.630	0.427	−0.794	1.001
Inner diameter	**4.216**	**0.040**	**0.051**	**0.025**	1.162	0.281	−0.043	0.040	0.756	0.385	0.052	0.060
Impressiveness	0.010	0.919	0.021	0.207	0.349	0.554	0.195	0.329	**6.497**	**0.011**	**−1.312**	**0.515**
Roundness	0.249	0.618	−0.089	0.178	0.509	0.475	−0.199	0.278	**5.172**	**0.023**	**1.022**	**0.450**
Male courtship initiation	**19.034**	**0.000**	**0.687**	**0.157**	–	–	–	–	–	–	–	–
Female visit	–	–	–	–	**7.708**	**0.005**	**1.077**	**0.388**	–	–	–	–
Circling	–	–	–	–	–	–	–	–	**6.350**	**0.012**	**0.795**	**0.315**

Variables included in the respective final model are in bold print. Statistical parameters of variables which are only significant in one of the three models are shown in standard print where they are non-significant. These statistical parameters are given when single variables are included in the previously identified final model by the method "enter". Additionally, the following factors were tested that had no significant effect on any model: outer crater diameter, crater inner depth, crater rim height, amount of stones incorporated into crater rim, percentage of sand covering the ground around the crater and crater rim sharpness
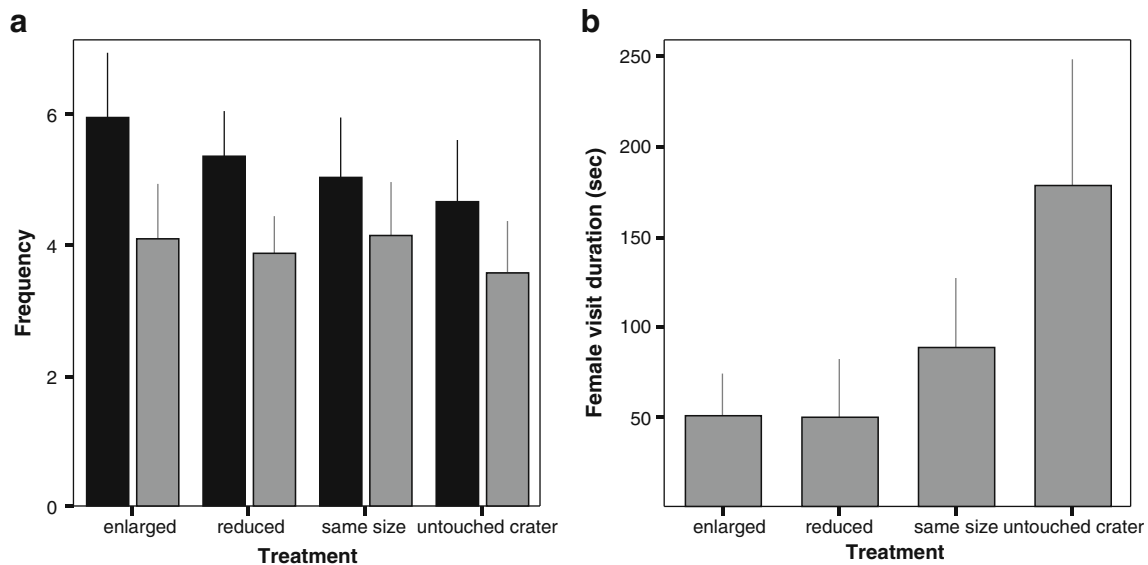
Fig. 3 **a** Frequency (mean ± SE) of female following (*black bars*) and female visits (*grey bars*) of *Cyathopharynx furcifer* per hour in the crater size manipulation experiment (*n*=12, 12, 12, 7); **b** female visit duration (mean ± SE) in the crater size manipulation experiment (same sample sizes)

df=108, *P*=0.986), but females stayed significantly shorter in the size-manipulated craters (treatments 1 and 2) compared to the controls (treatments 3 and 4) (Fig. 3b; *t* test—*t*= −3.818, *df*=240, *P*<0.001). In contrast, size manipulation (treatments 3 and 4 against treatments 1 and 2) did not affect female courtship behaviour (frequency of female following, GLM—$F_{1,41}$=0.742, *P*=0.394; female visits, GLM—$F_{1,41}$=0.004, *P*=0.948; circling, Mann–Whitney *U* test—*Z*=−1.176, *P*=0.239). The crater manipulation itself (treatment 4 against treatments 1, 2 and 3) had no effect on female preference (frequency of female following, GLM—$F_{1,41}$=0.423, *P*=0.519; visits, GLM—$F_{1,41}$=0.207, *P*=0.652; circling, Mann–Whitney *U* test—*Z*=−1.217, *P*=0.223).

Does crater size manipulation in the field influence male building activity?

The frequency with which a male spat sand on the crater rim showed neither a treatment effect (GLM; treatment—$F_{3,39}$=0.708, *P*=0.553), nor a manipulation effect (treatment 4 against treatments 1, 2 and 3; *t* test—*df*=41, *t*= −1.365, *P*=0.180), nor a size-change effect (treatments 3 and 4 against 1 and 2; *t* test—*df*=41, *F*=1.158, *P*=0.254), nor a size effect (treatment 1 against 2; *t* test—*t*=0.194, *df*= 22, *P*=0.848). Also, the amount of time a male invested in rearranging sand in the crater was neither affected by treatment (Kruskal–Wallis test—χ^2=2.748, *P*=0.432), nor manipulation (treatment 4 against treatments 1, 2, 3; Mann–Whitney *U* test—*Z*=−1.345, *P*=0.179), nor on size change (treatments 3 and 4 against treatments 1 and 2; Mann–Whitney *U* test—*Z*=−1.184, *P*=0.249).

Does male building activity relate to female choice?

Both the building frequency and the time spent building (log transformed) were analysed for correlations with female choice. Correlation analyses were performed over all treatments, except for the female visit duration, since females stayed significantly longer in the control craters. As female following and frequency of visits were highly correlated (Pearson correlation analysis; *n*=43, *r*=0.914, *P*<0.001), we only used visit frequency in this analysis. Male building was roughly 30 times more frequent than female visiting. Number of female visits correlated positively with both measurements of building behaviour (Fig. 4; Pearson correlation—visits vs. frequency of building, *r*=0.325, *P*< 0.05; Spearman rank correlation—visits vs. time of building, *ρ*=0.459, *P*<0.01; the latter remains significant with Bonferroni correction *α*=0.025). Circling frequency did not correlate with building activity (Spearman rank correlation— visits vs. frequency of circling, *ρ*=0.226, *P*=0.145). Male building activity was not significantly related to male body size or male courtship activity (Pearson correlation—building activity vs. body size *n*=32, *r*=−0.144, *P*=0.431; Spearman rank correlation—building activity vs. male courtship initiation *n*=19, *ρ*=0.333, *P*=0.163).

Female preference experiment in the laboratory

Does manipulated crater size influence female preference?

We observed no effect of the treatment on the frequencies of visits and circlings, but females visited males quicker in smaller craters (Fig. 5a; GLM—treatment, $F_{1,7}$=6.789, *P*=
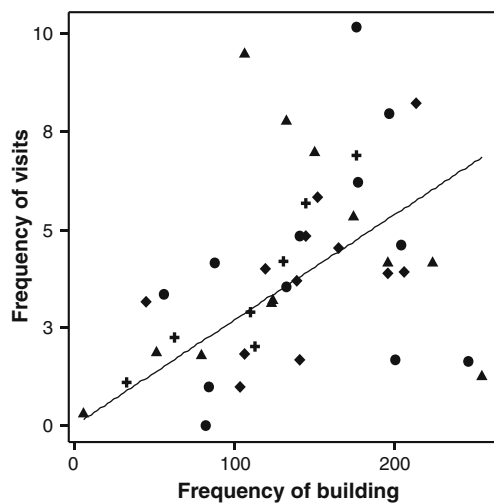
Fig. 4 Correlation between frequency of male building behaviour and frequency of female visits in the field in the fish *Cyathopharynx furcifer* (treatments—*filled circles* enlarged craters, *filled diamonds* reduced craters, *filled triangles* same-sized craters, *crosses* untouched craters)

0.035; female, $F_{19,7}=2.039$, $P=0.170$). Also, they started to circle quicker in smaller craters, where males showed more building behaviour (Fig. 5b, circling latency; GLM—treatment, $F_{1,20}=8.121$, $P=0.010$; covariate rearranging sand, $F_{1,20}=5.586$, $P=0.028$).

Does crater size manipulation in the laboratory influence male behaviour?

Crater size manipulation was successful since crater diameter was significantly different between the two treat-

ments during the whole experiment (*t* test, after 24 h—$t=8.245$, $df=84$, $P<0.001$). When receiving a small crater, males rearranged sand significantly more often (Fig. 6; GLM—treatment, $F_{1,20}=10.776$, $P=0.004$; random factor female, $F_{23,20}=3.266$, $P=0.005$). Male sand-transport behaviour from outside the crater, defending and swimming were not influenced by the crater size manipulation (sand transfer, GLM—treatment, $F_{1,16}=1.899$, $P=0.187$; random factor female, $F_{22,16}=1.171$, $P=0.379$; defending, GLM—treatment, $F_{1,20}=0.186$, $P=0.671$; random factor female, $F_{23,20}=3.060$, $P=0.007$; swimming, *t* test, $t=1.362$, $df=16$, $P=0.192$).

Discussion

Female *C. furcifer* consider non-bodily and behavioural courtship signals throughout different stages of mate choice. Our field observations revealed that they visit larger craters and more actively courting males more frequently and seem to use qualitative crater characteristics for their decision as to where to lay eggs. Similarly, mate-searching females of the satin bowerbird, *P. violaceus*, use different signals during courtship. First, females inspect decorated bowers in the absence of owners. Later on, only a subset of those bowers is visited again when male bower owners are actively courting (Coleman et al. 2004). Since male courtship can frighten female satin bowerbirds, mainly inexperienced females rely predominantly on non-bodily ornaments like bower decorations (Coleman et al. 2004). In *C. furcifer*, however, male courtship behaviour seems to be especially important at initiation, while different compo-
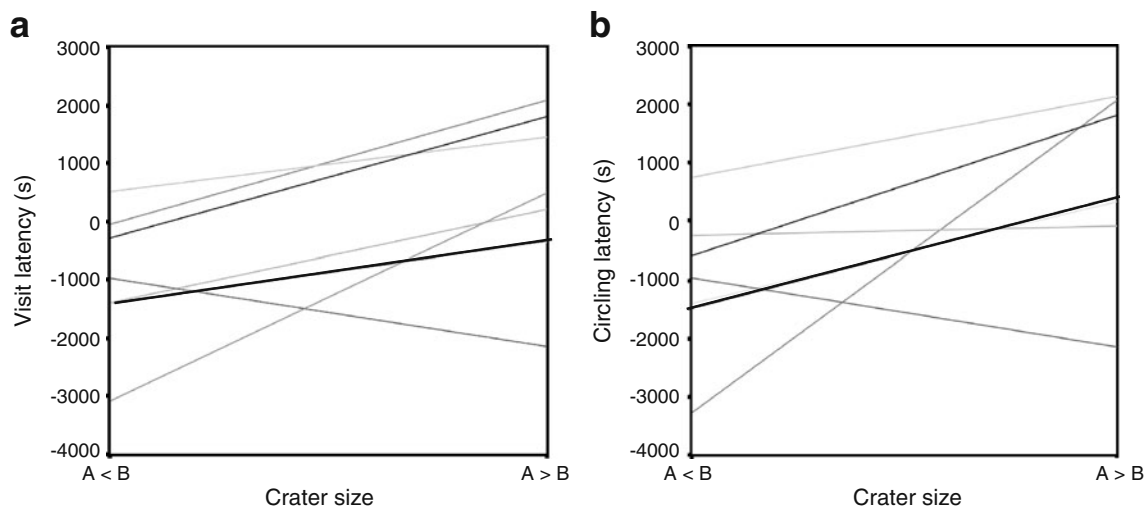

Fig. 5 a Difference of visit latency of the first female visit at crater A minus her visit latency at crater B, depending on treatment (relative crater size) in the laboratory preference test of *Cyathopharynx furcifer*. A negative value means that male A was visited earlier than male B.

b Difference of latency of the first circling by females depending on treatment. A negative value means that the female circled earlier with male A than with male B
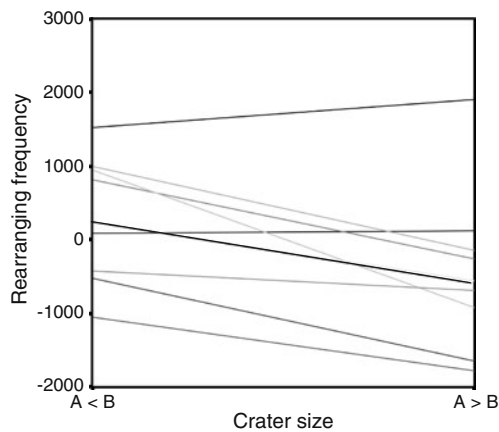
Fig. 6 Difference of the frequencies of "rearranging" behaviour of male A minus "rearranging" frequencies of male B, depending on treatment (relative crater size) in male *Cyathopharynx furcifer*. For example, the *third line from top intersecting the left ordinate* shows results of a tank where male A built about 1,000 times more often than male B when A had the smaller crater. However, at the intersection with the right ordinate the same line reveals that when A had the larger crater, it built about 900 times less often than B. Thus, among the two males in the same tank, the male with the smaller crater was usually more actively building, which can be seen by the negative slope of most lines

nents of the non-bodily ornament seem to influence female mate choice throughout as suggested by our stepwise analysis of the courtship sequence.

The initial attraction of females to larger craters and to more active males might be influenced by their greater conspicuousness. In spotted bowerbirds, *C. maculata*, Borgia (1995) suggested that long-distance ornaments like bleached bones allow a preliminary assessment from above the bower. Similarly, female preference for taller craters in *Lethrinops* c.f. *parvidens* in Lake Malawi was attributed to their increased conspicuousness (Kellog et al. 2000). An initial attraction depending on the size of sand structures, such as hoods or pillars next to the burrow entrance, was also found in fiddler crabs, e.g. *Uca musica* and *Uca beebei*. Further investigation, however, showed that female fiddler crabs use these sand structures for orientation and hiding from aerial predators (Christy et al. 2002, 2003a, b). Hence, sand structures in these crabs are probably attractive because of their direct benefit to females and not because they provide mate-searching females with additional information on male quality. We should like to point out that no relationship between female choice and crater characteristics was found in a population of *C. furcifer* of the northern tip of the lake (Karino 1997). This discrepancy to our findings at the southern tip of the lake might be due to population differences in female choice (Endler and Houde 1995; Gabor and Ryan 2001; Dunn et al. 2008; Maan et al. 2010), or to different observation and analysis methods.

In the Malawi cichlid *Hemitilapia oxyrhynchus*, male reproductive success also relates to male courtship initiation frequency, and to crater height and position (Genner et al. 2008). The further progression of the courtship sequence was not significantly influenced by any crater characteristics in this species. However, courtship was often terminated prematurely (92%), which is similar to our data of courtship sequences terminated before egg-laying (91.5%). Genner and co-authors (2008) hypothesised that females consider additional, unmeasured behavioural or morphological traits for their spawning decisions. Indeed, in *C. furcifer*, the final decision whether or not to lay eggs apparently depends on additional, qualitative crater characteristics. It seems that craters provide more information than is conveyed simply by their size (see Table 2, crater 'impressiveness' and 'roundness'). To our knowledge, no study of crater building cichlids has yet considered such characteristics of crater quality.

In contrast to the observational data, our experiments did not reveal a female preference for larger craters. One obvious explanation of this discrepancy could be that crater manipulation repelled females. However, females did not seem to respond to our crater manipulation *per se* (treatments 3 and 4 in the field), but whether craters changed in size: female visit duration was significantly longer if craters were unmanipulated or rebuilt to the same size, compared to craters which were enlarged or reduced in size. A proximate mechanism for this result may be that crater manipulations elicit a change in male behaviour, for example in crater building, even though we did not find a difference in male building frequency or duration between the two controls versus the two treatments. In the laboratory experiment, however, we observed an increased building activity when crater owners were assigned to a smaller crater. Females visited these downsized craters quicker, probably due to the increased male building activity. This is corroborated by our results of the field experiment that showed more female visits to more actively building males, regardless of the treatment. A similar case, where the construction behaviour of a non-bodily ornament is apparently more important than the ornament itself, has been observed in black wheatears, *Oenanthe leucura*, where males pile up stones in front of their nest cavity. After manipulating the number of stones artificially, female investment in breeding depended on the amount of stones carried by the individual male, but not on the number of stones present at the nest entrance (Soler et al. 1996).

In this study, we did not address the potential effects of crater size on male–male competition and intrasexual selection. Genner and co-authors (2008) hypothesised that in *H. oxyrhynchus*, crater characteristics play a role in male hierarchical assessment and are thus under indirect mate choice, as females of this species showed no preference for

any crater characteristics. A hint in this direction was found in the bower-building Malawi cichlid *Nyassachromis* cf. *microcephalus*, where conspecific male aggression decreased on tall artificial bowers (Martin and Genner 2009). In *C. furcifer*, crater size may also be important for male–male competition, as males with experimentally enlarged craters reduced crater size quickly (Schaedelin and Taborsky 2006). Similar voluntary diminution of a sexual signal was found in spotted bowerbirds, *C. maculata*, where male bower owners with experimentally augmented berry number removed surplus berries, even though berry number correlates with male mating success (Madden 2002). Probably the increased attractiveness to females does not outweigh the greater risk of bower destruction by surrounding bourgeois males if their resource holding potential does not match the quality of their non-bodily ornament.

Multiple signals may be used by females to acquire information on different aspects of male quality (Candolin 2003). We found that female *C. furcifer* consider multiple traits of male behaviour and non-bodily ornaments, such as building behaviour and crater characteristics, throughout the courtship sequence. This may allow females to assess male quality more accurately than when solely observing male courtship. Crater size and quality may reflect the males' past investment over a longer period, whereas his courting behaviour might indicate the males' current condition. Considering a male's building behaviour might even help to discriminate against secondary, transient crater owners that just temporarily take over abandoned craters without investing adequately in their maintenance. Our data suggest that females prefer larger craters early in the choice sequence, whereas qualitative crater characteristics are important later on. This might reflect different possibilities to assess different crater characteristics in dependence of the distance to the crater, with crater size being discernible from far away, but qualitative crater characteristics being better appraised from the crater centre.

So far only few studies investigated the role of the sensory environment and the receiver physiology and psychology (Espmark et al. 2000; Candolin 2003), but considering multiple traits at different stages of the courtship sequence may increase mate search efficiency and reduce errors. Besides the assessment of crater characteristics, we found that the crater construction behaviour *per se* affects female choice in *C. furcifer*. A combination of non-bodily ornaments with display behaviour has been observed also in several species of birds (Soler et al. 1996; Borgia and Presgraves 1998; Coleman et al. 2004). In addition to the potential benefit of thereby providing information on different aspects of a male's quality, this might increase the perception probability of females, for example by the benefit of involving multiple

sensory channels (Hebets and Papaj 2005) or by the possibility that males can actively draw the attention of potential mates to their costly non-bodily ornaments.

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