



Mating craters of *Cyathopharynx furcifer* (Cichlidae) are individually specific, extended phenotypes

FRANZISKA C. SCHAEDELIN & MICHAEL TABORSKY

Department of Behavioural Ecology, Institute of Zoology, University of Bern

(Received 7 January 2005; initial acceptance 18 March 2005;
final acceptance 7 November 2005; published online 17 August 2006; MS. number: 8417)

Sexually selected traits have been intensively studied in the recent past, but there is comparatively little information about the signalling value of the extended phenotype, despite its unique potential in mate choice and intersexual competition. Individuals manipulating their environment to create a nonbodily ornament may reveal their immediate quality more reliably than by using conventional signals. Nonbodily ornaments may also integrate a bearer's behaviour over a recent interval, which would save the potential receiver repeated or prolonged sampling of the signaller's behaviour. We investigated factors involved in the production of a nonbodily ornament and assessed its potential as a signal in the reproductive context. The crater-building behaviour of the Lake Tanganyika cichlid *Cyathopharynx furcifer* was observed and manipulated in the field and laboratory. Craters were maintained for prolonged periods, and crater size correlated with male body size, building behaviour and crater location in the lek. Larger craters had a higher 'neatness index', and this index correlated negatively with a male condition factor. Behaviour of cichlids after a storm and our manipulations of crater size showed that crater size is a repeatable, individual character; destroyed craters were rebuilt to their original sizes roughly within 1 day and both, experimentally enlarged and diminished craters were immediately reconstructed to their original sizes. We conclude that mating craters are an individually characteristic, extended phenotype of the building males and potentially a suitable signal for conspecifics, providing information about the owner's size, capability and condition.

© 2006 The Association for the Study of Animal Behaviour. Published by Elsevier Ltd. All rights reserved.

Dawkins (1978) introduced the term 'extended phenotype' to describe organisms' manipulations of their environment, assuming that there is a genetic basis to such behaviour. This concept refers also to the elaborate mating structures that males of some species build to attract females (e.g. bowers, Borgia et al. 1985; Diamond 1986; Borgia 1995). Structures requiring time, energy or skills to be constructed could reliably signal the amount of investment made over a prolonged period and hence reflect the producer's capabilities (Borgia & Gore 1986). Extended phenotypic traits may signal a potential mate's current condition more accurately than any morphological characteristic developed over much longer or different intervals, such as during an individual's ontogeny. In addition, any nonbodily ornament produced by an

individual can inform passing receivers about the producer's quality, even during his absence (Coleman et al. 2004).

Especially in the context of sexual selection, extended phenotypic traits may provide valuable information to potential mates and competitors. The evolutionary importance of secondary sexual characteristics has been intensively studied (Darwin 1871; Fisher 1930; Zahavi 1975, 1977; Lande 1981; Hamilton & Zuk 1982; Andersson 1982, 1994), but studies have usually focused on bodily ornaments. The same evolutionary mechanisms as described for sexual ornaments may apply to nonbodily ornaments, addressing conspecifics in the context of reproduction (Borgia 1985b; Borgia et al. 1985, 1987; McKaye et al. 1990; Madden 2003; Madden & Tanner 2003; Coleman et al. 2004).

Apart from the often spectacular bowers of bowerbirds (Diamond 1986; Borgia 1995), some components of nest structures may have a signal function in reproduction (e.g. Hoi & Valera 1994; Barber et al. 2001). If there is a relation between nest building and the quality of the producer, the evolution of nest building may partly depend

Correspondence and present address: F. C. Schaedelin, Konrad Lorenz Institute for Ethology, Austrian Academy of Sciences, Savoyenstrasse 1a, 1160 Vienna, Austria (email: F.Schaedelin@klivv.oew.ac.at). M. Taborsky is at the Department of Behavioural Ecology, Zoological Institute, University of Bern, Ethologische Station Hasli, Wohlenstrasse 50a, CH-3032 Hinterkappelen, Switzerland.

on sexual selection mechanisms (Andersson 1994; see also Soler et al. 1998). In the common goby, *Pomatoschistus microps*, for example, nest cover and thus nest quality depend on male condition (Kvarnemo et al. 1998). Similarly, the production of a sticky secretion to secure the algal nest is costly for male sticklebacks, *Gasterosteus aculeatus*; consequently, only males in good condition are able to build neat nests (Barber et al. 2001), which are preferred by females (Östlund-Nilsson 2001; Östlund-Nilsson & Holmlund 2003). In some crater-building cichlids, females in search of mates consider characteristics such as the height or location of a crater (McKaye 1983; McKaye et al. 1990, 2001; Taylor et al. 1998; Kellog et al. 2000). While the display character of a stickleback or goby nest may be secondary to its breeding function, the sand constructions of these mouthbrooding cichlids have no brood care function at all. After laying an egg, the female cichlid typically picks it up immediately and then leaves the crater to brood the eggs in her mouth somewhere else. Therefore, cichlid sand craters are a secondary sexual character similar in function to bowers, mainly serving to attract mates (McKaye et al. 1990; Taylor et al. 1998; Kellog et al. 2000).

In the lekking Lake Tanganyika cichlid *Cyathopharynx furcifer*, sexually active males build mating craters several times larger than the male's body size (Karino 1997; Rossiter 1997). We assessed the potential signalling value of these mating craters and asked whether they are individually distinct, repeatable traits of males. Crater building and maintenance is demanding (Rossiter 1997; Bucher 2004), so natural variation in the ability of males to bear these costs may result in substantial differences in crater characteristics, which should influence male–male competition and female choice. We hypothesized that a crater's attributes are a characteristic that signals individual traits of its constructor. To test this hypothesis, we identified factors influencing crater size and analysed the reaction of crater builders to natural and artificial modifications of crater size. Behavioural observations and experiments were carried out mainly in the field, but complemented with data from aquaria. In this paper, we do not consider the costs of crater building (Rossiter 1997; Bucher 2004) or the benefits derived from different crater sizes (Karino 1997; Rossiter 1997).

METHODS

Study Species

Cyathopharynx furcifer is a lekking cichlid with maternal mouthbrooding that is endemic to Lake Tanganyika, Africa. Sexually active males have elongated pelvic fins with yellow tips and iridescent, gaudy body coloration. These males show elaborate courtship displays and build mating craters by picking up sand with their mouths and spitting it on to the rim of a perfectly circular wall. This activity results in an impressive sand crater with a diameter several times larger than the male's body size.

The rather drab, silver-grey females and juveniles form schools in mid-water at some distance from the leks. Single females occasionally visit a lek and move between craters, apparently inspecting available mates. Males try to

lead females into their crater by spreading their pelvic fins and wriggling the body. If a female follows, the male swims in circles in the crater in front of the female. After circling a few rounds, the male positions himself perpendicular to the crater rim, head out and upwards, and he wriggles with the tail, presumably releasing sperm before leaving the crater. The female stays in the crater and may lay an egg, after which she will spin around and pick it up immediately. After a short excursion the male returns to the crater and starts circling with the female again. This sequence is repeated up to 40 times until the female leaves the crater (Rossiter 1997; personal observations).

Housing Conditions

In the laboratory, at the University of Bern, *C. furcifer*, obtained from cichlid traders in Germany or from a laboratory population, were kept in small (<10), mixed-sex groups in 1000-litre aquaria (260 × 65 cm and 65 cm high). The water temperature was kept at 27°C and the light:dark cycle was 13:11 h light:dark. The fish were fed 6 days per week, with dry flake food (Tetra) or frozen tropical food mix (Artemia, mosquito larvae, daphnia and cyclops), supplemented with chopped organic spinach twice a week. All aquaria had a 5-cm layer of fine river sand (0.1–2 mm), a biological filter and an air stone. In these mixed-sex groups, the biggest males were usually sexually active and built craters in the same way as in the field. Observations and experiments were carried out between August 2001 and January 2004 with permits from the local Veterinary Authority of Bern, Switzerland.

Field Observations

The field site was at Kasakalawe point, Zambia, 4 km west of Mpulungu at the southern tip of Lake Tanganyika (8°46.849'S, 31°04.882'E). All observations were conducted by SCUBA diving and snorkelling from February to May in 2002 and 2003. We made observations throughout the daylight period, but an initial survey showed that crater-building activity declined after 1500 hours. Therefore, all behavioural recordings were done between 0700 and 1400 hours. We investigated three leks at depths of 2–6 m. One lek, extending 50 m at a depth of 2–3.5 m, consisted of 37 craters in 2002. The other two leks were at depths of 4.5–6 m and each contained up to 200 mating craters in 2003. A small, fourth lek at a depth of 9 m was briefly surveyed in 2003. At all leks, the bottom was partly covered with rocks of ca. 15–20 cm in diameter scattered on a sandy substrate. We found no occupied craters outside of these leks.

We measured mating craters and the distances between them (± 0.5 cm). Crater measurements included inner diameter, outer diameter, height of rim from the bottom and depth of crater in its centre. The water depth was measured at the crater base. We also noted crater appearance and assigned numbers to each crater (1–4) to classify quality on an ordinal scale for six criteria. We measured the following variables: (1) relative impressiveness: how large the crater was compared to the surrounding craters; (2)

roundness (4: perfect circle; 3: small imperfection; 2: large imperfection; 1: polygon); (3) proportion of stones incorporated into the crater (4: none; 3.5: $<1/3$; 3: $1/3-1/2$; 2.5: $1/2-2/3$; 2: $2/3-3/4$; 1: $>3/4$); (4) substrate (4: fine sand; 3: more than half fine sand; 2: more than half gravel; 1: only gravel; gravel was small pieces of broken shells and coarse sand grains more than about 3 mm in diameter); (5) type of ground on which the crater was built (4: 90–100% sand; 3: ca. 75% sand; 2: ca. 50% sand; 1: ca. 25% sand); (6) rim sharpness (4: very sharp; 3: rather smooth; 2: round; 1: no recognizable edge). For the analysis, we calculated the mean of all six crater appearance criteria to produce a 'neatness index', ranging from 4 (neatest) to 1 (least neat).

During quantitative behavioural observations of crater owners, we recorded the frequencies of the following behaviours: feeding, shaking of the body (a comfort behaviour), picking up sand, spitting sand onto the crater rim, rearranging sand within the crater, chasing away other fish, courting females, leading females and number of circlings with females. The total time spent picking up a mouthful of sand and swimming back to the crater was also recorded within each observation period. We recorded these behaviours for 289 5-min periods for 38 crater-owning males on 19 days within 1 month in 2002; target craters were chosen randomly ($\bar{X} \pm SE = 8 \pm 0.815$ observations/male). We used the means of all observations of each male. Each crater was measured three times, with a minimum of 7-day intervals between measurements. A stopwatch was used to measure time, and data were recorded on a PVC board with a soft pencil.

At the end of both field seasons, we captured 78 crater owners and measured the following: standard length (SL; tip of the mouth to the base of the tail fin), fork length (FL; tip of the mouth to the sinus of the forked tail fin), length of the forked tail fin at the top and at the bottom, length of the dorsal fin, length of both pelvic fins and maximal body height. We also measured the wet weight of 36 males. As a measure of body condition we used the standard ratio of body weight (w) divided by standard length to the power 3 (L^3). After capture, males usually abandoned their crater and left the lek. New males reoccupied the abandoned craters within a few minutes, enabling us to investigate the body characteristics of new owners in relation to previous owners.

Individual Identification

Since fin clipping turned out to be too invasive (around 10 fish were marked and they all abandoned their territories), we identified 24 crater owners in 2003 by the individual pattern of iridescent green spots on their dorsal flanks and individual fin characteristics. We checked the presence of individual males approximately every 2 weeks.

Experiments

Storm effect

Directly before and after a storm during the night of 21 March 2002, we checked two leks, one of 34 craters of 2 m

depth and one of 35 craters at 5 m depth. We measured 15 craters of the shallower lek before and after the storm.

Destruction experiment

We intentionally destroyed 22 craters by scattering the sand. Afterwards, we measured the diameter of the craters that had been reconstructed by their owners, on each of the next 3 days, and on days 9 and 13 after the destruction. As a control, we also measured 40 untouched craters on the same lek before and after the destruction experiment.

We repeated the destruction experiment in the laboratory. We measured 12 craters before destruction and 3 h, 1 day and 10 days afterwards. We also measured six of these craters 23 days after destruction. This allowed us to observe the change in crater size in an undisturbed environment over a longer period than in the field.

Crater size manipulation

In 2003, in a lek 5 m deep we chose sets of four craters that were relatively close to each other and assigned them haphazardly to one of the following four treatments: (1) enlargement of crater size by a quarter of the diameter; (2) reduction of crater size by a quarter of the diameter; (3) moving sand near the crater to cause a similar disturbance, but without touching the crater, to control for the influence of observer disturbance (control 1); (4) crater destruction and rebuilding it to its original size by the experimenter, to control for the influence of crater manipulation (control 2). With these manipulations, we were able to assess the effect of manipulation on crater size and on the behaviour of crater owners. Crater diameters were measured two or three times after manipulation on the same day and once on the following day.

Statistical Analyses

For statistical analyses we used SPSS 11.0 (SPSS Inc., Chicago, IL, U.S.A.). Data distributions were checked for normality with Kolmogorov–Smirnov tests. When data were normally distributed, we tested correlations with Pearson correlation analyses; otherwise we used Spearman rank correlation tests. Comparisons between means of two samples were analysed with Student's t tests (for normally distributed data) or Mann–Whitney U tests. The choice of ANOVA procedures was also determined in response to underlying distributions. All tests were two tailed. To identify the relation between crater characteristics, crater owners and crater location on the lek, we used a backward binary logistic regression analysis. Craters were divided into two categories, according to the measured distances to all other craters on the lek: we classified craters above the median as peripheral and those below the median as central. The crater-holding duration of individual males was assessed with a survival analysis, and the relation between crater size, male size, lek affiliation and water depth was analysed with a generalized linear model (GLM).

Ethical Note

In the field, the males that we caught for measuring abandoned their territories, but they remained in the general area after being released and a few took over a crater in the vicinity. Experimental crater destruction and crater size manipulations usually did not cause males to abandon their territory, but instead resulted in immediate crater rebuilding (see Results). In the laboratory, fish were kept in mixed-sex groups in spacious tanks allowing them to show their complete behavioural repertoire. Fish were not obviously affected by the experimental manipulations and continued with courtship. The breeding programme and the experiments were approved by the local Veterinary Authority in Bern, Switzerland.

RESULTS

Description of Leks and Craters

Crater-building *C. furcifer* males spat sand on to the rim on average every 15 s ($\bar{X} \pm SD = 15.5 \pm 9.6$ s). We found actively maintained craters of *C. furcifer* at depths of 1–10 m, but most were at 4.5–5.5 m. Leks were 50–200 m apart. Craters on a lek were not randomly distributed but were grouped along a depth contour, which was most pronounced in the largest lek (lek B; data from 2003).

We found considerable variation in crater size on the leks (Fig. 1). For a detailed analysis of crater size, we selected the two large leks of 2003. The larger crater was more than twice the size of the smaller one and the coefficients of variation within leks were 12% for the larger lek ($N = 90$) and 10% for the smaller lek ($N = 58$). In the backward logistic regression analysis of the relation between crater location on the lek and several characteristics of the crater and its owner, only inner crater diameter was a significant factor ($\chi^2_1 = 5.303$, $P < 0.05$), and central craters were larger than peripheral ones. Male body size, male condition and crater neatness did not significantly influence the model. Nevertheless, when we quantitatively determined centrality of craters by measuring the distance to all other craters on the lek and used it as a continuous variable, central craters were not only larger (Spearman correlation: $r_s = -0.478$, $N = 26$, $P < 0.05$), but also 'neater' according to the neatness index ($r_s = -0.474$, $N = 22$, $P < 0.05$; Fig. 2). Males replacing a removed crater builder were significantly smaller than the original owners (Student's t test: $t_{81} = -3.795$, $P < 0.001$). The coefficients of variation of male body size were 5% for the larger lek ($N = 90$) and 3.5% for the smaller one ($N = 58$). Based on survival analysis in leks A and B with individually identified owners checked in 2003 ($N = 24$ craters), the median crater-holding period ranged from 42 to over 46 days.

Relations Between Craters and Crater Owners

Crater sizes and owners' body sizes were positively correlated (field: Pearson correlation: $r_{157} = 0.426$, $P < .001$; laboratory: Spearman correlation: $r_s = 0.811$, $N = 15$, $P < 0.001$; Fig. 3), as were crater size and building

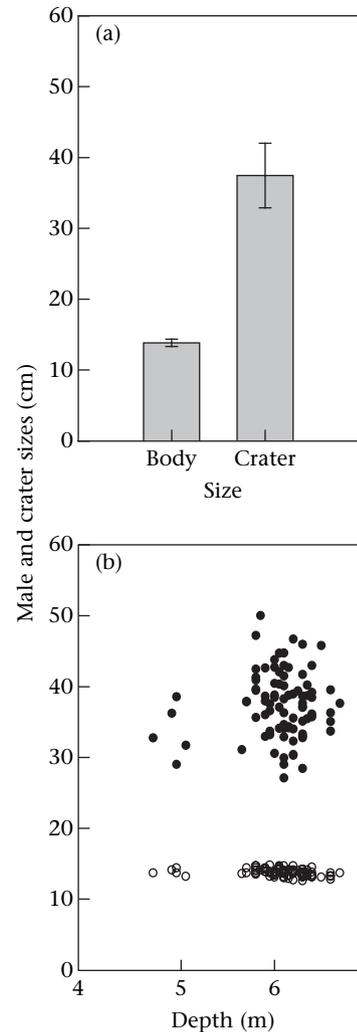


Figure 1. (a) Mean \pm SD male body size and crater size. (b) Individual male (○) and crater (●) sizes at different water depths.

activity of the owner (Spearman correlation: $r_s = 0.353$, $N = 38$, $P < 0.05$; Fig. 4a). Male body size and lek affiliation had a significant influence on crater size (univariate GLM: fork length: $F_{1,81} = 4.87$, $P < 0.05$; lek: $F_{1,81} = 20.779$, $P < 0.001$), whereas the depth of crater location had no effect ($F_{1,81} = 0.0$, $P = 0.988$).

Larger craters were neater, based on a significant positive correlation between crater size and the neatness index (Pearson correlation: $r_{160} = 0.387$, $P < 0.001$; Fig. 4b). Male body condition correlated negatively with crater neatness index (Spearman correlation: $r_s = -0.477$, $N = 22$, $P < 0.05$).

Crater Size Manipulations

Craters destroyed by storm

Craters were affected by wave action, and heavy storms destroyed them. On both leks, most craters were still occupied by the males the day after the storm on 21 March 2002 (numbers of occupied craters before and after the storm, Fisher's exact test: $P = 0.428$). Thus, the storm

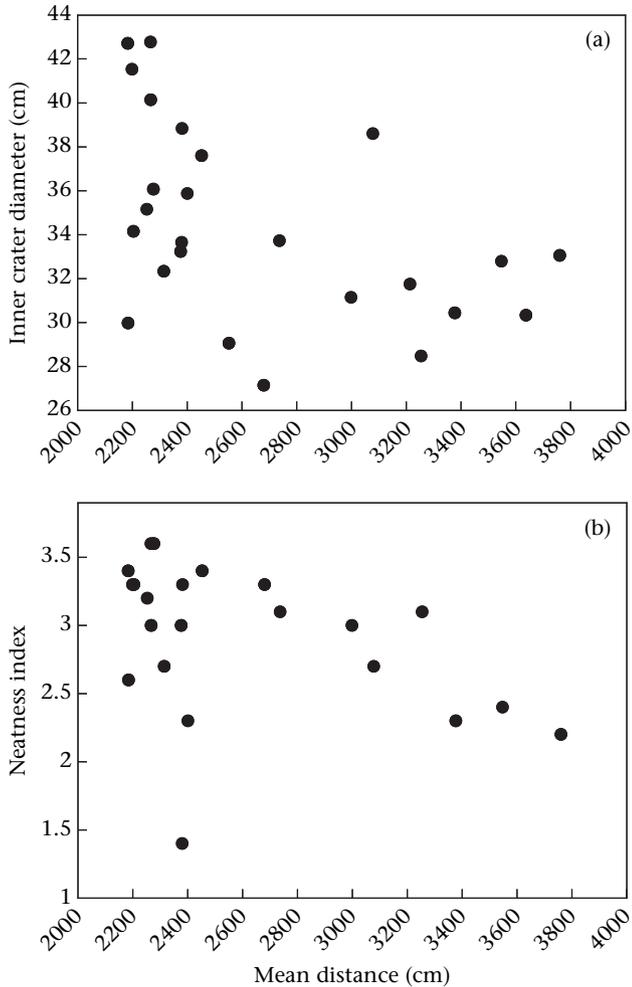


Figure 2. Relation between crater location within the lek (i.e. how central a crater was, as measured by the average distances to all other craters) and (a) inner crater diameter and (b) neatness index (4: nearest crater; 1: least neat).

did not force males to abandon their craters. However, while 91% of the craters in the deeper lek were intact about 9 h after destruction, only 65% of the craters in the shallower lek had been rebuilt (Fisher’s exact test: $P < 0.01$). Fifteen hours after complete destruction by the storm, the sizes of rebuilt craters in the shallow lek were again similar to the sizes before the storm (Fig. 5).

Destruction experiment

In the field, rebuilding of a crater after complete experimental destruction took, on average, 2–3 days. From an initial small depression in the sand bottom, craters grew steadily in diameter and height for several days. Already after 1 day, new crater diameters were not significantly different from the respective diameters of the craters that they replaced (paired t test: $t_{21} = 1.787$, $P = 0.088$). The steady growth of crater diameters continued beyond the original crater size, but at a slower rate; at 9 and 13 days after destruction, average crater diameters were slightly larger than they had been before the

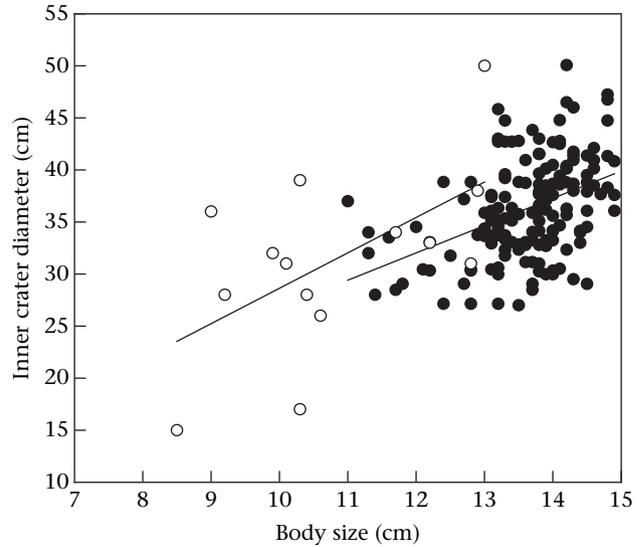


Figure 3. Relation between male body size (fork length) and inner crater diameter in the field (●) and in aquaria (○). Regression lines are shown.

destruction (paired t test: after 9 days: $t_{21} = -2.870$, $P < 0.01$; after 13 days: $t_{20} = -3.226$, $P < 0.01$). During the same interval, the inner crater diameters of 40 untouched craters on the same lek did not change significantly (paired t test: $t_{40} = -0.805$, $P = 0.426$).

In the laboratory, crater reconstruction started immediately, but crater size was still significantly smaller 3 h after the destruction (paired t test: $t_{11} = 3.377$, $P < 0.01$). Similar to result in the field, 1 day after the destruction the diameters of new craters were not significantly different from the respective original diameters (paired t test: $t_9 = 1.652$, $P = 0.133$). Once the original crater size was reached, crater size stayed constant. Crater diameter did not differ significantly from the respective crater diameters before destruction after either 10 days (paired t test: $t_{11} = -0.444$, $P = 0.666$) or 23 days ($t_5 = 1.474$, $P = 0.200$).

Size manipulation experiment

After the crater size manipulation, males immediately rebuilt the craters to their original sizes (Fig. 6). Against our prediction, males quickly rebuilt not only the reduced but also the enlarged craters. There was no difference in inner crater diameters between treatments before the experiment (Kruskal–Wallis test: $H_3 = 0.091$, $P = 0.993$). After only 1 h in the reduced and enlarged treatments, the crater diameters differed significantly from the respective diameters just after the manipulation (paired t tests: reduced treatment: $t_{10} = -7.953$, $P < 0.001$; enlarged treatment: $t_{10} = 2.305$, $P < 0.05$). There was no significant difference in crater diameter between the different treatments 1 day after manipulation (Kruskal–Wallis test: $H_3 = 6.103$, $P = 0.103$) and between the two types of controls (Mann–Whitney U test: $U = 22.5$, $N_1 = 6$, $N_2 = 9$, $P = 0.607$). In both controls there was no significant change in crater diameter during the experiment (repeated measure ANOVA: $F_{1,9} = 0.630$, $P = 0.448$).

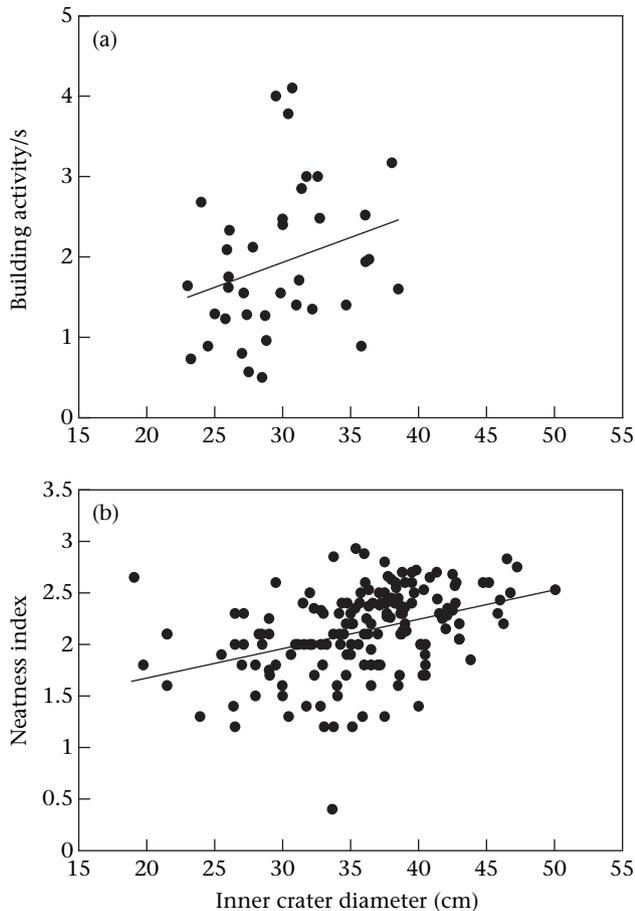


Figure 4. Relation between inner crater diameter and (a) building activity and (b) neatness index (4: neatest crater; 1: least neat).

DISCUSSION

Craters built by individual male *C. furcifer* are a highly repeatable characteristic. Regardless of whether the crater was destroyed by a storm or experimentally, fish rebuilt craters immediately. Both in the destruction and in the manipulation experiments, craters had about the same size as before within a day. Similarly, in *Copadichromis eucinostomus* the top diameter of craters was not significantly different from that of the craters in the control group 1 day after destruction (McKaye et al. 1990). However, the crater destruction in the field in our study had an unexpected long-term effect. After 13 days, the destroyed craters were significantly larger than before the destruction, while there was no change in size in undestroyed craters elsewhere on the lek. We found no long-term effect of crater destruction on size over an even longer interval in the laboratory. The destruction of some craters under natural conditions might have caused an undetected ownership change, with new crater owners perhaps building slightly larger craters.

Surprisingly, fish reconstructed craters to their original size not only after a complete destruction or a reduction in size, but also after enlargement. We therefore concluded that crater size is an individual characteristic of a male. A similar reconstruction effort after experimental manipulation of an animal's construction was observed in the

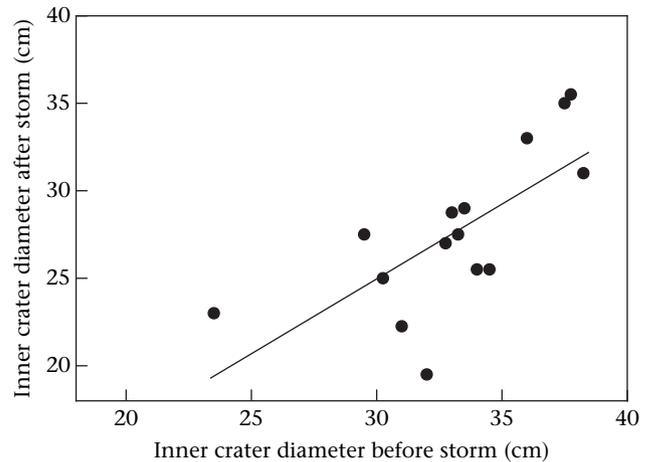


Figure 5. Inner crater diameters before and after a storm, measured in the shallows of two leks 15 h after complete destruction (Pearson correlation: $r_{13} = 0.708$, $P < 0.01$).

stone-provisioning behaviour of chinstrap penguins, *Pygoscelis antarctica* (Moreno et al. 1999) and the black wheatear, *Oenanthe leucura* (Soler et al. 1996). Whereas stone provisioning in chinstrap penguins is apparently an adaptive mechanism to attain prime nest insulation properties (Fargallo et al. 2001), stone piling of black wheatears does not seem to have direct functional significance (Moreno et al. 1994). In this species males pile up large numbers of stones near the nest entrance after pairing, and females modulate their brood care investment according to the observed stone-collecting activities of their mates. After an experimental manipulation of stone piles, males adjusted their stone-collecting activities to the presence of new stones and replaced removed stones (Soler et al. 1996), which resembles the reactions of *C. furcifer* males to our crater manipulations.

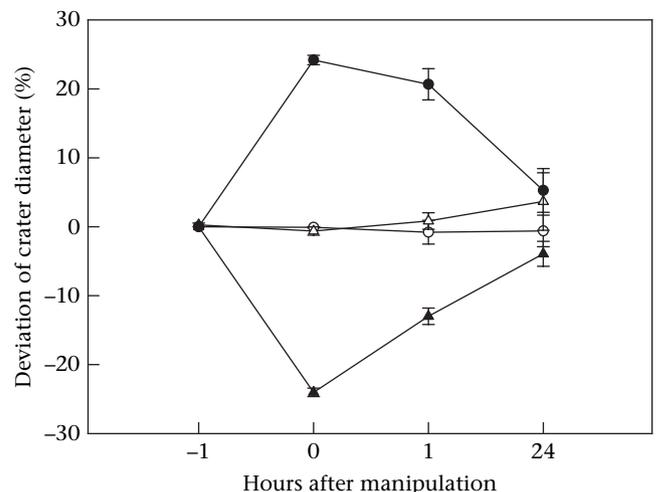


Figure 6. Percentage change in inner crater diameter from the original crater size during the manipulation experiment. The two treatments were 'enlarged' (●) and 'reduced' (▲) crater sizes, the controls were 'untouched' (○) and 'same size' (△). Artificial manipulation took place between the hours -1 and 0.

Since crater size is a highly repeatable, individual characteristic, craters should be viewed as an extended phenotype of the constructor. Several hypotheses have been suggested to explain the crater-building behaviour in cichlids. McKaye (1983) proposed that sand structures may help to collect the gametes and thereby increase fertilization success. However, the large crater size and an unsuitable profile of craters for this purpose (McKaye 1991) mean that, in many species, this cannot be an important function of craters. In addition, if selective processes shaped crater size and form, we would expect one single crater shape and size to be the best. However, we found large variation in crater size in *C. furcifer*. The manipulation of differently sized craters in our experiments also showed that each male reshaped the crater to its own, preferred size and not to a common, 'best' crater diameter.

Alternatively, Barlow (2000) suggested a species recognition function of sand craters. However, this hypothesis can explain neither the repeatability of crater size within males nor the large variation in inner crater diameters on the lek. Furthermore, when *C. furcifer* builds craters on rocks, the crater form is different from the crater shape that we observed at Kasakalawe (personal observation).

A third hypothesis is that craters have a signalling function for conspecifics (McKaye 1983, 1991). Since craters are an individual characteristic of their constructor, they could inform conspecifics about individual properties like any bodily trait. Craters could also provide information that is otherwise not available or difficult to acquire. As a nonbodily ornament, craters also signal properties of the constructor in his absence. Furthermore, the coefficient of variation was two to three times larger for crater size than for body size. Even if crater size correlates with male body size, males of a given size still build differently sized craters, which may contain important information about the constructor's qualities in addition to body size.

Apart from crater size, we also investigated qualitative characteristics of craters. Research on three-spined sticklebacks, *Gasterosteus aculeatus*, suggests that the neatness of nest structures may work as an ornament revealing male health status and androgen level (Barber et al. 2001; Östlund-Nilsson & Holmlund 2003). The glycoprotein production serving to glue nests correlates with food intake in fifteen-spined sticklebacks *Spinachia spinachia*, providing females with an honest nonbodily ornament (Östlund-Nilsson 2001). In *C. furcifer*, crater 'neatness' was positively correlated with crater size and male body size, but males owning a neater crater were in poorer condition, and there was no relation between crater size and body condition. Since the neatness of a crater is probably a good indicator of the male's maintenance activity on a particular day, newly built craters are always neat. During the long crater-holding period of a male, a crater remains neat only if the male continuously maintains it. This crater maintenance over the course of weeks may negatively affect the crater owner's condition. This hypothesis is supported by the observation that newly recruited crater-owning males had the best body condition, but with continued ownership, condition decreased (Rossiter 1997).

To spare building effort, males can incorporate stones into their sand structures. This activity appears economical if stones of the right size are available, because for the volume made up by a stone, the male does not need to transport sand. The economy of using rocks in crater building may explain why leks were located in a mixed rock–sand habitat and not on uniform sand planes. The amount of stones incorporated into the crater did not correlate with crater neatness.

In many lekking species, males, and females choosing mates, favour central positions on leks (Höglund & Alatalo 1995). In *C. furcifer*, in our study more central craters were significantly larger and neater, which suggests that crater position on the lek is important. In addition to male body size and male building behaviour, centrality in the lek is apparently a third factor relating to crater size. The immediate take-over of abandoned craters after experimental removal of male *C. furcifer* in our study suggests that a large reserve of noncrater holders is ready to take over a crater. Within seconds of the removal of the original owners, much smaller males with no elongated fins took over the abandoned crater and started to display. A few minutes later they were usually replaced by larger males. Nevertheless, these replacing males were significantly smaller than the original crater owners. The outcome of aggressive encounters in fish is usually predicted by body size (Koops & Grant 1993), so this result suggests that larger, more dominant males exclude smaller males from owning a crater on the lek.

Male–male competition could also explain why males reduced the size of an enlarged crater in the manipulation experiment. Males often inspect neighbouring craters on the lek, so competitors are probably well informed about available craters. A male with a crater that is too large for his resource-holding power (Parker 1974) might not be able to defend his crater against potential intruders, so bluffing may not pay. Consequently, in a low-competition situation, we would not expect males to reduce the size of experimentally enlarged craters. In the laboratory, if only two males shared a tank they did not reduce enlarged craters, but they reconstructed reduced craters to their original size within 1 day (unpublished data). Similarly, in bowerbirds, the male dominance hierarchy is reflected by the quality and persistence of a bower (Borgia 1985a; Borgia & Gore 1986). Artificially supplemented bowers of spotted bowerbirds, *Chlamydera maculata*, suffer from increased levels of destruction by other males (Miles & Madden 2002). Bower owners seem to realize this risk and actively remove supplemented decorations. Furthermore, satin bowerbird, *Ptilonorhynchus violaceus*, males with an experimentally provided supply of blue chips did not add as many new chips as did those males that were not provided with chips (Borgia 1993), even if they were available free and despite blue decoration pieces being a key factor in the successful attraction of females. These results are compatible with the hypothesis that bower decorations are used as an honest signal.

Male *C. furcifer* are constantly busy either defending the crater against intruders or rearranging sand in the crater. In the present study, this building activity was positively

correlated with crater size, indicating that maintenance of larger craters demands a higher initial building effort and more building investment. Therefore, a large crater signals to a conspecific that the crater owner is able to invest much time and energy in crater building. The crater, as a nonbodily ornament, may allow a more accurate and reliable assessment of male quality than a bodily ornament does. A bodily ornament takes longer to develop and therefore might be influenced by variable environmental circumstances that are unknown to the receiver. The receiver may not be able to judge whether a high-quality bodily ornament is the result of the favourable environmental conditions during its development or whether it represents the individual's special ability to cope with environmental stress. A reflection of momentary investment and capability is a common advantage of behavioural signals. However, the physical presence, shape and quality of the crater are an integrative outcome of a behaviour performed over several days. Therefore, conspecifics may obtain an appropriate assessment of the crater at the first visit and spare the time and energy needed for repeated or prolonged sampling.

What mechanism is behind the evidence that crater size in *C. furcifer* is an individual character? Each male apparently has a concept of his specific crater size and keeps it over prolonged periods, even though he could probably build any other crater size as well. Alternatively, crater size could be a mere by-product of the building procedure, which may itself depend on a certain trait of the male. The procedure is the same in all males: they pick up sand somewhere around the crater, swim through the middle of the crater and spit the sand out onto the crater rim opposite to where they first passed it. Thus, crater radius might be determined just by the swimming speed or by male body size. However, body size had only a limited (although significant) influence on crater size. Also, the course of the reconstruction in the destruction experiment showed a steady growth of the inner crater diameter. Therefore, a purely mechanistic explanation based only on the building procedure seems unlikely.

In conclusion, mating craters in *C. furcifer* are individually characteristic and highly repeatable extended phenotypes. As a nonbodily ornament, mating craters may signal aspects of male quality such as body size, resource-holding power, investment during the recent past and individual building capabilities.

Acknowledgments

We thank Valerio Rizzo, Katharina Peer and Oliver Otti for field assistance and the anonymous referees for helpful comments on the manuscript. We thank H. Phiri, R. Shapola, L. Makasa, D. Sinyinza and C. Lukwesa from the Fisheries Department, Mpulungu, Zambia and the Ministry of Agriculture and Co-operatives of Zambia, in particular Director C. Kapasa, for support. We thank the members of the Lake Tanganyika Diving Expeditions 2002 and 2003 for their assistance and R. Eggler, S. Maurer and P. Stettler for helping to organize these expeditions. We are particularly grateful to Dik Heg for valuable suggestions.

The project was supported by a grant from the Swiss National Science Foundation (no. 3100-064396) to M.T.

References

- Andersson, M. 1982. Female choice selects for extreme tail length in a widowbird. *Nature*, **299**, 818–820.
- Andersson, M. 1994. *Sexual Selection*. Princeton, New Jersey: Princeton University Press.
- Barber, I., Nairn, D. & Huntingford, F. A. 2001. Nests as ornaments: revealing construction by male sticklebacks. *Behavioral Ecology*, **12**, 390–396.
- Barlow, G. W. 2000. *The Cichlid Fishes: Nature's Grand Experiment in Evolution*. Cambridge, Massachusetts: Perseus.
- Borgia, G. 1985a. Bower destruction and sexual competition in the satin bowerbird (*Ptilonorhynchus violaceus*). *Behavioral Ecology and Sociobiology*, **18**, 91–100.
- Borgia, G. 1985b. Bower quality, number of decorations and mating success of male satin bowerbirds (*Ptilonorhynchus violaceus*): an experimental analysis. *Animal Behaviour*, **33**, 266–271.
- Borgia, G. 1993. The cost of display in the non-resource-based mating system of the satin bowerbird. *American Naturalist*, **141**, 729–743.
- Borgia, G. 1995. Complex male display and female choice in the spotted bowerbird: specialized function for different bower decorations. *Animal Behaviour*, **49**, 1291–1301.
- Borgia, G. & Gore, M. A. 1986. Feather stealing in the satin bowerbird (*Ptilonorhynchus violaceus*): male competition and the quality of display. *Animal Behaviour*, **34**, 727–738.
- Borgia, G., Pruett-Jones, S. G. & Pruett-Jones, M. A. 1985. The evolution of bower-building and the assessment of male quality. *Ethology*, **67**, 225–236.
- Borgia, G., Kaatz, I. M. & Condit, R. 1987. Flower choice and bower decoration in the satin bowerbird *Ptilonorhynchus violaceus*: a test of hypotheses for the evolution of male display. *Animal Behaviour*, **35**, 1129–1139.
- Bucher, M. 2004. The costs of a non-bodily ornament: crater building in the cichlid fish, *Cyathopharynx furcifer*. M.Sc. thesis, University of Bern.
- Coleman, S. W., Patricelli, G. L. & Borgia, G. 2004. Variable female preferences drive complex male displays. *Nature*, **428**, 742–745.
- Darwin, C. 1871. *The Descent of Man and Selection in Relation to Sex*. London: Murray.
- Dawkins, R. 1978. Replicator selection and extended phenotype. *Zeitschrift für Tierpsychologie*, **47**, 61–76.
- Diamond, J. 1986. Animal art: variation in bower decorating style among male bowerbirds *Amblyornis inornatus*. *Proceedings of the National Academy of Sciences, U.S.A.*, **83**, 3042–3046.
- Fargallo, J. A., De Leon, A. & Potti, J. 2001. Nest-maintenance effort and health status in chinstrap penguins, *Pygoscelis antarctica*: the functional significance of stone-provisioning behaviour. *Behavioral Ecology and Sociobiology*, **50**, 141–150.
- Fisher, R. A. 1930. *The Genetical Theory of Natural Selection*. Oxford: Clarendon Press.
- Hamilton, W. D. & Zuk, M. 1982. Heritable true fitness and bright birds: a role for parasites? *Science*, **218**, 384–387.
- Hoi, H. & Valera, F. 1994. Female mate choice and nest desertion in penduline tits, *Remiz pendulinus*: the importance of nest quality. *Animal Behaviour*, **48**, 743–746.
- Höglund, J. & Alatalo, R. V. 1995. *Leks*. Princeton, New Jersey: Princeton University Press.
- Karino, K. 1997. Female mate preference for males having long and symmetric fins in the bower-holding cichlid *Cyathopharynx furcifer*. *Ethology*, **103**, 883–892.

- Kellog, K. A., Stauffer, J. R. J. & McKaye, K. R. 2000. Characteristics that influence male reproductive success on a lek of *Lethrinops* c.f. *parvidens* (Teleostei: Cichlidae). *Behavioral Ecology and Sociobiology*, **47**, 164–170.
- Koops, M. A. & Grant, J. W. A. 1993. Weight asymmetry and sequential assessment in convict cichlid contests. *Canadian Journal of Zoology*, **71**, 475–479.
- Kvarnemo, C., Svensson, O. & Forsgren, E. 1998. Parental behaviour in relation to food availability in the common goby. *Animal Behaviour*, **56**, 1285–1290.
- Lande, R. 1981. Models of speciation by sexual selection on polygenic traits. *Proceedings of the National Academy of Sciences, U.S.A.*, **78**, 3721–3762.
- McKaye, K. R. 1983. Ecology and breeding behaviour of a cichlid fish, *Cyrtocara eucinostomus*, on a large lek in Lake Malawi, Africa. *Environmental Biology of Fishes*, **8**, 81–96.
- McKaye, K. R. 1991. Sexual selection and the evolution of the cichlid fishes of Lake Malawi, Africa. In: *Cichlid Fishes: Behavior, Ecology and Evolution* (Ed. by M. H. A. Keenleyside), pp. 241–257. New York: Chapman & Hall.
- McKaye, K. R., Louda, S. M. & Stauffer, J. R. 1990. Bower size and male reproductive success in a cichlid fish lek. *American Naturalist*, **135**, 597–613.
- McKaye, K. R., Stauffer, J. R., Turner, G. F., Konings, A. & Sato, T. 2001. Fishes, as well as birds, build bowers. *Journal of Aquaculture and Aquatic Science*, **9**, 121–133.
- Madden, J. R. 2003. Male spotted bowerbirds preferentially choose, arrange and proffer objects that are good predictors of mating success. *Behavioral Ecology and Sociobiology*, **53**, 263–268.
- Madden, J. R. & Tanner, K. 2003. Preferences for coloured bower decorations can be explained in a nonsexual context. *Animal Behaviour*, **65**, 1077–1083.
- Miles, A. J. & Madden, J. R. 2002. Bower location by the spotted bowerbird (*Chlamydera maculata*). *Emu*, **102**, 187–193.
- Moreno, J., Soler, M., Møller, A. P. & Linden, M. 1994. The function of stone carrying in the black wheatear, *Oenanthe leucura*. *Animal Behaviour*, **47**, 1297–1309.
- Moreno, S., Moreno, J. & De Leon, A. 1999. The effect of nest size on stone-gathering behaviour in the chinstrap penguin. *Polar Biology*, **22**, 90–92.
- Östlund-Nilsson, S. 2001. Fifteen-spined stickleback (*Spinachia spinachia*) females prefer males with more secretional threads in their nests: an honest-condition display by males. *Behavioral Ecology and Sociobiology*, **50**, 263–269.
- Östlund-Nilsson, S. & Holmlund, M. 2003. The artistic three-spined stickleback (*Gasterosteus aculeatus*). *Behavioral Ecology and Sociobiology*, **53**, 214–220.
- Parker, G. A. 1974. Assessment strategy and the evolution of fighting behaviour. *Journal of Theoretical Biology*, **47**, 223–243.
- Rossiter, A. 1997. Intraspecific plasticity in the social system and mating behaviour of a lek-breeding cichlid fish. In: *Fish Communities in Lake Tanganyika* (Ed. by H. Kawanabe, M. Hori & M. Nagoshi), pp. 194–217. Kyoto: Kyoto University Press.
- Soler, J. J., Møller, A. P. & Soler, M. 1998. Nest building, sexual selection and parental investment. *Evolutionary Ecology*, **12**, 427–441.
- Soler, M., Soler, J. J., Møller, A. P., Moreno, J. & Linden, M. 1996. The functional significance of sexual display: stone carrying in the black wheatear. *Animal Behaviour*, **51**, 247–254.
- Taylor, M. I., Turner, G. F., Robinson, R. L. & Stauffer, J. R. 1998. Sexual selection, parasites and bower height skew in a bower-building cichlid fish. *Animal Behaviour*, **56**, 379–384.
- Zahavi, A. 1975. Mate selection: a selection for a handicap. *Journal of Theoretical Biology*, **53**, 205–214.
- Zahavi, A. 1977. The cost of honesty. *Journal of Theoretical Biology*, **67**, 603–605.