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Sexual conflict over breeding substrate causes female expulsion and offspring loss in a cichlid fish

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Females of the Lake Tanganyika cichlid *Lamprologus callipterus* exclusively breed in empty snail shells that males collect in their territories. Male–male competition for shells is severe, leading to frequent shell stealing and territory takeover. As a consequence, males have breeding females in their shells that spawned with competitors. In this field study, we investigated both naturally occurring and experimentally induced encounters of territorial males with females that had spawned with other males. We found that the breeding success of females that were taken over by a different male was significantly reduced. Behavioral observations after experimental shell relocation further showed that males recognized females that they had not spawned with: males directed more exploration and manipulation behavior toward such shells compared with controls. Reoccupation rate of emptied experimental shells was significantly higher than that of unmanipulated empty shells. This indicates that shell stealing and nest takeover, followed by female expulsion, contribute to the reproductive success of *L. callipterus* males. We also found that female mate choice reduces expulsion risk: females preferred to mate with large males, and male size correlated with dominance. We conclude that the limited availability of breeding substrate is a key determinant of both intrasexual competition and intersexual conflict in this species. *Key words:* cichlid fish, infanticide, Lake Tanganyika, *Lamprologus callipterus*, resource defense polygyny, shell brooding. *[Behav Ecol 19:302–308 (2008)]*

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Conflicts of interest between males and females inevitably arise from differential reproductive investment (Arnqvist and Rowe 2005). One extreme expression of such conflict is infanticide, which has been studied most extensively in mammals (e.g., primates [Dunbar 1988], cats [Natoli 1990], and rodents [Lonstein and De Vries 2000]). In mammals, a widespread functional cause of infanticide is that males force females to become receptive again when they are caring for offspring that were sired by another male (Hrdy 1974; Grinnell and McComb 1996).

A variety of female counterstrategies has been reported, such as cooperation among females (Hrdy 1974; Grinnell and McComb 1996) or cooperation of females with subdominant males (Struhsaker and Leland 1985; Harcourt and Greenberg 2001), pseudoestrus (Hrdy 1974; Jeppsson 1986; Zinner and Deschner 2000), and confusion of paternity by extrapair copulations (Reichard 1995; Brockman and Whitten 1996). Female choice for high-quality males may decrease the risk of infanticide by intruders in primates (Paul 2002).

In fish, infanticide typically takes the form of filial cannibalism: the consumption of one's own offspring, which is particularly common in species with paternal care (Sargent 1997; Manica 2002). Due to reduced feeding opportunities and energetic costs associated with paternal care, male physical condition deteriorates during the breeding cycle, and cannibalism is a way to replenish energy reserves (e.g., sticklebacks [Rohwer 1978], river bullheads [Marconato et al. 1993], bluegill sunfish [Coleman and Fischer 1991]), but other functions of cannibalism by brood-caring males have been suggested (Belles-Isles and Fitzgerald 1991; Payne et al. 2002; Klug and St Mary 2005). To dilute the risk of filial cannibalism by males, females of several species preferentially lay their eggs in nests already containing high numbers of eggs (e.g., sand gobies [Forsgren et al. 1996], blennies [Kraak and Weissing 1996], river bullheads [Marconato and Bisazza 1986]) or supplement their clutches with "dummy eggs" that do not contain yolk (Kume et al. 2002). Finally, female choice for males in good physical condition may in some cases be driven by cannibalism avoidance (Manica 2002).

Here, we study the polygynous African cichlid *Lamprologus callipterus*, in which reproductive conflict leads to infanticide by nesting males. In this species, infanticide appears to serve a very different purpose than hitherto discussed: it makes breeding substrate available for new mates.

The mating system of *L. callipterus* is characterized by resource defense polygyny (Emlen and Oring 1977). This cichlid actively gathers resources that are necessary for reproduction: males collect empty snail shells (*Neothauma tanganicense*) in their territories and females breed in these shells. In order to reproduce, females rely exclusively on these shells (Sato 1994; Schütz and Taborsky 2000). In fact, female and male sizes are limited by the sizes of available shells, albeit in opposite directions (Schütz and Taborsky 2005). Nest males are more than 12 times larger than females (body weight; Schütz and Taborsky 2000). Males are subject to intense intrasexual selection in which the possession of suitable shells is of crucial importance (Taborsky 2001; Sato et al. 2004; Schütz and Taborsky 2005; Schütz et al. 2006). Indeed, only a minor proportion of males defend a territory at any given point in time. Sato (1994) showed that territories of larger males contain more shells and that these males have higher reproductive success. He observed that territory owners frequently

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intrude into neighboring nests to steal shells or take over the entire territory. In both these cases, the males are aggressive toward the breeding females inside the shells. Sato (1994) proposed that by expelling females that had spawned with other males, the territory owner creates breeding space for new females that are ready to spawn with him.

Thus, in this species there is not only male–male but also male–female competition for breeding substrate, with severe consequences for females. When expelled, females will lose their offspring, but unlike in many mammalian species, in *L. callipterus* such females will not spawn with the infanticidal male. This is because they need a few weeks to replenish resources to be able to lay eggs again (Schütz 1998; Schütz et al. 2006).

Laboratory experiments (Taborsky M, unpublished data) suggest that *L. callipterus* males discriminate between females they spawned with and strange females. When presented with a nest containing shells with breeding females, takeover males expelled these females by burying the shells under sand. In contrast, when females were offered that were ready to spawn, males spawned with them and accepted them for their entire breeding period.

In this field study, we investigate both naturally occurring and experimentally induced encounters of territorial males with females that have spawned with other males. We test whether males discriminate between offspring they have sired and offspring sired by other males. In experimental manipulations, we further investigate whether expulsion behavior of males and resistance of females are influenced by the breeding stage of the female. We expect that a male, confronted with a strange female in her final stages of brooding the fry, will not expel her if this involves costs to him because she will leave the shell soon anyway. Similarly, for a female it would not pay to submit to male aggression and leave the shell because due to the advanced stage of her offspring they constitute an important part of their reproductive value. In contrast, in the early breeding stages a male's potential benefit from female expulsion is high because he would gain considerable opportunity to accommodate a new female. At the same time, the cost of leaving for the female is relatively low as the offspring are still young and their survival probability is low. Males should thus try to acquire information about females and the developmental stage of the offspring and, depending on the costs involved in female expulsion, predominantly expel them during the earlier breeding stages. We test this hypothesis by varying the stage of the breeding cycle in which shells are experimentally relocated. We further investigate how shell stealing and female expulsion influence male reproductive success. We test whether the number of shells in a territory influences female choice and would thereby function as an extended phenotype signal, and we quantify the reoccupation rates of emptied shells. Finally, we ask whether females choose superior males that defend their territories well to reduce the risk of territory takeover or shell stealing by intruder males.

METHODS

Study area

During a period of 48 days (January–February 1997), we studied the behavior of *L. callipterus* in an area of 144 000 m^2 at Kasakalawe Point west of Mpulungu, Zambia, at the southern tip of Lake Tanganyika, using scuba diving. The study area extended from 9 to 11 m depth and consisted of sandy bottom covered with rocks. We observed 34 nests. The distance between nests was 4.9 ± 2.4 m (mean ± standard deviation). All shells occupied with a female were marked with elastic rubber bands with numbered labels. These were prepared beforehand and put around the shells under water. In addition, we used wax pencils to mark shells under water.

Experiments and controls

To test for male response to offspring sired by other males, we exchanged shells that were occupied by brooding females ($n = 68$) between nests. To increase the chance that territory owners would notice the change, experimental shells were placed at approximately 10-cm distance from the original position of the shells for which they were exchanged but always within the perimeter of the nest. Every shell transfer from the original nest to another nest is considered a replicate. For the following 3 days or more, we checked whether the exchanged shell was still occupied. In the control treatment, we took shells from nests and returned them to the same nest ($n = 30$) after transporting them for 2–5 min, which matched the time used for exchange of shells between nests in the experimental treatment. Again, the shells were placed at a distance of approximately 10 cm from their original positions, within the nest perimeter.

Experiments and controls were done in 3 breeding stage categories: days 1–3 (egg stage, 37 experiments and 16 controls), days 4–6 (early larval stage, 25 experiments and 10 controls), and days 7–9 (late larval stage, 6 experiments and 5 controls). Of all experiments and controls performed, we could record breeding success of 54 experimental females ($n = 29$, 20, and 5 for breeding stages 1, 2, and 3, respectively) and 28 control females ($n = 14$, 9, and 5). The other manipulated shells were stolen, involved in nest takeovers, or disappeared. Successful experiments and controls involved 26 territories and at least 30 males (due to nest takeovers and incomplete marking of individual males [see below], we can only make a minimum estimate of the total number of males involved). No male was used more than once in manipulations of shells in the same breeding stage. Thus, the number of experiments and controls performed in each breeding stage represents the number of males used.

Nest takeovers: male catching and marking

To determine when nest takeovers occurred, we marked 20 territory owners. They were caught with a fence net and hand nets and subsequently marked by injecting ink under the skin or into scale pouches (see Taborsky 1984). Additionally, 5 males were caught and not returned to their territories in order to create opportunities for other males to take over these nests.

Female choice

We measured total length of 13 territory owners (with calipers, to the nearest 0.1 mm), counted the number of breeding females (as a measure of female choice), and took several measures of territory quality: the total number of shells, the number of intact shells, and the size of intact shells (with calipers, shell length from tip to most distant point of opening, to the nearest 0.1 mm).

Nest checks and behavioral observations

We checked all nests for the presence of territory owners and females once or twice a day. In addition, we performed 10-min focal male observations immediately after experiments (27 observations) and controls (24 observations), in which the following behaviors of the territory owners were recorded.

Shell exploration—the male pushes his head into the shell entrance and makes sniffing movements: the fish opens and closes its mouth and opercula and thereby creates a water current. *Shell manipulation*—a shell is pushed, turned, moved, or picked up and thrown about by the territory owner.

During observations, we recorded whether these behaviors were directed toward the experimental shells or toward other occupied shells in the nest. To compare the activity of nest males toward experimental shells with that toward other shells in the nest, we divided the frequencies of behaviors directed toward other shells by the number of occupied shells in the nest. We only considered occupied shells for this analysis because these behaviors are very rarely directed toward empty shells (Maan ME and Taborsky M, personal observation).

Underwater video

With unmanned underwater video cameras, we made time-lapse recordings for additional 10-min observations after experiments ($n = 6$) and controls ($n = 1$). To determine the natural frequency of shell exploration and manipulation behavior of undisturbed territory owners, we also made fifteen 10-min observations of 4 nests at days when they were neither involved in experiments nor controls. Finally, to estimate the cost of female expulsion for males, we observed the behavior of 3 territory owners toward experimentally relocated shells continuously up to the moment that the female left the shell.

Calculations

To quantify the effect of experiments, controls, natural shell theft, and nest takeover and to compare this with unmanipulated shells, we calculated breeding success rates. Based on 23 known cases of successful broods, we calculated the average leaving day of successful females, which was day 12. This matches earlier observations (Takamura [1987]: 10–14 days and Sato [1994]: up to 17 days). Thus, females that stayed for at least 10 days inside shells, that is, that left at day 11 or later, were considered to have produced successful broods. The breeding success rate is the proportion of successful broods in relation to the total number of breeding attempts within a category and is expressed as percentage.

To compare the overall success rates of manipulated females with unmanipulated ones, we used subsamples of unmanipulated shells that had the same distribution of breeding stages as the manipulated sample. This was necessary because breeding success rates varied with female breeding stage (see Results). The size of these subsamples differs for each comparison because the proportion of females in different breeding stages differs for each group of manipulated females (i.e., experiment, control, and females involved in nest takeover or shell theft).

To determine the effect of female expulsion on male reproductive success, we calculated reoccupation rates of experimental shells that were emptied by nest owners and compared those with the occupation data of 100 randomly selected unmanipulated shells. Reoccupation rate was defined as the number of shells that was occupied within 3 days after being emptied.

Estimation of censored data

We did not always have complete information about shells and females. For example, shells containing breeding females disappeared or lost their marking. In such cases, we estimated the total occupation period in order to be able to include these females in the calculations rather than disregarding them. This was done because the number of these cases is considerable: 163 out of 454. Moreover, the chance that the information about a female breeding cycle is not complete increases with occupation duration. Therefore, disregarding all cases with censored data would bias the results toward shorter incubation period estimates. Using day 12 as the average leaving day, the chances of leaving at any given day were calculated for each of the uncertain females, assuming for simplicity that leaving chances were the same for each day. Consider, for example, a shell with a breeding female that disappeared on the fifth day after spawning. This female may have left the shell on any day between days 5 and 12. It follows that the leaving probability at any of these days is 1/7. In the estimation of success rate, this female would be included with 2/7: the probability that she left on day 11 (1/7) or day 12 (1/7). If she left on days 6, 7, 8, 9, or 10, she would be considered unsuccessful (5/7).

Statistics

All statistics were carried out using SPSS 10.0 (SPSS Inc, Chicago IL) and applying 2-tailed tests throughout. Breeding success was analyzed using chi-square and Kruskal–Wallis tests. Male behavior toward experimental, control, and unmanipulated control shells was analyzed with Mann–Whitney U tests for independent comparisons (between males) and Wilcoxon signed-rank tests for paired comparisons (within males). Correlations between male size, territory characteristics, numbers of females in a territory, and the time interval until shells were emptied were analyzed with Spearman rank correlations. Male size was normally distributed (Kolmogorov–Smirnoff test, $P > 0.9$), and we therefore used an independent sample t-test to analyze the size difference between males that were subject to nest takeover and those that were not.

RESULTS

Shell stealing and nest takeovers

We observed 3 spontaneous nest takeovers, and we removed 5 territory owners. Within 24 h of male removal, new territory owners were present. Forty-four marked occupied shells were present in these territories. Of these, 12 shells disappeared, 12 shells were stolen (see below), and 20 shells remained. All remaining shells were emptied within the next 48 h. During nest takeovers, shell thieves did not show a preference for either occupied or empty shells: of 44 occupied and 39 empty shells, 12 occupied (27%) and 8 empty (21%) shells were stolen ($\chi^2 = 0.39$, degrees of freedom [df] = 1, $P = 0.53$).

We recorded 13 natural instances of shell stealing involving occupied shells that were not related to territory takeovers. Including the shells that were stolen during nest takeovers, breeding success of stolen females was 20%. This is significantly lower than the success rate of a subsample of unmanipulated shells with the same distribution of breeding stages ($n = 100$, success rate = 44%): $\chi^2 = 5.32$, df = 1, $P = 0.017$. Of the females that were stolen in breeding stage 1 ($n = 8$) and 2 ($n = 7$), none were successful (compared with unmanipulated shells: stage 1: $\chi^2 = 1.95$, df = 1, $P = 0.16$; stage 2: $\chi^2 = 4.40$, df = 1, $P = 0.033$). Of the 10 females that were stolen in stage 3, 5 were successful which is not significantly different from unmanipulated shells ($\chi^2 = 0.91$, df = 1, $P = 0.29$). Most shells were stolen from territories of nearest neighbors (including empty shells, 42 out of 57 stolen shells = 74%).

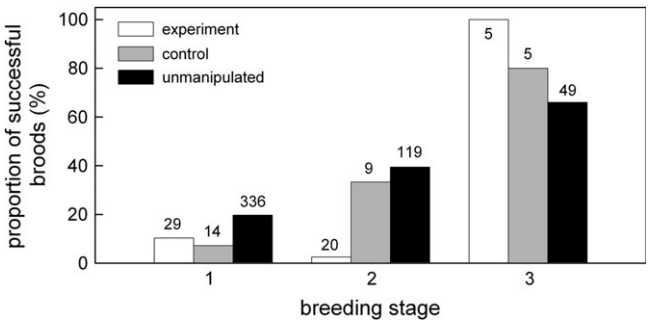

Figure 1
Breeding success of experimental, control, and unmanipulated females for different breeding stages. Sample sizes are given above each bar.

Experiments and controls: breeding success

The breeding success of experimental females was 16% (9 out of 54) and that of control females 29% (8 out of 28). This difference is not significant ($\chi^2 = 1.26$, df = 1, $P = 0.26$). We compared these overall success rates with a subsample of unmanipulated shells with the same distribution of breeding stages. Experimental manipulation significantly reduced breeding success (unmanipulated sample: $n = 270$, success rate = 31%, $\chi^2 = 4.60$, df = 1, $P = 0.022$), but control manipulation did not (unmanipulated sample: $n = 252$, success rate = 34%; $\chi^2 = 0.35$, df = 1, $P = 0.53$).

Breeding success increased significantly with breeding stage (Figure 1; general linear model [GLM] estimate = 1.06 ± 0.22, $F_{1,7} = 25.25$, $P = 0.002$). There was a significant interaction effect of experimental treatment and breeding stage on breeding success: GLM estimate = 0.35 ± 0.09, $F_{1,7} = 16.21$, $P = 0.005$. This was due to a lower breeding success of experimental females in stage 2 (compared with controls: $\chi^2 = 9.15$, df = 1, $P = 0.003$; compared with unmanipulated females: $\chi^2 = 11.13$, df = 1, $P < 0.001$, Figure 1). In breeding stages 1 and 3, breeding success did not differ between treatment groups ($\chi^2 < 2.9$, df = 2, $P > 0.2$). There was no difference between controls and unmanipulated females in any of the breeding stages: $\chi^2 < 1.4$, df = 1, $P > 0.2$.

Behavior of nest males toward experimentally transferred shells

Territory owners showed increased levels of both exploration and manipulation behavior toward experimental shells compared with unmanipulated shells in their territories (Figure 2; Wilcoxon signed-rank test, $n = 32$, exploration: $Z = -2.79$, $P = 0.005$ and manipulation: $Z = -3.21$, $P = 0.001$) but not toward control shells ($n = 24$, exploration: $Z = -0.30$, $P = 0.77$ and manipulation: $Z = -0.61$, $P = 0.54$).

In a direct comparison between experimental shells and controls, the difference in exploration behavior was not significant (Mann–Whitney U test, $n_1 = 32$, $n_2 = 24$, $Z = -1.792$, $P = 0.073$), but the difference in manipulation behavior was highly significant ($Z = -2.935$, $P = 0.003$).

The behavior of territory owners toward experimental shells did not differ between observations carried out while diving and observations from video recordings (Mann–Whitney U tests; $n_{diving} = 26$, $n_{video} = 6$; exploration: $Z = -0.22$, $P = 0.83$; manipulation: $Z = -0.36$, $P = 0.76$). Similarly, male behavior toward unmanipulated shells during randomly collected video observations did not differ from male behavior during diving observations after experiments and controls (Kruskal–Wallis tests; $n_{experiments} = 26$, $n_{controls} = 23$, $n_{video} = 15$; exploration: $\chi^2 = 3.48$, df = 2, $P = 0.18$; manipulation: $\chi^2 = 0.76$, df = 2, $P = 0.69$). This indicates that observer disturbance was negligible.

Although breeding success of experimental females was reduced in the second breeding stage only, breeding stage was not significantly related to exploration or manipulation frequencies toward experimental shells (Kruskal–Wallis test; $n_1 = 18$, $n_2 = 12$, $n_3 = 2$; exploration: $\chi^2 = 0.30$, df = 2, $P = 0.86$; manipulation: $\chi^2 = 0.40$, df = 2, $P = 0.82$).

Continuous video observations of 3 territory owners after experiments showed that they manipulated the experimental shells for at least 70, 27, and 22 times until the female left, taking 187, 230, and 390 min, respectively.

Why do males steal shells and expel females?

If males expel females because they need breeding substrate, their expulsion effort of experimental shells should be influenced by the number of available shells in the territory. The

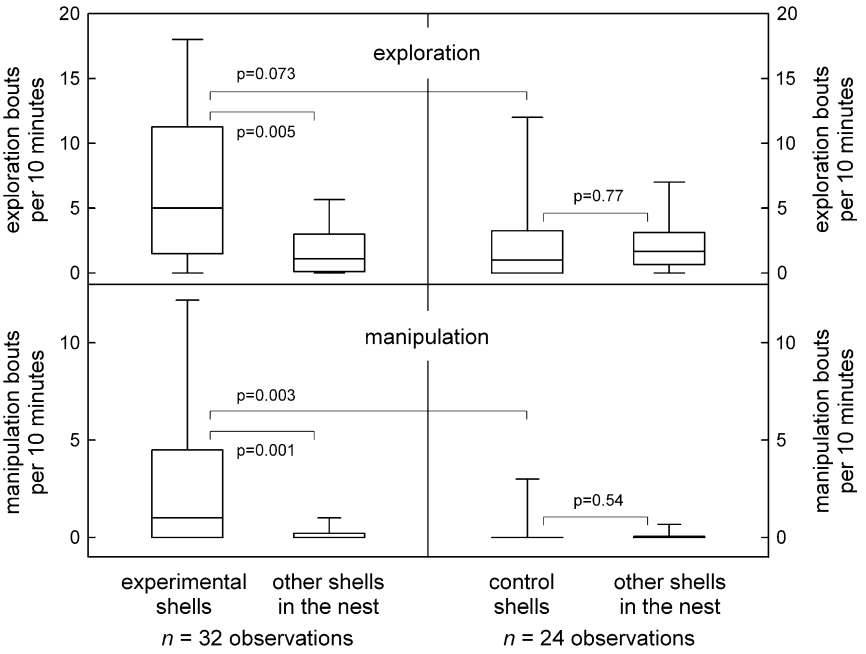

Figure 2
Exploration and manipulation behavior of territory owners toward manipulated shells (experiment and control) and unmanipulated occupied shells in their territories. Boxes indicate the 25 and 75 percentiles and median, whiskers indicate the data range.

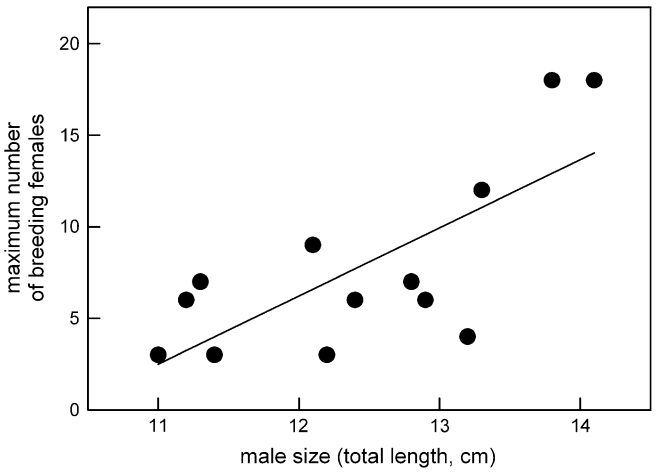

Figure 3
The relationship between male size and the maximum number of females simultaneously breeding in his territory (regression line: $y = 3.7x - 38.5$).

data did not support this hypothesis (Spearman rank correlations between the number of available shells [i.e., empty and intact] and exploration frequency [$n = 29$, $r = -0.08$, $P = 0.67$], manipulation frequency [$n = 29$, $r = -0.21$, $P = 0.28$], and the time interval until shells were emptied [$n = 54$, $r = -0.18$, $P = 0.20$]).

The time interval until an experimental shell was emptied was positively correlated with the number of females already breeding in the territory (Spearman rank correlation, $n = 54$, $r = 0.47$, $P < 0.001$). This relationship was absent in control shells ($n = 27$, $r = -0.18$, $P = 0.46$). There was no evidence, however, for a change in the behavior of males toward experimental shells in relation to the number of females present (Spearman rank correlations between the number of females already breeding and 1) male exploration frequency: $n = 32$, $r = -0.16$, $P = 0.38$ and 2) male manipulation frequency: $n = 32$, $r = -0.11$, $P = 0.54$).

To test whether shell stealing and subsequent expulsion of females increased the reproductive success of males, we compared the occupation rate of experimental shells after female expulsion with that of unmanipulated shells after females left on their own accord. The proportion of reoccupation of experimental shells was significantly higher than that of unmanipulated shells (74% vs. 21%, $n_1 = 31$, $n_2 = 34$, $\chi^2 = 10.10$, $P = 0.0015$).

Female choice

The number of breeding females in a territory was positively correlated with the size of the territory owner (Spearman correlation, $n = 13$, $r = 0.61$, $P = 0.026$; Figure 3). Large males had more intact shells and larger shells in their territories (Spearman correlations, $n = 9$, $r = 0.69$, $P = 0.039$ and $r = 0.70$, $P = 0.038$), but these traits did not correlate with the number of breeding females in the nest (Spearman correlations, $n = 8$, $r = 0.14$, $P = 0.74$ and $r = -0.08$, $P = 0.84$), indicating that females chose large males rather than high-quality nests.

Our data support the hypothesis that large males are better nest defenders. We recorded 3 natural instances of nest takeovers. These 3 males that were chased away from their territories were smaller than males that were not chased away (total length, mean ± standard error = 11.3 ± 0.2 vs. 12.4 ± 0.3 cm, t-test, $n_1 = 3$, $n_2 = 12$, $t = -2.99$, df = 7.51, $P = 0.02$).

DISCUSSION

Female reproductive success was considerably reduced by nest takeovers and shell stealing by males: the vast majority of occupied shells involved were emptied within 48 h. Furthermore, both shell stealing and experimental exchange of shells from one nest to another significantly decreased female breeding success.

Increased exploration and manipulation behavior by males after experiments indicated that they discriminated between females that they had spawned with and females that had spawned with other males. During these behavioral observations we never saw a female leaving an experimental shell, indicating that 10 min of male manipulation is not sufficient to expel a female and that the costs of female expulsion are not negligible to males. Indeed, video observations suggested that males continue to manipulate experimental shells for several hours until the female leaves. This continued manipulation behavior also explains why we did not find an effect of breeding stage on male behavior in the 10 min directly after experimental shell relocation, whereas the long-term effect of experimental manipulation strongly depended on breeding stage of the experimental females.

Consistent with our prediction, experimental relocation of females in the third breeding stage did not affect breeding success. This can be explained by the costs associated with female expulsion by males, the relatively low benefit given that the female would soon leave anyway, and the increasing benefits of resistance with breeding stage for females. However, we hypothesized that males would expel females in both the first and the second stages of breeding but found that experimental manipulation reduced female breeding success in stage 2 only. Possibly, decreased breeding success was not detected in manipulated shells in the first breeding stage because the probability that a clutch of eggs reaches free swimming stage was low even in the unmanipulated situation (20%). Alternatively, males may be limited in their ability to detect strange offspring in the egg stage. This has been shown for bluegill sunfish males (Neff 2003; Neff and Sherman 2005): in the face of cuckoldry by parasitic males, parental bluegill males use olfactory cues from the offspring to detect genetic relatedness and adjust their level of paternal care accordingly. This mechanism however does not operate until the eggs have hatched (Neff 2003). Likewise, *L. callipterus* males may be unable to discriminate against offspring sired by competitors until the fry stage is reached. This hypothesis predicts increased levels of expelling behavior right after hatching, a prediction that could be tested in laboratory conditions where the timing of hatching and subsequent male behavior can be closely monitored.

It is unknown to what extent females may resist male manipulation. Given that male and female interests change in the same direction with progressing breeding stage, we cannot easily determine to what extent female departure is a direct effect of male manipulation alone or also affected by female resistance. Yet, whereas female expulsion rate varied significantly with breeding stage, male exploration and manipulation behavior immediately after experiments did not. This may hint that female motivation contributes to the observed expulsion pattern. Again, detailed behavioral observations in the laboratory may help to answer this question.

Our results indicate that female expulsion contributes to male reproductive success: reoccupation rate of emptied experimental shells was significantly higher than that of unmanipulated empty shells. Thus, in contrast to male infanticide

in many mammal species, female expulsion by male *L. callipterus* acts to increase the availability of breeding substrate for "new" females, rather than enhance the receptivity of the aggressed female. Female *L. callipterus* may detect previous shell occupation and use this as an indicator of shell quality. We expected males to expel females especially when the number of suitable empty shells in their territory was limiting but found no support for this. In contrast, expelling latency was positively correlated with the number of females already breeding in a territory. This may be due to a dilution effect on male attention.

We did not find any evidence that shell stealing itself (of empty shells) increased male reproductive success: nests containing high numbers of intact shells did not accommodate more breeding females. Instead, the data suggest that females were attracted to the territories of large males. We cannot rule out that male size correlates with some unmeasured aspect of territory quality that affects the distribution of breeding females, such as particular characteristics of shells. Yet, our results indicate that female choice for large males may be adaptive because large males were better nest defenders. Female choice for large males may reduce the risk of being stolen or taken over by another male and as such be instrumental in infanticide avoidance. This is consistent with laboratory experiments in which large males were shown to be more aggressive and to hold their territories for longer periods (Schütz and Taborsky 2005). However, female choice for large males may have other benefits as well (Manica 2002). Male size may be an indicator of heritable quality in terms of "good genes" for survival, for instance (Brooks and Kemp, 2001). Analysis of *L. callipterus* otholiths however indicates that within the size range of territorial males, that is, above 9 cm standard length, size and age are not correlated (Rijneveld C, Ripmeester E, Taborsky M, unpublished data). Adult *L. callipterus* males do not hold territories continuously, they spend considerable periods of time without a territory (Sato 1994; Maan ME and Taborsky M, personal observation). In these periods, they are likely to replenish resources and growth rates are likely to be higher than in territory-holding periods. Thus, male size may not indicate heritable quality in this species, and direct benefits are likely to be more important for female choice.

As a result, female choice for large males is expected to be especially strong when shell stealing and nest takeovers are common. Variation in shell abundance between populations and over time, and the prevalence of shell stealing and nest takeover contingent on this variation, may explain why female choice for large males was not found in another *L. callipterus* population (Schütz and Taborsky 2005). In this population, shells were almost 10 times more abundant than in the population studied here. Sato (1994) studied yet another population, in which suitable shells were very scarce, and male reproductive success was related to both male size and the number of intact shells in a territory. These data suggest that when shells are overabundant, shell stealing and nest takeover are rare and females do not prefer to mate with large males. Similar environmental variation in the intensity of sexual conflict has been demonstrated in guppies, in which the abundance of predators influences the frequency of female harassment by males (Magurran and Seghers 1994; Godin and Dugatkin 1995; Croft et al. 2006) as well as female behavior and preference (Godin and Dugatkin 1996; Dill et al. 1999; Evans et al. 2002).

We do not know of other examples of infanticide associated with takeovers of females, breeding substrate, or nests in fish. In several polygynous freshwater fishes, nest usurpation and egg stealing by intruder males do occur but result in allopaternal care rather than infanticide (e.g., fathead minnow [Wootton 1971; Unger and Sargent 1988], three-spined sticklebacks [Wootton 1971], and striped darter [Porter et al. 2002]; see Wisenden [1999] for a review). This behavior may be driven by females preferring to spawn in nests already containing eggs due to female mate choice copying or because females aim to reduce the risk of filial cannibalism. Female three-spined sticklebacks however initiate nest raids in which they consume the eggs and often spawn with the nest owner (Fitzgerald and Van Havre, 1987). This phenomenon could be considered analogous to the expulsion behavior of *L. callipterus* males, as it makes breeding substrate (i.e., space in the male stickleback's nest) available for the egg-consuming females—albeit with reversed sex roles.

To conclude, our data suggest that male *L. callipterus* increase their reproductive success by acquiring shells through nest takeover or shell stealing and subsequently expelling the females that breed in them. Females may reduce this risk by choosing large males as mates. Earlier work showed that the particular breeding substrate of *L. callipterus* is the driving force behind an extreme sexual size dimorphism (Schütz and Taborsky 2000; Schütz and Taborsky 2005; Schütz et al. 2006). Our study shows that its limited availability also constitutes a key component of sexual conflict in this species.

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