

Male and female shell-brooding cichlids prefer different shell characteristics

Jeremy S. Mitchell*, Sabine Wirtz Ocana, Michael Taborsky

Department of Behavioural Ecology, University of Berne, Switzerland



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In resource defence polygyny, where males defend resources that females use for reproduction, the resource characteristics preferred by the two sexes are expected to match. We tested this expectation by comparing the shell characteristics preferred by males and females in the shell-brooding cichlid fish *Lamprologus callipterus*. In this species, males attract females by collecting and defending shells within which females breed. We added shells to males' nests and found that females were more likely to occupy large shells but made no distinction between new, smooth shells and old shells coated with mineral deposits. In contrast, when we placed additional shells adjacent to males' nests, males were more likely to retrieve shells covered in mineral deposits but showed no significant preference for large shells over small shells. Furthermore, many shells in males' nests were smaller than the smallest shell that females used for breeding. The discrepancy between male and female preferences suggests that empty shells in *L. callipterus* nests may have additional functions, beyond serving as breeding substrate. We discuss the possibility that shells may also be extended phenotype signals analogous to the decorations of a bower. © 2014 The Association for the Study of Animal Behaviour. Published by Elsevier Ltd. All rights reserved.

Resource defence polygyny refers to a mating system in which males acquire multiple mates by monopolizing access to resources that are necessary for female reproduction (Emlen & Oring, 1977). Females choose or compete for resource patches that maximize their reproductive success. A male's reproductive success is determined by the quality and quantity of the resource that he defends, which can in turn determine the number and quality of the females that he attracts (Davies, 1991). Thus, in species where resource defence polygyny occurs, characterizing the resource is central to understanding the mating system.

If the resource is used exclusively for breeding, then the resource characteristics that males prefer are expected to match those that females prefer (1) because both sexes gain similar reproductive benefits and (2) because males that preferentially secure the resources that females prefer will attract more and higher-quality mates than those that do not. Many examples of resource defence polygyny appear broadly consistent with this expectation, but characteristics of the mating system and the nature of the resource often complicate interpretation. For example, female *Calopteryx maculata* dragonflies lay their eggs on floating

plant material. Females are attracted to sites where vegetation has been added, and males compete for control of these territories. This pattern is consistent with the expectation of matching preferences. However, female preferences also depend on the number of other females already present (Alcock, 1987; Waage, 1987). Side-blotched lizards (*Uta stansburiana*) prefer sites that contain a range of different temperature microhabitats. Larger, more competitive males secure superior territories, and females prefer territories where the range of microhabitats has been experimentally increased. Again, this result is consistent with the expectation of matching preferences. However, the territory type also affects risk of predation, and territory preferences are modified by interactions with male reproductive strategies (Calsbeek & Sinervo, 2002a, 2002b). In both systems, indirect female choice of males is, potentially, a further complication: if high-quality males secure high-quality territories, then a female's territory choice can be an indirect way of choosing a high-quality mate. Finally, in both examples, and in most systems where resource defence polygyny has been studied, resources are an aspect of the territory (Andersson, 1994), which means that preferences for resource characteristics must be inferred from territory preferences, rather than being measured directly. In such systems, we may expect males to identify crucial reproductive resources, but we will not necessarily expect the two sexes to define high-quality territories in exactly the same way (cf. Greenfield, 1997). Matching male and female

* Correspondence and present address: J. S. Mitchell, Ocean Sciences Centre, Memorial University of Newfoundland, St John's, NL A1C 2E3, Canada.

E-mail address: [jsmithell@mun.ca](mailto:jsmitchell@mun.ca) (J. S. Mitchell).

resource preferences would be predicted in systems in which the resource is used exclusively for reproduction and is as distinct as possible from the territory that contains the resource.

In this study, we contrast male and female preferences for spawning habitat in the Lake Tanganyika cichlid fish, *Lamprologus callipterus*. This system appears to be a straightforward 'textbook' example of resource defence polygyny (Alcock, 2005). For *L. callipterus*, the resource is an empty snail shell. Females breed exclusively in empty shells, and territorial males defend collections of shells on territories that are just large enough to contain these collections and that contain no other resources. The reproductive ecology of *L. callipterus* is described in detail elsewhere (e.g. Sato, 1994; Schütz & Taborsky, 2000, 2005; Taborsky, 2001; Sato, Hirose, Taborsky, & Kimura, 2004). We refer to a male's territory and shell collection as that male's 'nest'. A male adds to his shell collection by retrieving shells from the lake floor (holding a shell in his mouth by the edge of the shell opening and swimming with it back to his nest) and by stealing shells from his neighbours (Maan & Taborsky, 2008). Female *L. callipterus* inspect males' collections until they locate a suitable shell, enter the shell to lay their clutch, and remain in the shell to care for the clutch and brood. Under experimental conditions and when choice is not constrained by the presence of competitors, females preferentially occupy large shells, in which they can lay more eggs and in which a larger proportion of broods survives (Schütz & Taborsky, 2005). Nonbreeding females do not occupy shells. Males do not participate in direct parental care. A territorial male's reproductive success is determined by the number and fecundity of the females that breed in his shells, and hence by the number and size of the shells in his collection (Sato et al., 2004; Schütz, Parker, Taborsky, & Sato, 2006; Schütz & Taborsky, 2005; Taborsky, 2001). A successful male's collection may contain more than 100 shells, with different females breeding in as many as 30 of these shells concurrently. Territorial males are much too large to enter shells (Schütz & Taborsky, 2000), so shells appear to function exclusively as shelters for females and their broods. In this system, we expect natural selection to favour males that preferentially collect large shells, because these are the shells that large, fecund females prefer to occupy (Schütz & Taborsky, 2005). Furthermore, males should not show preferences for shell characteristics that females ignore, because such preferences confer no advantage to a male and may result in a failure to collect shells that females would prefer.

Although *L. callipterus* appears to be a particularly straightforward example of resource defence polygyny, three aspects might still give rise to differences between male and female shell preferences. First, males must find and retrieve shells, so the reproductive benefit of a large, attractive shell may be offset by the ease of detecting it or by the cost of retrieving it. Collecting shells involves an energetic cost (Schütz & Taborsky, 2005), which is potentially important given that territorial males appear to be capital breeders (Schütz, Pachler, Ripmeester, Goffinet, & Taborsky, 2010). In this case, males should prefer large shells when they are nearby, but may shift their preference to smaller shells when the retrieval distance is greater. Second, in *L. callipterus*, a 'dwarf' male morph spawns parasitically by swimming past a spawning female into the inner whorl of a shell, from where it can fertilize the majority of a female's eggs (Sato et al., 2004; Taborsky, 1998, 2001; Wirtz Ocana, Meidl, Bonfils, & Taborsky, 2014; Wirtz Ocana, Schütz, Pachler, & Taborsky, 2013). Dwarf males seem to be more successful at entering larger shells, and especially shells that are large relative to their female occupants (Sato et al., 2004; S. Wirtz Ocana & M. Taborsky, personal observations). For a territorial male, the benefits of owning a large, attractive shell may be offset by the risks that dwarf males pose. In this case, territorial males will not necessarily prefer the largest shells available, but should still

restrict their collections to shell sizes that are large enough for females to use. The third possibility is that shells have some value other than as spawning sites. We consider these three possibilities in the discussion of our results.

To test whether male and female *L. callipterus* have matching shell preferences, we measured all intact shells in males' collections and noted which shells contained females. We then conducted shell preference experiments for both sexes. To assess males' preferences, we placed sets of shells near males' nests and recorded which shells were retrieved (experiments 1 and 2). To assess females' preferences, we placed additional shells within males' nests and recorded which shells females occupied (experiments 3 and 4). We were initially interested only in shell size, because shell size has an established effect on female reproductive success. However, during preliminary trials, preferences also seemed to be affected by a shell's age or by the amount of mineral deposits on its surface (Lake Tanganyika's water chemistry is such that, over time, 'old' empty shells become covered in mineral deposits, whereas 'new' shells are smooth). Therefore, in experiments 2 and 4, we considered the effects of both shell size and age on male shell collection and female shell occupancy decisions. While we had no a priori reason to predict a preference for old shells, we did expect that any preference for old or new shells would be consistent between males and females, for the reasons outlined above.

METHODS

Study Area and Preliminary Observations

All observations and experiments were carried out by diving using SCUBA at an *L. callipterus* colony at Kasakalawe Point, near Mpulungu, Zambia. At this site, *Neothauma tanganicense* is the only snail species whose shells are used by *L. callipterus*. The study colony was at 11–12 m depth and contained approximately 50 active male nests. Centrally located nests were less than 1 m apart. Nests on the perimeter of the colony were more widely spaced (generally >4 m apart). Before initiating preference trials, we used slide callipers to make in situ measurements of the long axes of all intact shells in a subset of male nests. This measure is a good correlate of shell volume (Schütz & Taborsky, 2005). Based on these measurements, we determined the range of shell sizes for use in the preference experiments.

Shells used in preference experiments were obtained from abandoned male nests outside the study area or by digging beneath cobble and boulders on the lake floor (for old, mineralized shells), or were collected from the shoreline (for new, smooth shells). All shells used in preference experiments were rinsed to remove any sand or detritus, dried, and then measured and numbered with an indelible marker. Shells were then organized into size-based sets according to the needs of each experiment. Shells that were similar to the very largest occupied shells found naturally in males' nests could not be used in experimental presentations because we could not obtain sufficient numbers. Note that the size-related terminology (large, medium, small) in the four experiments below always refers to relative sizes of shells that were presented in sets in one of the four experiments. This means that a shell size class termed 'large' in one experiment may overlap with a size class termed 'small' in another (see below). This variation does not affect conclusions regarding relative preferences with respect to shell size.

Because of the size of the colony, and because not all nest were suitable for experiments, the same male nests were used in separate experiments (i.e. the male nests used in experiment 1 were a subset of those used in experiment 2). Trials for separate experiments were never run concurrently.

Females prospecting for shells were abundant throughout the study period. Therefore, although females were not tagged, we consider it unlikely that individual females were recorded in multiple shells during successive trials in experiment 3 or 4.

Experiment 1: Male Collection of Large, Medium and Small Shells

One small (45–46 mm), one medium (48–49 mm) and one large (51–52 mm) shell were placed together at 0.5 m intervals beginning 0.5 m from the perimeter of a male's nest and ending 4.0 m from the nest perimeter (24 shells in total). The nest was revisited the following day and the location of each experimental shell was recorded. Shells that had been moved at least 0.5 m closer to the focal male's territory were recorded as moved. Presentations were made at six male territories, using a different set of shells in each trial, for a total of 144 shell presentations. Trials were conducted using both old and new shells, and shell sizes used for the three size classes differed among trials. However, within a trial, shells were either all old or all new, were size-matched to less than 1 mm within each size class, and were 3 mm larger or smaller than shells in the next size class. All trials were conducted at territories on the perimeter of the colony, and with the line of shells directed away from the colony, in order to minimize the risk of shells being collected by nonfocal males.

Experiment 2: Male Collection of Large vs Small and Old vs New Shells

In experiment 2, shells were presented to 23 different males. Each male was presented with a set of five shells: one large old, one small old, one large new, one small new and one control (see below). Small shells were 49–52 mm. Large shells were 52–55 mm. The exact size of each shell differed among trials but, within each trial, large and small shells were matched to less than 1 mm and large shells were 3 mm larger than small shells. The single control shell was 36–38 mm, which was less than the minimum occupied shell size observed in the colony (see Results, Fig. 1), and could be either old or new. Our expectation was that control shells would never be collected. The five shells were placed together 50 cm from the perimeter of a male's nest. The shells'

positions relative to one another were randomized. The male was then observed for 5 min to determine which shells he retrieved. If no shells were retrieved, the trial was repeated the following day. If the second trial was also unsuccessful, the presentation was repeated using a different male at a different territory. Twelve sets of shells were used in experiment 2. Eleven of these sets were each presented to two different males, while the 12th set was only presented to a single male (23 males in total).

Experiment 3: Female Occupancy of Large, Medium and Small Shells

Fifteen empty shells were added to each of 15 males' nests. Each experimental nest received five small (45–47 mm), five medium (48.5–50.5 mm) and five large (52–54 mm) shells. Five sets of shells were used, with each set presented at three different male nests (15 male nests in total). Shells were placed in a ring around the perimeter of the nest, abutting the male's existing collection. The nest was then revisited to determine which shells females had occupied. Females were removed from their shells and their total length was measured. Shells were placed in the morning. In most trials, the nest was revisited the afternoon of the same day. In some trials, nests were not revisited until the morning of the following day, but in no case was the delay long enough for all shells of a particular size class to have been occupied by females. Thus, possible effects of competition among females for a preferred shell size class were reduced (cf. Schütz & Taborsky, 2000, 2005). To limit the risk of shell theft by neighbouring males, all trials were conducted using nests on the perimeter of the colony, where male nests were farther apart.

Experiment 4: Female Occupancy of Large vs Small and Old vs New Shells

Immediately following the 5 min shell presentation in experiment 2, the five shells that had been presented to the male were placed within that male's nest. Shell placement was haphazard. The nest was revisited the following day and female occupancy of those shells was recorded. A female occupancy trial was conducted regardless of whether the male had retrieved any shells. One additional female shell preference trial was conducted at a nest

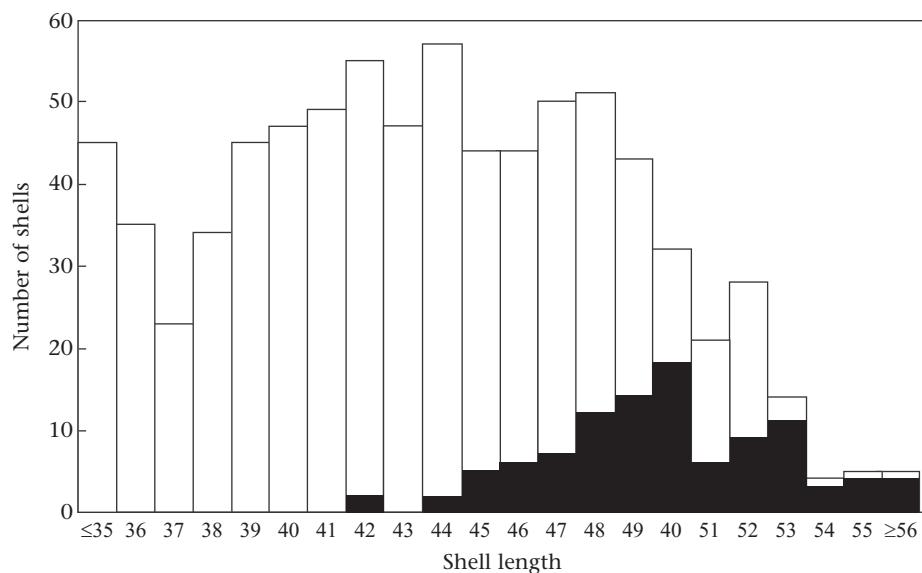


Figure 1. Size distribution of shells found in the collections of 21 males (white bars: all shells, $N = 778$; black bars: subset that were occupied by females, $N = 103$). Occupied shells were found in the collections of 15 males; all shells in the collections of the other six males were empty.

where there was no corresponding male shell preference test. Thus, in experiment 4, each of the 12 sets of five shells was presented at two nests (24 nests in total).

Statistical Analyses

Probabilities of shell retrieval by males and occupancy by females were fitted using logistic mixed-model regressions in R (version 3.0.1, [R Development Core Team, 2013](#)), with the `glmer` function (package `lme4` version 0.999999-2, [Bates, Maechler, & Bolker, 2013](#)). Shell size category (all experiments) and age (experiments 2 and 4) were treated as fixed factors. 'Shell set' (the set of shells presented at a particular male's nest) was treated as a random factor. When appropriate, 'male nest' was included as a second random factor nested within shell set. In experiment 1, the distance from the shell to the male nest was included as a covariate. In experiments 2 and 4, control shells were not included in the analyses. In experiment 3, we also examined the relationship between shell size and the size of the occupying female: treating female total length as the response, shell size category (large versus medium and small, i.e. data for medium and small shells pooled) as a fixed factor, and shell set and male nest as random factors. In experiment 4, we included prior collection by the male (i.e. whether the shell had been collected by the male in experiment 2) as an additional predictor of occupancy by a female. Finally, in experiment 3, we repeated the first analysis with the data set restricted to females smaller than the median female length. Interactions between fixed effects were never significant ($P > 0.6$), so models were rerun including only main effects. P values associated with fixed effects were calculated using likelihood ratio chi-square tests to compare models with and without the effect of interest. P values from these tests can be anticonservative. However, in this study, the qualitative differences between the responses of males and females were clear, and marginal P values (for shell size in experiment 4 and for small females in experiment 3) were consistent with the unambiguous result for all females in experiment 3.

Ethical Note

This study conformed to the laws of Switzerland and Zambia (ethical permissions of the Kantonale Veterinäramt Bern licence no. 41/05 to M.T.)

RESULTS

Size Distributions of Shells in Males' Collections

We measured 778 shells from the collections of 21 males (Fig. 1). Shell lengths ranged from 22.7 to 60.1 mm. Females occupied 103 shells, in nests of 16 males. Larger shells were more likely to be occupied ($\chi^2_1 = 141.6$, $P < 0.001$). The smallest occupied shell was 41.3 mm long. Approximately one-third of the shells in males' collections were smaller than this minimum length. Males' nests also contained broken shells and shell fragments that were not usable as brood shelters. Nests can be maintained for long periods by successive males, so many of the broken shells may have been originally collected as intact shells. However, we also directly observed males retrieving shell fragments that we had placed near their nests. All shells in males' collections were old (covered in mineral deposits). Both new shells and live snails were present in male nests outside the study area, but we did not observe any new shells within the study area during our observations.

Experiment 1: Male Collection of Large, Medium and Small Shells

Seventy of 144 presented shells (22 small, 26 medium, 22 large) were at least 0.5 m closer to the focal male nests when the nests were revisited (Fig. 2). A shell's probability of being collected decreased significantly as its distance from a male's nest increased ($\chi^2_1 = 14.8$, $P < 0.001$) but was independent of the shell's size ($\chi^2_2 = 1.2$, $P = 0.54$). In several cases, presented shells were found wedged between stones adjacent to males' nests, presumably after being dropped by the male during retrieval, or washed out of his nest after retrieval by wave swells. The 0.5 m criterion allows us to recognize that the male expressed a relevant preference for these shells, while excluding shells that were moved exclusively by wave swells, without any evidence of attempted retrieval by the male. The qualitative result held if the count was restricted to shells that had been moved completely into males' nests.

Experiment 2: Male Collection of Large vs Small and Old vs New Shells

Thirteen of the 23 males used in experiment 2 each retrieved at least one shell during the 5 min observation period. These focal

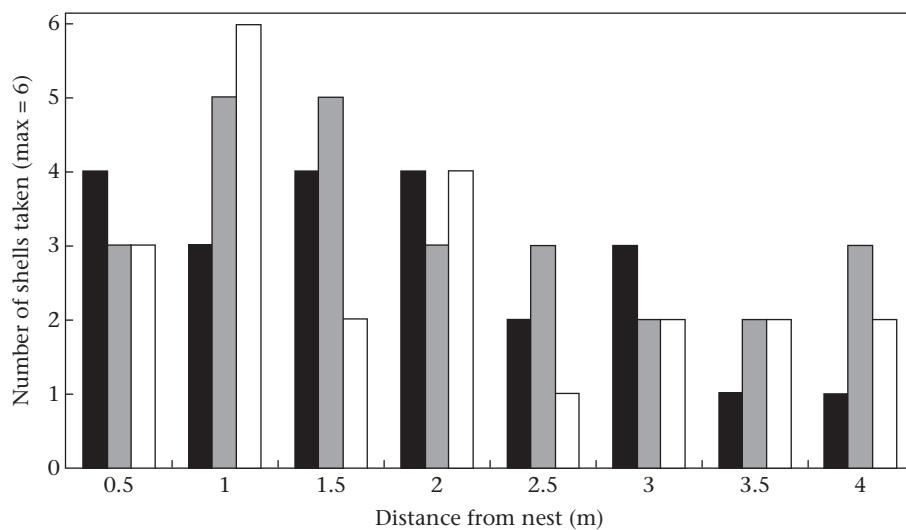


Figure 2. Numbers of small (black bars), medium (grey) and large (white) shells retrieved by males at different distances from their nests (experiment 1).

males retrieved a total of 24 noncontrol shells (one male collected all four noncontrol shells). The old large shell from a 14th trial was excluded from analysis because it was taken by a neighbouring male. Males were significantly more likely to collect old shells than new shells ($\chi^2_1 = 8.1, P = 0.004$) but were equally likely to collect small and large shells ($\chi^2_1 = 0.46, P = 0.49$; Fig. 3). In two trials, the control shell was also collected (one old control, one new control).

Experiment 3: Female Occupancy of Large, Medium and Small Shells

Larger shells were more likely to be occupied by females ($\chi^2_2 = 38.0, P < 0.001$); 2 of 74 small shells, 10 of 75 medium shells and 29 of 74 large shells were occupied. At least one shell was occupied in each experimental trial. One large shell was found in the nest of a neighbouring male (the neighbour had apparently stolen the shell; cf. Maan & Taborsky, 2008). One small shell was occupied by a dwarf male (see Discussion). On average, the females that occupied large shells were larger than females that occupied small and medium-sized shells ($\chi^2_1 = 10.8, P = 0.001$). This pattern arose because large females used large shells almost exclusively, whereas some small females used small or medium-sized shells. However, shell occupancy by smaller females was still biased towards large shells: females smaller than the median female length occupied two small, six medium and 10 large shells. The effect of shell size on occupancy by small females was significant regardless of whether we assumed that small females chose from among all experimental shells ($\chi^2_2 = 4.1, P = 0.04$), or that small females' options were restricted to the shells left vacant by larger females (i.e. to 74 small, 71 medium and 55 large shells) ($\chi^2_2 = 9.4, P = 0.009$).

Experiment 4: Female Occupancy of Large vs Small and Old vs New Shells

Forty-two of the 96 shells that had been placed in males' nests were occupied by females. One shell (old, large) was found, occupied, in the nest of a neighbouring male. Two large shells (one new, one old) could not be relocated. At least one experimental shell was occupied in 19 of the 24 male nests. Large shells were more likely to be occupied than small shells ($\chi^2_1 = 4.1, P = 0.04$; Fig. 3). In addition, shells that males had collected in experiment 2 were more

likely to be occupied than shells that had not been collected ($\chi^2_1 = 11.2, P < 0.001$; Table 1). The effects of shell size and prior collection by a male were independent. Shell age had no effect on female occupancy ($\chi^2_1 = 2.1, P = 0.15$). Control shells were never occupied.

DISCUSSION

Territorial males' collection decisions did not match females' occupancy decisions. Males did not preferentially collect large shells in either experiment 1 or 2. However, males in experiment 2 did have a clear preference for old, mineralized shells. We consider possible explanations for male shell preference below. Even if currently none of those possibilities offers a convincing explanation for the old shell preference, this preference confirms that males in experiment 2 were distinguishing among shells and that our design allowed us to detect males' preferences. Had males shown a similar preference for large shells, we should have detected it in experiment 2. The absence of any detectable preference for large shells in experiment 1 is consistent with this interpretation. Experiment 1 may be a weaker test of male choosiness, because the maximum shell size in experiment 1 (52 mm) was slightly less than that in experiment 3 (54 mm) and in experiments 2 and 4 (55 mm), respectively. With a larger shell, a unit increase in shell length corresponds to a greater increase in shell volume. However, shell collection in experiment 1 was potentially more costly, because males had to carry shells much further and hence to leave their nests for longer periods.

In contrast to males, females in experiment 4 were equally likely to occupy old and new shells. Indeed, fewer old shells were occupied than new shells. And, in both experiment 3 and 4, females were much more likely to occupy large shells than small shells. The preference for large shells is consistent with the results of previous, aquarium-based experiments (Schütz & Taborsky, 2000, 2005) and with observational field data (Schütz & Taborsky, 2000), and has a straightforward, adaptive interpretation: a female can lay more eggs and raise a larger brood in a larger shell; even after controlling for female body size, more young survive in a larger shell (Schütz & Taborsky, 2005). Our interpretation of experiment 3's results assumes that, by adding 15 shells, we gave each female the opportunity to choose her preferred shell size. In that case, several small

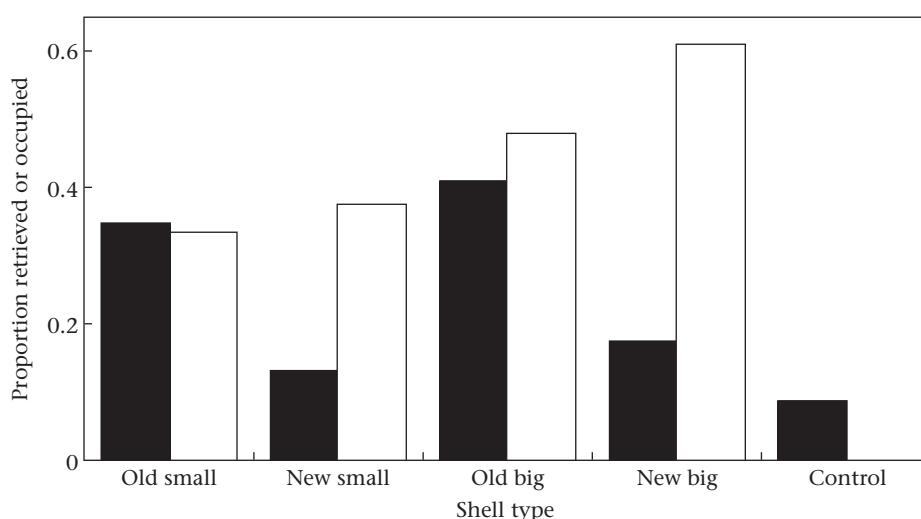


Figure 3. Proportion of presentations of shells with different characteristics that were retrieved by males (black bars, experiment 2) and occupied by females (white bars, experiment 4). Sample sizes (male, female) are as follows: old small: 23, 24; new small: 23, 24; old big: 22, 23; new big: 23, 23; control shells: 23, 24; note that control shells were not included in the statistical analyses described in the text.

Table 1

Coincidence of shell retrieval by a male (experiment 2) and occupancy by a female (experiment 4)

Retrieved by male	Occupied by female	
	Yes	No
Yes	14	10
No	24	41

For statistical comparison, see text.

females preferred small shells but most small females and all large females avoided small shells; that is, although females in laboratory-based experiments prefer large shells irrespective of the female's own size (Schütz & Taborsky, 2000), free-living small and large females may have slightly different preference functions (*sensu* Stinchcombe, Function-valued Traits Working Group, & Kirkpatrick, 2012). However, we should still expect males to prefer large shells, even if females' preference functions differ, because most females preferred large shells, especially large, more fecund females, and because large shells and large female body size both increase breeding success (Schütz & Taborsky, 2005). If some degree of competition for preferred shells remained, or if females perceived a potential for competition (cf. Schütz & Taborsky, 2000), then our test of female shell size preferences is conservative, because an overall preference for large shells was apparent despite that competition. In experiment 4, females were also more likely to occupy shells that males had retrieved. This result may indicate that males and females did agree on other, unidentified, shell characteristics. Alternatively, it is possible that males influence females' shell choices, for example by placing their own preferred shells in particular places within their nests, or by directing their courtship behaviour in relation to such shells. However, the apparent agreement on an unidentified shell characteristic was independent of the female preference for large shells, a preference that males did not share. Thus, the discrepancies between male and female shell choices remain.

These discrepancies are surprising. The implication is that, even in a system with a discrete reproductive resource that is distinct from a male's territory, the costs or benefits associated with resource characteristics differ for males and females. The scope for such differences is limited because, if shells are used exclusively for reproduction, then most consequences of shell variation will affect male and female fitness in a similar way. The most obvious difference in shell use by males and females is that males must find and retrieve the shells, so shell collection by males may reflect differences in the probability of detecting or ease of retrieving different shells. Our results are not consistent with this interpretation. In experiment 1, males collected shells that were closer to their nests, presumably because those shells were more likely to be detected and were easier and cheaper to collect. However, there was no interaction between shell size and placement distance (i.e. no indication that a preference for a particular shell size class developed as the energetic cost of retrieval increased). In experiment 2, males may have had a better-developed search image for old, mineralized shells because primarily old shells occurred naturally at the study site, or mineralized shells might be easier to carry. But, given the short (50 cm) retrieval distance, we would also have expected males to prefer larger shells. They did not. Indeed, two males also collected control shells that were too small to be used by females at all. Furthermore, large numbers of small, unusable shells were found within males' nests independently of experimental presentations. The males that collected these shells incurred an energetic cost and an opportunity cost, because the time spent collecting unsuitable shells could have been spent defending an

existing collection or searching for suitable shells. Even if males are trading off shell quality with cost of retrieval, shells that have no value to females should not be collected.

The collection of small shells and shell fragments, unsuited for female spawning, is also inconsistent with the possibility that the preference mismatch is due to risk of parasitic spawning by dwarf males. Although the risk posed by dwarf males might discourage territorial males from collecting the largest shells, shells that are too small for breeding should also be avoided. Indeed, the presence of dwarf males should further discourage collection of small shells: because dwarf males are smaller than females, small shells can provide shelter for a dwarf male within a territorial male's nest (cf. Sato et al., 2004).

In our opinion, the most likely explanation for the shell preference mismatch is that a shell's utility extends beyond its function as a breeding site. We hypothesize that a shell may also function as one element of a shell collection. Experiments 3 and 4 tested for female shell preferences within a male's collection. However, females must also choose among males or male nests. Just as females in other systems may use male territories to evaluate territory owners, so may female *L. callipterus* use males' shell collections to choose among potential mates. In addition to providing breeding substrate, shells may serve as extended phenotypic signals (or 'ornaments'; Schaedelin & Taborsky, 2009), much as bowers and bower decorations are used in mate choice by female bowerbirds (e.g. Borgia, 1985; Madden, 2003a, 2003b). The shell attributes that contribute to a collection's perceived quality will not necessarily be the same attributes that make an individual shell more suitable for breeding. We might still expect larger shells to be more impressive ornaments, because they are more difficult and expensive to carry (Schütz & Taborsky, 2005). But, larger shells might not always be the most effective additions to a male's collection if females' decisions are influenced by other characteristics of a collection (e.g. the number or variety of shells, or the area that the shells cover; cf. Borgia, 1985; Madden, 2003b), and not exclusively by characteristics of individual shells. In that case, males' decisions should reflect efforts to establish attractive collections. Our incidental observations of males collecting shell fragments, and the broad range of shell sizes found in male nests are consistent with this interpretation. Tests of this possibility require an appropriate means of describing shell collections. Schütz and Taborsky (2005) reported a positive correlation between the number of intact shells in a male's collection and the number of nesting females, and Maan and Taborsky (2008) found that the number of breeding females in a male's nest correlated with male body size, which was in turn correlated with the number of shells in his nest. However, because a larger collection may be more likely to contain a single preferred shell, those correlations are expected even if females are only considering characteristics of individual shells. Future experimental manipulations of the material within males' shell collections might provide insight into the importance of a collection's characteristics, as distinct from the characteristics of individual shells. Those manipulations might also suggest an explanation for the males' old shell preference.

Shell-brooding cichlids like *L. callipterus* are potentially informative and tractable study systems: a shell is a discrete, quantifiable resource that can be easily manipulated and that has a direct connection to both male and female reproductive success. The mismatch between male and female shell preferences in *L. callipterus* is particularly intriguing because of the system's apparent simplicity. Indeed, it is a system in which it should be possible to progress from the preference patterns that we describe here to quantitative preference functions (Stinchcombe et al., 2012). The suitability of using *L. callipterus* to study relationships between habitat characteristics and mating patterns suggests that

resolving the remarkable mismatch between male's and female's breeding substrate preferences is a worthwhile goal for future studies.

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