



Male and female shell-brooding cichlids prefer different shell characteristics



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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

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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.

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