

Experimental Evidence of Female Choice in Lake Malawi Cichlids

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To date, most research on sexual selection has focused on the discrimination between attributes of individuals of the opposite sex. We have demonstrated female discrimination of a male behavioral character, bower size, by experimentally manipulating bower height in a lek of cichlid fishes from Lake Malawi, Africa. Eggs increased significantly ($p < 0.01$) with large (15 cm) and extra large (30 cm) artificial bowers. Males with extra large bowers received a 50% greater increase in eggs laid than those with just large bowers.

THE driving mechanism for the speciation events that led to the explosive radiation of the haplochromine cichlids in the Great Lakes of Africa is undiscovered; the two most widely proposed methods are allopatric speciation (Fryer and Iles, 1972) and intrinsic isolating mechanisms (McKaye and Stauffer, 1986). Several authors (Lande, 1981; West-Eberhard, 1983; Turner and Burrows, 1995) proposed that rapid divergence of mate recognition via sexual selection could promote behavioral isolation and facilitate speciation. Runaway sexual selection has been proposed to partially explain the rapid radiation of these haplochromines (McKaye, 1991), and Deutsch (1997) provided evidence that sexual selection may be associated with the color diversification of the Lake Malawi rock-dwelling cichlids.

Wiley and Poston (1996) distinguished between direct mate choice, which requires discrimination of individual attributes including behavior, and indirect mate choice, which occurs when females do not respond differentially to male features. Most research on sexual selection has focused on male attributes (Wiley and Poston, 1996). Vocal advertisement of fertility has been documented in Tungara Frogs, *Physalaemus pustulosus* (Ryan et al., 1996) and Archbold's Bowerbird, *Archboldia papuensis* (Frith et al., 1996). Additionally, Borgia (1995) studied the manifestation of a behavioral character, bower decoration, in male success. His observations showed that male courtship success was positively correlated with counts of bone and glass used to decorate bowers of Spotted Bowerbirds, *Chlamydera maculate*. Östlund-Nilsson and Holmlund (2003) showed that females of the Three-spined Stickleback, *Gasterosteus aculeatus*, were more attracted to males that decorated their nests than to males that did not. McKaye et al. (1990) found a preference for larger bowers in the female cichlid fish *Copadichromis conophorus*. This species formed huge leks that contained more than 50,000 males at

the height of the breeding season (McKaye, 1983, 1984). In comparisons between pairs of bowers, males on larger bowers received a 2- to 3-fold increase in female attention (bower entry and circling behavior) over males on smaller bowers. In a smaller lek, occupied by 20 to 50 *Otopharynx* c.f. *argyrosoma* males, individuals occupying bowers closest to the center of the lek received approximately three times as many matings per male as those around the periphery (McKaye, 1991). On a third, multi-specific breeding arena, occupied primarily by *Lethrinops* c.f. *parvidens* (approximately 150 individuals), we found that both bower height and location within the lek were important (Kellogg et al., 2000). It is our contention that a simple correlation between mating success and male attributes was not sufficient evidence of direct female choice (Cox and LeBoeuf, 1977); thus, the purpose of this study was to investigate if females were selecting males based on bower size, independent of location within the lek, by experimentally manipulating bower size in a lek of *Lethrinops* c.f. *parvidens* from Lake Malawi, Africa.

MATERIALS AND METHODS

The study site was located in the southeastern arm of Lake Malawi, Africa (34°56'E, 14°00'S) on a lek approximately 22 m x 15 m (see Fig. 1 in Kellogg et al., 2000). We constructed artificial bowers of tin with heights of either 15 cm (tall) or 30 cm (extra tall) as compared to the mean height of 9 cm for natural bowers. The tin bowers were coated with epoxy and covered with sand. As part of another study (Kellogg et al., 2000), all the males on the bowers were marked using Floy-T tags with individual identification marks. Fifteen *L. c.f. parvidens* males were randomly selected from different areas in the lek. Each male was observed for 15 10-minute observation periods during the seven days prior to the installation of the artificial bowers, and the

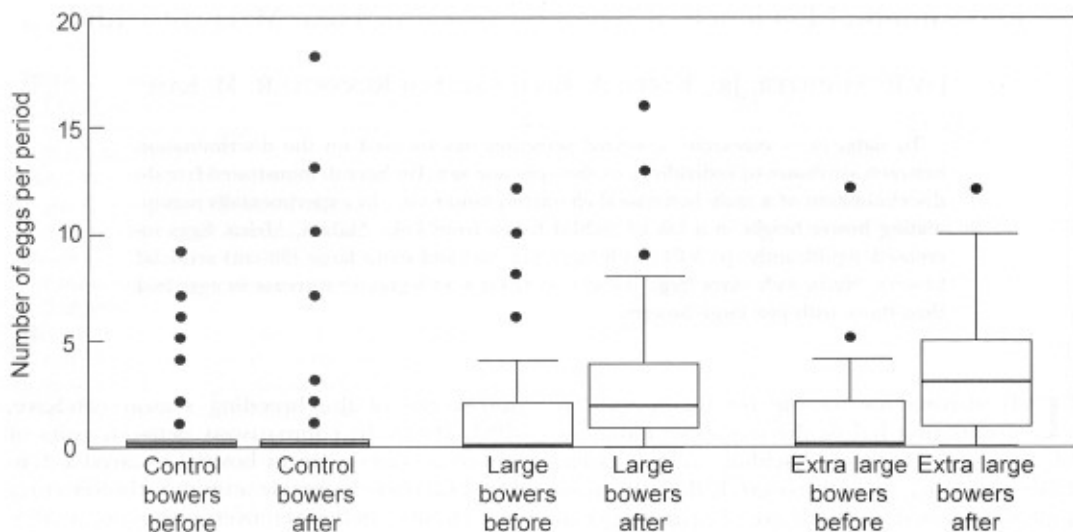


Fig. 1. Number of eggs laid per 10 minute observation in control, large, and extra large bowers before and after bower manipulation. Egg-laying increased significantly in bowers that were replaced with either the large (15 cm) ($N = 72$; $Z = -3.052$; $p < 0.01$) or extra large (30 cm) ($N = 75$; $Z = -4.733$; $p < 0.01$) artificial bowers, whereas no significant difference ($N = 75$; $Z = -1.203$; $p > 0.05$) was observed in the control bowers.

number of eggs laid by females entering the bowers was recorded. On the eighth day, the original bowers of ten of the males were destroyed and replaced with one of the two types of artificial bowers. The bowers of the five remaining males were slightly disturbed by moving the sand by hand. All males returned to their original bowers immediately after manipulations, and again observed for 15 10-minute observation periods during the seven days following the manipulation. A Wilcoxon signed-rank test for related or paired variables (SPSS 11.15 for Windows) was used to evaluate the differences ($p < 0.01$) in male mating success before and after manipulations of the control, large, and extra large bowers.

RESULTS

Egg-laying increased significantly in bowers that were replaced with either the large (15 cm) ($N = 72$; $Z = -3.052$; $p < 0.01$) or extra large (30 cm) ($N = 75$; $Z = -4.733$; $p < 0.01$) artificial bowers, whereas no significant difference ($N = 75$; $Z = -1.203$; $p > 0.01$) was observed in the control bowers (Fig. 1). Note that several observation periods for the large bowers were excluded from the analysis because of interruptions during the observation period. Furthermore, males with extra large bowers received a 50% greater increase in number of eggs laid than those with just large bowers.

DISCUSSION

Lekking (arena) behavior among animals has attracted considerable recent attention among behavioral and evolutionary biologists (see Johnsgard, 1994; Höglund and Alatalo, 1995 for reviews). These breeding aggregations of males offer excellent opportunities for examining: 1) the processes of mate choice when a large number of partners are available (Bradbury et al., 1985); 2) the evolution of sexual preference, and a "runaway" nonadaptive feedback leading to the rapid formation of new species (Fisher, 1958; Lande, 1981; Dominey, 1984); and 3) whether or not females are looking for "good-genes," and gain genetic benefits by producing fitter young (Hamilton and Zuk, 1982).

Speculation and research upon these fundamental questions has a long history. Darwin (1871) first addressed the role of intersexual selection (female choice) as an evolutionary force for producing seemingly maladaptive traits; when males provide no resources or parental care and females have numerous males among which to choose, "extravagant" male secondary characteristics could result solely from sexual selection.

We propose that the construction of large bowers by males is directly a result of female preference for large bowers. These bowers are built by the males moving one mouthful of sand at a time and are thus energetically costly to build. Furthermore, while these large bowers

advertise to potential mates, they also advertise to predators such as mormyrids and bagrid catfish, both of which move into the shallows to feed at dusk.

Theoretically, positive "runaway" feedback provides a mechanism that could accelerate the joint evolution of female mate choice and male secondary sexual attributes. Fisher (1958) hypothesized that "an evolution of sexual preference due to this cause would establish an effective isolation between two differentiated parts of a species, even when geographical and other factors were least favorable to such separation." Furthermore, Fisher (1958) postulated that the following conditions would result under his model of runaway sexual selection: 1) the development of a male character and female choice for such a character would advance together until checked by severe counter-selection; 2) the rate of development of this character would be proportional to the development already attained; 3) the selected character would increase with time exponentially as a result of this relationship; and 4) this "runaway" process could begin from small differences soon achieving major proportions.

Lande (1980, 1981) expanded upon Fisher's original thesis and hypothesized that divergence in male traits such as behavioral patterns, color, and size could originate rapidly throughout the range of a species due to local population differences in female choice. In particular, Arnold (1983) argued that lek-breeding species should exhibit "extraordinary geographic variation in male attributes." Stauffer et al. (1993) demonstrated both shape and size differences among bowers of three allopatric *Copadichromis* species in Lake Malawi.

Bower-building cichlids of Africa (McKaye, 1991; McKaye et al., 1993; Stauffer et al., 1993) present an excellent opportunity to examine the behavioral patterns and processes necessary to test the ideas behind the various models of mating preferences and sexual selection. These results experimentally demonstrate that male *Lethrinops* c.f. *parvidens* with the tallest bowers (30 cm) are more successful in attracting females than males with large bowers (15 cm), which in turn are more successful than those with short bowers (5–9 cm). Thus, increased bower height in male *L. c.f. parvidens* is selected for by female mating preferences. This study provides experimental evidence that females respond differently to differing male attributes; thus, this experimental evidence coupled with the observations of the species specific bower shape (Stauffer et al., 1993) lends support to the hypothesis that sexual selection contributed

to the rapid radiation of Lake Malawi cichlids. In addition, this study is unlike manipulation experiments conducted on other organisms (e.g., Long-tailed Widowbirds, Andersson, 1982; Swordtail Fish, Basolo, 1990) in that the preference demonstrated here is for a non-morphological trait, but rather a manifestation of a behavioral character (i.e., bower building).

ACKNOWLEDGMENTS

The authors wish to thank the government of Malawi for providing the necessary permits to collect fishes. Fishes were collected and processed under the research permit issued to the Molecular Biology and Ecology Research Unit (MBERU), University of Malawi and the approval of the Animal Use and Care Committee at Pennsylvania State University (IACUC #16945; 00R084). Partial funding was provided by the NSF/NIH joint program in ecology of infectious diseases (DEB0224958) and the World Wildlife Fund (Finland).

LITERATURE CITED

- ANDERSSON, M. 1982. Female choice selects for extreme tail length in a widowbird. *Nature* 299:818–820.
- ARNOLD, S. J. 1983. Sexual selection: the interface of theory and empiricism, p. 67–108. *In: Mate Choice*. P. Bateson (ed.). Cambridge University Press, Cambridge, Massachusetts.
- BASOLO, A. 1990. Female preference predates the evolution of the sword in swordtail fish. *Science* 250: 808–810.
- BORGIA, G. 1995. Threat reduction as a course of differences in bower architecture, bower decoration and male display in two closely related bowerbirds, *Chlamydera nuchalis* and *C. maculata*. *Emu* 95:1–12.
- BRADBURY, J. W., S. L. VEHCAMP, AND R. GIBSON. 1985. Leks and the unanimity of female choice, p. 301–314. *In: Evolution: Essays in Honour of John Maynard Smith*. P. J. Greenwood, P. H. Harvey, and M. Slatkin (eds.). Cambridge University Press, Cambridge, Massachusetts.
- COX, C. R., AND B. J. LEBOEUF. 1977. Female incitation of male competition: a mechanism in sexual selection. *Am. Nat.* 111:317–335.
- DARWIN, C. 1871. *The Descent of Man and Selection in Relation to Sex*. John Murray, London.
- DEUTSCH, J. C. 1997. Colour diversification in Malawi cichlids: evidence for adaptation, reinforcement or sexual selection. *Biol. J. Linn. Soc.* 62:1–14.
- DOMINEY, W. J. 1984. Effects of sexual selection and life history on speciation: species flocks in African cichlids and Hawaiian *Drosophila*, p. 231–249. *In: Evolution of Fish Species Flocks*. A. A. Echelle and I. Kornfield (eds.). University of Maine Press, Orono, Maine.

- FISHER, R. A. 1958. *The Genetical Theory of Natural Selection* (2nd ed.). Dover Pub., Inc., New York.
- FRITH, C. B., G. BORGIA, AND D. W. FRITH. 1996. Courts and courtship behaviour of Archbold's Bowerbird *Archboldia papuensis* in Papua New Guinea. *Ibis* 138:201-211.
- FRYER G., AND T. D. ILES. 1972. *The Cichlid Fishes of the Great Lakes of Africa: Their Biology and Evolution*. Oliver and Boyd, London.
- HAMILTON, W. D., AND M. ZUK. 1982. Heritable true fitness and bright birds: a role for parasites? *Science* 218:384-387.
- HÖGLUND, J., AND R. V. ALATALO. 1995. *Leks*. Princeton University Press, Princeton, New Jersey.
- JOHNSGARD, P. A. 1994. *Arena Birds: Sexual Selection and Behavior*. Smithsonian Institution Press, Washington and London.
- KELLOGG, K. A., J. R. STAUFFER, JR., AND K. R. MCKAYE. 2000. Characteristics that influence male reproductive success on a cichlid lek. *Behav. Ecol. Sociobiol.* 47:164-70.
- LANDE, R. 1980. Sexual dimorphism, sexual selection, and adaptation in polygenic characters. *Evolution* 34:292-305.
- . 1981. Models of speciation by sexual selection on polygenic traits. *Proc. Nat. Acad. Sci. USA* 78: 3721-3725.
- MCKAYE, K. R. 1983. Ecology and breeding behavior of a cichlid fish, *Cyrtocara eucinostomus*, on a large lek in Lake Malawi, Africa. *Environ. Biol. Fish.* 8: 81-96.
- . 1984. Behavioral aspects of cichlid reproductive strategies: patterns of territoriality and brood defense in Central American substratum spawners and African mouth brooders, p. 245-273. *In: Fish Reproduction: Strategies and Tactics*. G. W. Potts and R. J. Wootton (eds.). Academic Press, London.
- . 1991. Sexual selection and the evolution of the cichlid fishes of Lake Malawi, Africa, p. 241-257. *In: Cichlid Fishes: Behavior, Ecology and Evolution*. M. H. A. Keenleyside (ed.). Chapman and Hall, London.
- , J. H. HOWARD, J. R. STAUFFER, JR., R. P. MORGAN II, AND F. SHONHIWA. 1993. Sexual selection and genetic relationships of a sibling species complex of bower building cichlids in Lake Malawi, Africa. *Jap. J. Ichthy.* 40:15-21.
- , S. M. LOUDA, AND J. R. STAUFFER, JR. 1990. Bower size and male reproductive success in a cichlid fish lek. *Am. Nat.* 135:597-613.
- , AND J. R. STAUFFER, JR. 1986. Description of a gold cichlid (Teleostei: Cichlidae) from Lake Malawi, Africa. *Copeia* 1986:870-875.
- ÖSTLUND-NILSSON, S., AND M. HOLMLUND. 2003. The artistic Three-spined Stickleback (*Gasterosteus aculeatus*). *Behav. Ecol. Sociobiol.* 53:214-220.
- RYAN, M. J., A. S. RAND, AND L. A. WEIGT. 1996. Allo-syme and advertisement call variation in Tungara frog, *Physalaemus pustulosus*. *Evolution* 50:2435-2453.
- STAUFFER, J. R., JR., T. J. LOVULLO, AND K. R. MCKAYE. 1993. Three new sand-dwelling cichlids from Lake Malawi, Africa, with a discussion of the status of the genus *Copadichromis* (Teleostei: Cichlidae). *Copeia* 1993:1017-1027.
- TURNER, G. F., AND M. T. BURROWS. 1995. A model of sympatric speciation by sexual selection. *Proc. Roy. Soc. Lond. B Bio.* 260:287-292.
- WEST-EBERHARD, M. J. 1983. Sexual selection, social competition and speciation. *Quart. Rev. Biol.* 58: 155-183.
- WILEY, R. H., AND J. POSTON. 1996. Perspective: indirect mate choice, competition for mates, and co-evolution of the sexes. *Evolution* 50:1371-1381.
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