

An Investigation of the Utility of Feeding Angles Among Lake Malawi Rock-dwelling Cichlids (Teleostei: Cichlidae)

JAY R. STAUFFER, JR. AND ISA POSNER

Image analysis was used to measure feeding angles of *Labeotropheus trewavasae*, *Labeotropheus fülleborni*, *Melanochromis auratus*, *Metriaclima zebra*, *Petrotilapia* spp., *Pseudotropheus* c.f. *elongatus*, *Tropheops tropheops*, and *Tropheops gracilior* videotaped in Lake Malawi. *Petrotilapia* spp. fed on vertical, slanted, and horizontal slopes, *T. gracilior* grazed on vertical slopes approximately 60% of the time, and the other species spent at least 80% of the time feeding on horizontal slopes. The median feeding angles ranged from 35° to 90°. There are four significantly different groups of feeding angles among the eight rock-dwelling species that were examined: (1) *L. trewavasae* (35°), (2) *L. fülleborni*, *M. auratus*, and *P. elongatus* (44.8–48.5°), (3) *T. tropheops* (58.4°), and (4) *Petrotilapia* spp., *T. gracilior*, and *M. zebra* (84.2–90.2°). Feeding angles within a species did not vary with location or differences in fish community structure. Feeding angles were associated with a combination of mouth position and head shape. We hypothesized that feeding angles may be important in differential access to food.

CICHLIDAE are fishes of the lowland tropics (Stiassny, 1991), with eighty percent of all cichlid species found in Africa (Fryer and Iles, 1972). Although the estimate of the number of African cichlid species varies, it is generally accepted that the African rift valley lakes are the most speciose freshwater lakes in the world. Lake Malawi harbors the most speciose ichthyofauna of all freshwater lakes (Konings, 1989; Stauffer et al., 1997). This diversity results from the explosive radiation and speciation of the endemic cichlids (Regan, 1921; Trewavas, 1935; Greenwood, 1984). High trophic diversity of the Old World cichlids results in the consumption of virtually every food type available in the environment (Liem and Osse, 1975; Liem, 1979), with even slight morphological changes affecting the ability to exploit new food sources (Liem and Osse, 1975; Liem, 1980). The successful radiation of the rift valley cichlids is purported to be a result of their differential ability to acquire food (Axelrod and Burgess, 1979).

In cichlids, mouth structure, dentition, gill-raker number (Stauffer et al., 1995), and jaw structure vary tremendously, and this variation in structure seems to be tied to a variety of feeding techniques (Fryer and Iles, 1972). Documented feeding strategies of Lake Malawi fishes illustrated numerous feeding specializations, including death feigning (McKaye, 1981), paedophagy (McKaye and Kocher, 1983; Stauffer and McKaye, 1986), lepidiophagy (Ribbink, 1984), cleaning (Stauffer, 1991), and scraping of an algal, diatomaceous, and detritus biolayer (aufwuchs) from the rock surfaces (Fryer, 1959).

Among the rock-dwelling cichlids of Lake Malawi (mbuna), there are clearly defined

habitat preferences and depth distributions (Lewis, 1981; Witte, 1984). Distribution of several species of mbuna were correlated with depth, (Ribbink et al., 1983b), oxygen levels, algae production (Sharp, 1981; Reinthal, 1987), size of rock, interstitial space (Ribbink et al., 1983b), wave action, and sediment loading on the substrate (Ribbink et al., 1983a). Despite the specialized strategies employed by Lake Malawi cichlids, the diets of some rock-dwelling cichlids overlap (Fryer, 1959; Reinthal, 1987, 1990). Observations made while SCUBA diving in Lake Malawi indicate that many of the rock-dwelling cichlids appear to have specific feeding angles (angle ventral to the long axis of fish's body and the rocky substrate; Axelrod and Burgess, 1981, pers. obs.).

It was postulated that species-specific feeding angles are important in habitat partitioning and utilization among rock-dwelling cichlids in Lake Malawi; thus, we observed feeding angles of eight rock-dwelling fishes endemic to Lake Malawi. Six of these species have diets that overlap (*Labeotropheus fülleborni*, *Labeotropheus trewavasae*, *Melanochromis auratus*, *Petrotilapia* spp., *Pseudotropheus* c.f. *elongatus*, and *Tropheops gracilior*), and two (*Tropheops tropheops* and *Metriaclima zebra*) have diets that are significantly different from each other and from other rock-dwelling cichlids (Reinthal, 1989). The purposes of this study were to determine: 1) if there were different behaviors evident when the above species grazed from the substrate, 2) if there was specificity of substrate slope utilization, 3) if there were measurable differences in feeding angles among species *in situ*, and 4) if feeding angles changed within a species based on

community structure of these rock-dwelling cichlids.

MATERIALS AND METHODS

A Sony Hi 8 mm underwater video camera was used to record feeding fishes in the southeast arm of Lake Malawi. We were unable to distinguish between the video images of female *Petrotilapia genulutea* and *Petrotilapia nigra*, so they were combined as *Petrotilapia* spp. Individuals of the same species at a given locality were videoed on the same dive, and identifying marks (e.g., color differences) were noted to ensure that no individual fish was videoed more than once.

The videos were viewed to determine the general feeding behavior of these rock-dwelling fishes. Feeding angles, measured between the surface of the feeding substrate and the long axis of the fish, were measured only when the fishes' sides were parallel to the camera lens. The midpoint between the upper and lower lip served as the vertex of this angle, and the long axis was drawn between the vertex and the midpoint of the caudal fin. We used an image analysis program, MOCHA, to measure feeding angles.

Substrate slope was determined relative to the surface of the lake as horizontal, slanted, or vertical. "Horizontal" was arbitrarily defined as substrate between 0–30°, "slanted" was substrate from 31–60°, and "vertical" from 61–90°. When a feeding angle was measured, the slope category of the substrate was recorded. These data were used to calculate percentage of bites on substrates with different slopes and to determine if feeding angle changed with slope.

Fish community structure differs among sites in Lake Malawi as indicated by high site specific endemism (Stauffer et al., 1995). Behavioral changes of rock-dwelling cichlids as a response to other fishes has been well documented (Fryer and Iles, 1972). Therefore, a comparison of feeding angles of the same species at different sites (Harbor Island, Mazinzi Reef, and Mitande Rocks) was analyzed. The median feeding angles of each fish were used to compare the feeding angle of conspecific fishes among the localities.

One fish of each species was collected from the sites where video images were taken. Three-dimensional skull images were constructed from images taken with a Micro Photonics X-ray Micro-CT.

RESULTS

Feeding behavior and feeding territories differed among rock-dwelling cichlids. *Melanochromis auratus* took a single bite from one location,

moved approximately 3–8 cm and bit again. *Labeotropheus* spp., *M. zebra*, and *Petrotilapia* spp., on the other hand, had more restricted feeding ranges. *Labeotropheus* spp. tended to glean the substrate as they moved over the rocks, and *M. zebra* and *Petrotilapia* sp. repeatedly contacted the substrate in the same general location taking a single bite each time contact was made.

Labeotropheus spp., *M. auratus*, *M. zebra*, *P. c.f. elongatus*, and *T. tropheops* spent at least 80% of the time feeding on horizontal slopes. *Petrotilapia* spp. fed on vertical slopes about 40% of the time, and fed on slanted approximately 30% of the time, and on horizontal 30% of the time. *Tropheops gracilior* grazed from vertical slopes approximately 60% of the time. The median feeding angles for each species ranged between 35–90.2°. Within that range, there were four significantly different angle groups: 1) *L. trewavasae* (35°, $n = 8$), 2) *L. fuelleborni* ($n = 21$), *M. auratus* ($n = 33$), and *P. c.f. elongatus* ($n = 9$; 44–48°), 3) *T. tropheops* (58.4°, $n = 12$), and 4) *Petrotilapia* spp. ($n = 6$), *T. gracilior* ($n = 8$) and *M. zebra* ($n = 13$; 84.2–90.2°; Fig. 1; Kruskal-Wallis; $P < 0.05$). The number of bites recorded for each individual ranged from 14–29. A regression analysis of the sample size and feeding-angle variation confirmed that variation was not related to sample size ($R^2 = 0.07$). Feeding angles of the same species recorded at Harbor Island, Mazinzi Reef, and Mitande Rocks were not significantly different (Kruskal-Wallis, $P > 0.05$).

DISCUSSION

Although many of the rock-dwelling cichlids graze algae from the rock surface, many of the fishes feed in the water column when zooplankton is abundant (McKaye and Marsh, 1983). During periods of low zooplankton productivity (Hale and Stauffer, 1997), however, competition for aufwuchs may increase.

Despite the overlap of algae in stomach contents of epilithic rock-dwelling cichlids, the anatomical (e.g., gape differences, mouth position) and behavioral (e.g., feeding angle) specializations for feeding may have allowed for differential access to food (Fryer, 1959). Fryer (1959) suggested that larger fishes were unable to feed from narrow cracks and crevasses, whereas smaller species could feed from those sites. Much of the rocky substrate in Lake Malawi at our dive sites was irregular. Thus, we hypothesized that even when species are comparable in size, the feeding angle at which they graze may be important in fostering differential access to food.

The four different feeding-angle groups observed were associated with different combinations of mouth position and head shape as depicted in micro-CT scans (Fig. 1). *Labeotropheus trewavasae*, which fed at the smallest angle to the substrate, possessed an inferior mouth. The three species, which exhibited feeding angles ranging between 44.8 and 48.5° all had sub-terminal mouths, with just a slight overhang of

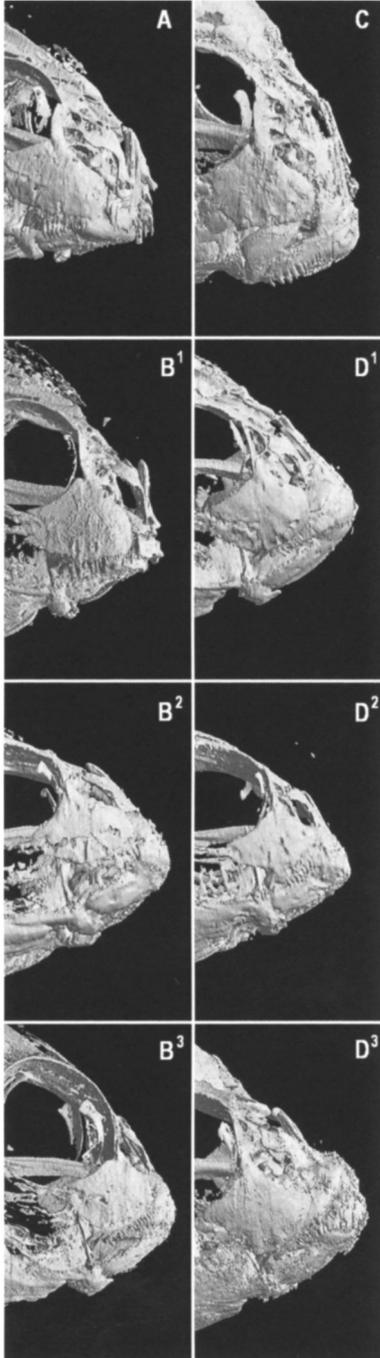
the snout. *Tropheops tropheops* (feeding angle, 58.4°) had a terminal mouth with a steeply downward sloping ethmo-vomerine block (Stauffer et al., 1997). Finally, the three species that fed at the most acute angle (84.2° to 90.2°) possessed a terminal mouth with a moderately sloping ethmo-vomerine block.

Alternative feeding strategies, such as differential use of substrate, slope, or feeding angle could minimize competition for food. Indeed, this study showed that there was spatial partitioning of resources among rock-dwelling cichlids. *Tropheops gracilior* and *Petrotilapia* spp. fed from slanted and vertical slopes, whereas all the other species predominately fed from horizontal surfaces.

A lack of abundant zooplankton in the water column may force the fishes to feed on aufwuchs in order to survive the seasonal shortages of planktonic food. If feeding angle provides a competitive advantage during food acquisition, then during times of abundant plankton, selective pressure on feeding method, e.g., feeding angle, would be minimal. Periodic low food availability, however, may result in competition among epilithic fishes and alternative feeding strategies such as differential use of substrate slope or feeding angle.

ACKNOWLEDGMENTS

We would like to extend our thanks to the Malawi government for the permits to conduct research in Lake Malawi. This work was funded in part by United States Agency for International Development (11.204; DHR-5600-G-1043-00; Program in Science and Technology Cooperation, Office of Science Advisor) and a Fulbright Research Award (Council for International



←

Fig. 1. Median feeding angle for eight species of rock-dwelling cichlids; n corresponds to the number of individuals observed; the number of observations of each individual ranged from 14–29. Those species with the same letter designation exhibited feeding angles that were not significantly different (Kruskal-Wallis, $P > 0.05$). In total, there were four significantly different feeding-angle groups. A—*Labeotropheus trewavasae* (mean feeding angle = 35.0°; SD = 5.3; $n = 8$). B¹—*Labeotropheus fulleborni* (mean feeding angle = 44.8; SD = 5.3; $n = 21$). B²—*Pseudotropheus* c.f. *elongatus* (mean feeding angle = 44.7°; SD = 7.9; $n = 9$). B³—*Melanochromis auratus* (mean feeding angle = 48.5°; SD = 9.8; $n = 33$). C—*Tropheops tropheops* (mean feeding angle = 58.4°; SD = 14.3; $n = 12$). D¹—*Metracilima zebra* (mean feeding angle = 84.2°; SD = 10.9; $n = 13$). D²—*Tropheops gracilior* (mean feeding angle = 85.9°; SD = 5.0; $n = 8$). D³—*Petrotilapia nigra* (mean feeding angle = 90.2°; SD = 6.7; $n = 6$).

Exchange of Scholars) to JRS. The research was conducted under the approval of the Animal Use and Care Committee at Penn State University (IACUC #16945; 00R084). Many thanks to T. Sledz and A. Tatiparthi from Micro Photonics, who took the micro-CT scans and constructed the 3-D images of the fish skulls.

LITERATURE CITED

- AXELROD, R. H., AND W. BURGESS. 1979. African Cichlids of Lakes Malawi and Tanganyika. 8th edition. T.F.H. Publications, Neptune City, New Jersey.
- FRYER, G. 1959. The trophic interrelationships and ecology of some littoral communities of Lake Nyasa with special reference to the fishes, and a discussion of the evolution of a group of rock-frequenting Cichlidae. *Proc. Zool. Soc. London* 132:153–281.
- , AND T. D. ILES. 1972. The Cichlid Fishes of The Great Lakes of Africa, Their Biology and Evolution. T.F.H. Publications, Neptune City, New Jersey.
- GEENWOOD, P. H. 1984. The cichlid fishes of Lake Victoria, East Africa: the biology and evolution of a species flock. *Bull. Br. Mus. Nat. Hist. (Zool.)*, Supp. 6:1–134.
- HALE, E., AND J. R. STAUFFER, JR. 1997. Lake Malawi fish production is linked to landscape geology. *Cichlid News* 6:10–12.
- KONINGS, A. 1989. Malawi Cichlids in Their Natural Habitat. Raket B.V., Pijnacker, Holland.
- LEWIS, D. S. C. 1981. Preliminary comparisons between the ecology of haplochromine cichlid fishes of Lake Victoria and Lake Malawi. *Neth. J. Zool.* 31:746–761.
- LIEM, K. F. 1979. Modulatory multiplicity in the feeding mechanism in cichlid fishes, as exemplified by the invertebrate pickers of Lake Tanganyika. *J. Zool. Lond.* 189:93–125.
- . 1980. Adaptive significance of intra- and interspecific differences in the feeding repertoire of cichlid fishes. *Amer. Zool.* 20:295–314.
- , AND J. W. OSSE. 1975. Biological versatility, evolution and food resource exploitation in African cichlids. *Ibid.* 15:427–454.
- MCKAYE, K. R. 1981. Field observation on death feigning: a unique hunting behavior by the predatory cichlid, *Haplochromis livingstoni* of Lake Malawi. *Environ. Biol. Fish.* 6:361–365.
- , AND T. KOCHER. 1983. Head ramming behaviour by three paedophagous cichlids in Lake Malawi, Africa. *Anim. Behav.* 31:206–210.
- , AND A. MARSH. 1983. Food switching by two specialized algae-scraping cichlid fishes in Lake Malawi, Africa. *Oecologia* 56:245–248.
- REGAN, C. T. 1921. The cichlid fishes of Lake Nyasa. *Proc. Zool. Soc. London.* 1921:675–727.
- REINTHAL, P. N. 1987. Morphology, ecology and behavior of groups of rock-dwelling cichlid fishes (Cichlidae: Perciformes) from Lake Malawi, Africa. Unpubl. Ph.D. diss., Yale University, New Haven, Connecticut.
- . 1989. The feeding habits of a group of herbivorous rock-dwelling cichlid fishes (Cichlidae: Perciformes) from Lake Malawi, Africa. *Environ. Biol. Fish.* 27:215–233.
- . 1990. The feeding habits of a group of herbivorous rock-dwelling cichlid fishes (Cichlidae: Perciformes) from Lake Malawi, Africa. *Ibid.* 27: 215–233.
- RIBBINK, A. J. 1984. The feeding behavior of a cleaner, scale and skin and fin eater of Lake Malawi (*Docimodus evelynae*, Pisces: Cichlidae). *Neth. J. Zool.* 34:182–196.
- , B. A. MARSH, A. C. MARSH, AND B. J. SHARP. 1983a. The zoogeography, ecology and taxonomy of the genus *Labeotropheus* Ahl, 1927, of Lake Malawi. (Pisces: Cichlidae). *J. Linn. Soc. (Zool.)* 79:233–243.
- , A. C. MARSH, A. C. RIBBINK, AND B. J. SHARP. 1983b. A preliminary survey of the cichlid fishes of rocky habitats in Lake Malawi. *Afr. J. Zool.* 18:149–310.
- SHARP, B. J. 1981. An ecological study of territoriality in four cichlid species resident on rocky shores near Monkey Bay, Lake Malawi. Unpubl. M.Sc. thesis, Rhodes University, Republic of South Africa.
- STAUFFER, J. R., JR. 1991. Description of a facultative cleanerfish (Teleostei: Cichlidae) from Lake Malawi, Africa. *Copeia* 1991:141–147.
- , N. J. BOWERS, K. A. KELLOGG, AND K. R. MCKAYE. 1997. A revision of the blue-black *Pseudotropheus zebra* (Teleostei: Cyprinidae) of hybrid origin from Lake Malawi, Africa, with a description of a new genus and ten new species. *Proc. Acad. Nat. Sci. Phila.* 148:189–230.
- , ———, K. R. MCKAYE, AND T. D. KOCHER. 1995. Evolutionary significant units among cichlid fishes: the role of behavioral studies. *Amer. Fish. Soc. Symposium* 17:227–244.
- , AND K. R. MCKAYE. 1986. Description of a paedophagous deep-water cichlid (Teleostei: Cichlidae) from Lake Malawi, Africa. *Proc. Biol. Soc. Wash.* 99:29–33.
- STIASSNY, M. L. J. 1991. Phylogenetic intrarelationships of the family Cichlidae: an overview, p. 1–31. *In: Cichlid Fishes Behaviour, Ecology, and Evolution.* M. H. A. Keenleyside (ed.). Chapman and Hall, London.
- TREWAVAS, E. 1935. A revision of the cichlid fishes of the genus *Lethrinops* Regan. *Ann. Mag. Nat. Hist.* 10:133–152.
- WITTE, F. 1984. Ecological differentiation in Lake Victoria haplochromines: comparison of cichlid species flocks in African lakes, p. 155–167. *In: Evolution of Fish Species Flocks.* A. A. Echelle and I. Kornfield (eds.). University of Maine at Orono Press, Orono, Maine.
- SCHOOL OF FOREST RESOURCES, 12 FERGUSON BUILDING, PENN STATE UNIVERSITY, UNIVERSITY PARK, PENNSYLVANIA 16802. E-mail: (JRS) vc5@psu.edu. Send reprint requests to JRS. Submitted: 16 Sept. 2005. Accepted: 30 Nov. 2005. Section editor: C. M. Taylor.