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Commensalistic Feeding Relationships of Three Lake Malaŵi Fish Species

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Abstract.—The endemic, haplochromine, cichlid species flock of Lake Malaŵi represents the most diverse assemblage of fishes of any of the world's freshwater lakes. Of particular interest are the interspecific relationships that permit so many species to coexist in this unique ecosystem. We hypothesized that a detailed study of the feeding associations among three sand-dwelling species, *Taeniolethrinops praeorbitalis, Cyrtocara moori,* and *Protomelas annectens,* would provide the necessary information needed to determine if these species are effective in harvesting specific food resources. *Taeniolethrinops praeorbitalis* feeds by plunging its snout into the sand, engulfing a mouthful of sand, retaining prey items, and expelling the sand through its gills. Immediately after *T. praeorbitalis* plunges into the sand, other species, including *C. moori* and *P. annectens,* move closer and begin to forage on the invertebrates suspended in the water column by the disturbance of the substrate or expelled through the gills of *T. praeorbitalis.* The gap between the gill rakers of *T. praeorbitalis* is significantly ($P < 0.05$) wider than that of the other two species; the interraker gaps of *C. moori* and *P. annectens* are not significantly ($P > 0.05$) different from each other. Most *P. annectens* consumed small Arthropoda and Cladocera (0.3–0.8 mm), whereas most *C. moori* and *T. praeorbitalis* consumed chironomids (mean prey size = 4.2 mm). Although there was an association with interraker gap size and prey size when *P. annectens* and *T. praeorbitalis* were compared, this relationship was not present when the stomach contents and interraker gap of *C. moori* was contrasted with those of the other two species. Thus, we concluded that differences in prey size among these three species is a function of interraker gap, prey selectivity, and foraging behavior.

The cichlid species flock of Lake Malaŵi, Africa, is believed to be the largest assemblage of unique vertebrate species in the world. This variety offers opportunities to investigate evolutionary processes leading to biological diversity and to study the interspecific relationships that permit so many species to occur in an ecosystem. The large trophic diversity exhibited by the ichthyofauna in Lake Malaŵi suggests that the species must be extremely effective at harvesting specific food resources.

Fishes commonly reduce competition through spatial, behavioral, and temporal partitioning of resources (Ross 1986; Angradi et al. 1991; Pitts 1991). Symbiotic feeding relationships between marine fishes, such as the association of cobias *Rachycentron canadum* with cownose rays *Rhinoptera bonasus,* have been documented (Magnuson 1971; Smith and Merriner 1982). Demetropoulos et al. (1990) associated resource partitioning between two sublittoral cottids, the longfinsculpin *Jordania zonope* and the scalyhead sculpin *Artedius harringtoni,* with morphological differences. Commensalistic feeding relationships between the moray eel *Gymnothorax griseus* and the groupers *Epinephelus fasciatus* (Karplus 1978), *Lycodontis javanicus,* and *Cephalopholis argus* (Fricke 1972) have been reported. Montogomery (1975) interpreted the association of the leather bass *Epinephelus dermatolepis* with fishes from seven different families (Tetraodontidae, Pomacentridae, Labridae, Scaridae, Balistidae, Acanthuridae, and Kyphosidae) as attempts "to facilitate predation on small benthic fishes." Additionally, many feeding symbioses involve interactions between fishes and invertebrates (Hoffman 1981; Castro 1988; Taylor 1990). Some of these relationships involve removal of parasitic copepods; thus, they represent protocooperation rather than commensalism (Creesey and Lachner 1970).

Documented interspecific associations of Lake Malaŵi fishes include: death feigning (McKaye 1981), paedophagy (McKaye and Mackenzie 1982; McKaye and Kocher 1983; Stauffer and McKaye, 1986), mutualistic defense of young (McKaye 1985), lepidiophagy (Ribbink 1984), and cleaning (Ribbink and Lewis 1982; Stauffer, 1991). Additionally, Fryer and Iles (1972) and Kocher and McKaye (1983) reported that *Cyrtocara moori* and *Protomelas annectens* form associations (1–3 fish) and feed on invertebrates that are suspended in the water column as a result of the feeding action of other cichlids, including *Taeniolethrinops praeorbitalis. Taeniolethrinops praeorbitalis* feeds by plunging its snout into the substrate, engulfing a mouthful of sand, and expelling the sand through its gills. Presumably the gill rakers in combination with mucous secretion enable the fish to retain and ingest macroinvertebrates. Immediately after a *T. praeorbitalis* plunges its snout into the sand, the associated *C. moori* and *P. annectens* move directly behind it and forage on invertebrates that are suspended in the water column by the disturbance of the substrate or expelled from the gills of *T. praeorbitalis.* An underwater videotape that records this behavior is held by the Pennsylvania State University Fish Museum (PSU 2735.1). An effective strategy for *C. moori* and *P. annectens* might be to ingest the smaller prey items that are not retained or selected by *T. praeorbitalis.* The purpose of this study was to investigate diet partitioning between *T. praeorbitalis* and *C. moori* and *P. annectens.*

Methods

Fishes were collected January–March 1989 off Nankumba peninsula between Songwe Hill (34° 56′E, 14°00′S) and Chigubi Point (34°56′E, 13° 57′S), Lake Malaŵi, Africa. Feeding groups were located by scuba diving and captured with a fine-mesh monofilament net (7 m × 1 m × 1.5 cm). Fish stomachs were injected with 10% formalin, and whole fish were preserved in the same solution. A feeding group was defined as a single feeding *T. praeorbitalis,* followed by one or more *C. moori* or *P. annectens.* Each feeding group was preserved separately, transferred to 70% ethanol, and placed in permanent storage in the Pennsylvania State University Fish Museum. Prey were identified to the lowest possible taxa, measured, and deposited in the Frost Entomological Museum, Pennsylvania State University (Voucher V-92-1).

Each fish was measured for standard length (SL) to the nearest 0.1 mm. The relationship between prey size and fish length was analyzed with Spearman's rank correlation coefficient. The gap between the base of each gill raker on the first ceratobranchial was measured to the nearest 0.01 mm by using a dissecting microscope, and a mean interraker gap was calculated for each individual. Interraker gap was regressed against standard length. Because interraker gap increases with standard length, the residuals were calculated and analyzed by analysis of variance (ANOVA) and Duncan's multiple-range test to determine if there were significant ($P < 0.05$) differences among species irrespective of size differences. Stomach contents were removed, identified to the lowest possible taxon, measured, and enumerated.

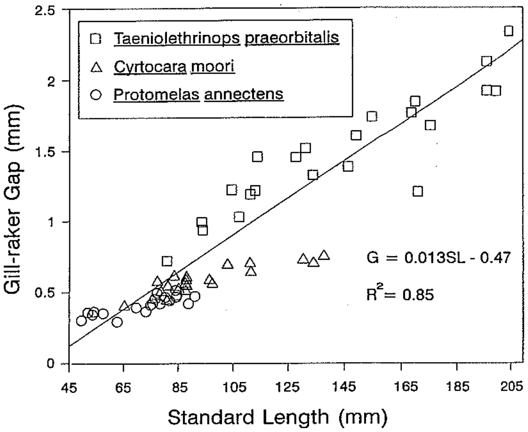

FIGURE 1.—Plot of gill raker gap versus standard length for *Taeniolethrinops praeorbitalis, Cyrtocara moori,* and *Protomelas annectens.*

Results

In all, 112 feeding groups were collected. These groups consisted of 57 pairs of *T. praeorbitalis* and *C. moori,* 52 pairs of *T. praeorbitalis* and *P. annectens,* 1 group of *T. praeorbitalis, C. moori,* and *P. annectens,* 1 group of *T. praeorbitalis* and 2 *C. moori,* and 1 group of *T. praeorbitalis* and 2 *P. annectens.* Mean standard lengths were 112.6 mm (SD = 32.4) for *T. praeorbitalis,* 88.5 mm (SD = 16.3) for *C. moori,* and 73.6 mm (SD = 9.0) for *P. annectens.*

When the three species were analyzed as a single group, the formula $G = 0.013\ \mathrm{SL} - 0.47$ ($R^2 = 0.85$) explained the relationship between interraker gap (G) and standard length (Figure 1). An ANOVA, in conjunction with Duncan's multiple-range test of the residuals, demonstrated that the interraker gap of *T. praeorbitalis* was significantly larger than that of the other two species. The interraker gaps of these two species were not significantly different.

A Spearman's rank correlation coefficient of 0.45, which was significantly different from zero, was calculated when the data from all the species were analyzed simultaneously. This positive correlation was probably caused by the fact that the larger *T. praeorbitalis* preyed upon larger prey

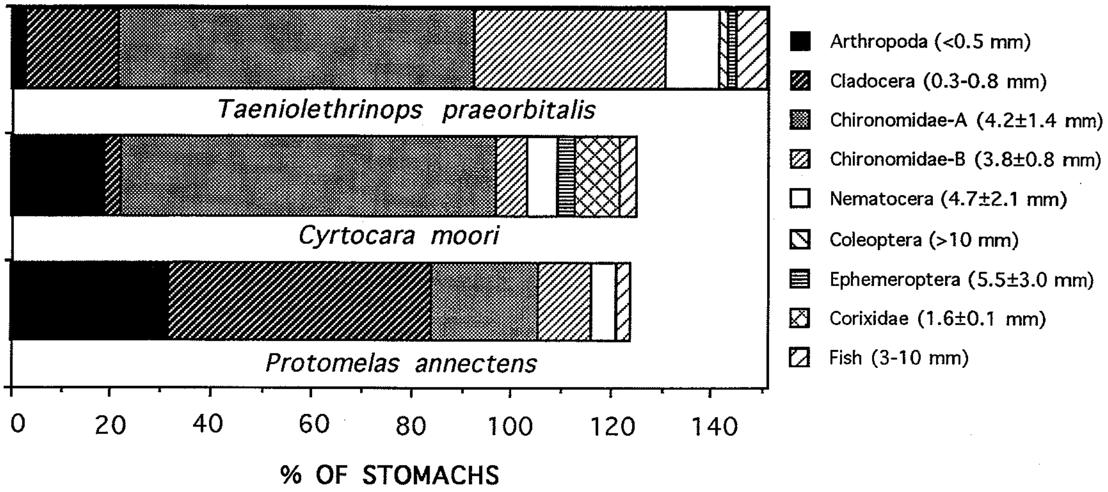

FIGURE 2.—Percentage of stomachs in which various prey items were found for *Taeniolethrinops praeorbitalis*, *Cyrtocara moori*, and *Protomelas annectens*. Percentages exceed 100 because many stomachs contained more than one prey taxa.

items than the smaller *P. annectens*. When the standard length of the fish was compared to prey length for each species separately, no coefficients were significantly different from zero.

Although many small *T. praeorbitalis* (40–70 mm SL) were observed while diving, the smallest one that was followed by *P. annectens* or *C. moori* was 68.8 mm. All *P. annectens* observed in association with *T. praeorbitalis* were 49.5–88.6 mm, and all *C. moori* were 65.3–137.7 mm.

The following prey items were identified in the stomachs: (1) Arthropoda, small specimens usually less than 0.5 mm in total length that were either too small or too digested to be identified to a lower taxon but could well be Cladocera; (2) Cladocera (0.3–0.5 mm), easily recognizable by their distinct carapace and antennae; (3) Chironomidae A, larvae 3–7 mm long that may have included more than one species; (4) Chironomidae B, larvae with large head capsules relative to their body length of 3–6 mm that probably represented a single species; (5) Nematocera, chironomid-type larvae or pupae that were unidentifiable to family level; (6) Coleoptera, a single individual in poor condition, with relatively intact elytron; (7) Ephemeroptera, 3–4-mm nymphs; and (8) Corixidae, adults about 1.6 mm in total length. All prey items were counted, except the Arthropoda and Cladocera, which were counted if less than 50 were found in a stomach but were put in the following numeric categories if 50 or more were found: 50–100, 101–200, 201–300, 301–400, 401–500, and >500.

TABLE 1.—Prey eaten by *Taeniolethrinops praeorbitalis* and *Protomelas annectens* associations.

Prey	Number of prey per fish	Number of *T. praeorbitalis*	Number of *P. annectens*
Arthropoda	1–50	1	
	200–300	1	
	301–500		1
	>500		10
Cladocera	50–100	3	
	101–200	2	3
	201–300	1	2
	301–400	1	4
	401–500		1
	>500		9
Chironomidae A	1–5	18	8
	10–14	4	
Chironomidae B	1	7	4
	2–7	3	
Nematocera	1	3	2
Coleoptera	1	1	
Fish eggs	1		1
Fish larvae	3–9	2	
None		20	16

Taeniolethrinops praeorbitalis and Protomelas annectens associations.—A comparison of stomach contents of *T. praeorbitalis* and *P. annectens* associations supports our initial hypothesis that *T. praeorbitalis* ingests larger food items than *P. annectens* (Figure 2). Arthropoda and Cladocera were usually less than 0.5 mm in total length. Arthropoda were consumed by two and Cladocera by seven *T. praeorbitalis*; 11 and 19 *P. annectens* preyed on Arthropoda and Cladocera, respectively (Table 1).

TABLE 2.—Prey eaten by *Taeniolethrinops praeorbitalis* and *Cyrtocara moori* associations.

Prey	Number of prey per fish	Number of *T. praeorbitalis*	Number of *C. moori*
Arthropoda	50–100		1
	200–500		1
	>500		4
Cladocera	50–100	3	
	300–500	1	
	>500	1	
Chironomidae A	1–5	21	17
	6–10	1	2
	>10	1	1
Chironomidae B	1–5	12	2
	6–10	3	
Nematocera	1–2	5	2
Ephemeroptera	1–5	1	1
Corixidae	1–8		1
	20		1
Fish larvae	1–5	1	1
None		28	27

A comparison of the larger prey items (2.7–7.3 mm) in the stomachs reverses this trend (Table 1). Twenty-two *T. praeorbitalis* ingested Chironomidae A, and only eight *P. annectens* ingested them. Nineteen *P. annectens* that were associated with *T. praeorbitalis* that ate Chironomidae A did not consume Chironomidae A. Ten *T. praeorbitalis* ate Chironomidae B, but only four *P. annectens* did. Twenty *T. praeorbitalis* and 16 *P. annectens* stomachs contained no identifiable organisms.

Taeniolethrinops praeorbitalis and Cyrtocara moori associations.—There was little distinction between prey size (Figure 2) and prey ingested by *T. praeorbitalis* and *C. moori*. Five *T. praeorbitalis* and 6 *C. moori* ingested Arthropoda and Cladocera (Table 2). For a given association, Chironomidae A were found in only *T. praeorbitalis* stomachs 12 times and only in *C. moori* stomachs 9 times. They were found in both species 11 times. Chironomidae B were found in 15 *T. praeorbitalis* but in only 2 *C. moori*. In all the fish sampled, 8 corixids were found in the stomach of 1 *C. moori* and 20 in the stomach of another. In 15 associations, both *T. praeorbitalis* and *C. moori* stomachs contained no identifiable prey, in 13 only *T. praeorbitalis* contained no identifiable prey, and in 12 only *C. moori* stomach contents were unidentifiable.

Discussion

Arthropoda and Cladocera, 0.3–0.8 mm, were found in more than 80% of the stomachs of *P. annectens* that contained identifiable prey (Figure 2). Conversely, Chironomidae (mean length = 4.2 ± 1.4 mm) was the prey item found in over 70% of the stomachs of both *C. moori* and *T. praeorbitalis* that contained prey. Observed differences in prey items may be a partial function of morphological differences (i.e., interraker distance) and prey selectivity. Standard length was discounted as a possible influence on prey size because there were no significant correlations between standard length and prey size when each species was analyzed independently. It was first postulated that the smaller interraker distance would enable *C. moori* and *P. annectens* to forage on the smaller prey items that *T. praeorbitalis* could not ingest. This hypothesis was supported when the prey size in the stomachs of *P. annectens* and *T. praeorbitalis* were compared because the interraker gap was significantly greater in *T. praeorbitalis*. Although the interraker distance between *C. moori* and *P. annectens* was not significantly different, *C. moori* consumed similar-sized prey as that ingested by *T. praeorbitalis* (Figure 2), suggesting that prey size is not solely dependent on interraker gap. Similarly, Drenner et al. (1987) showed that size-selective ingestion rates of gizzard shad *Dorosoma cepedianum* were associated with the cumulative frequency of gill raker gap; however, surgical removal of gill rakers did not affect particle selection of *Sarotherodon galilaeus* (=*Tilapia galilaea*). The retention of small prey items by a few *T. praeorbitalis* may be fortuitous or a function of entrapment in mucus, as suggested for other cichlids (Greenwood 1953; Fryer and Iles 1972).

Thus, we hypothesize that in addition to the influence of interraker gap, differences in prey size and composition are a function of prey selectivity and foraging behavior. For example, although chironomid A and chironomid B are of similar size, the data suggest that either *T. praeorbitalis* is selectively feeding on chironomid B or that *C. moori* is avoiding it. Certainly, neither *C. moori* or *P. annectens* require association with *T. praeorbitalis* for successful prey capture. The presence of Arthropoda and Cladocera in a large number of *P. annectens* stomachs probably results from foraging in the water column, as observed by Kocher and McKaye (1983). It may be that many of these organisms are disturbed from the substrate by *T. praeorbitalis* when it plows its snout into the sand. Consumption of corixids by *C. moori* may also be the result of these prey being suspended following foraging by *T. praeorbitalis* or may be the result of *C. moori* foraging independently of any association with *T. praeorbitalis*. Kocher and McKaye (1983) reported that *C. moori* switched hosts an average of 6.8 times per hour and spent 37.4% of its time alone. Because we captured the feeding associations as soon as they were observed, we cannot estimate the length of time each group was together. While videotaping the *T. praeorbitalis* and *C. moori* associations, however, we observed several groups that remained together for more than 30 min.

We categorized the relationships between *C. moori* and *P. annectens* with *T. praeorbitalis* as commensalistic because there was no evidence of any derived benefit to *T. praeorbitalis.* Perhaps the presence of the other two species better enables *T. praeorbitalis* to establish and defend a feeding territory. The results we present are consistent with observations of the foraging behavior of these three species. *Taeniolethrinops praeorbitalis* swims along the bottom and periodically plunges its snout into the sand. At no time did we observe it stop or reverse direction to selectively feed from the cloud of detritis it had disturbed; it simply continued swimming and plunging its snout into the substrate. The fact that chironomids constitute most of its prey is consistent with this feeding mode. Furthermore, at no time did we observe either *C. moori* or *P. annectens* foraging in the substrate. Because chironomids are not present in the water column, except for nocturnal vertical migrations and immediately before hatching, we concluded that the presence of chironomids in the diet of *C. moori* and *P. annectens* is a direct result of the suspension of these organisms by *T. praeorbitalis.* Because *T. praeorbitalis* does not selectively feed from the cloud of detritus created by its foraging, the organisms not taken directly into its mouth would not be ingested; thus, we conclude that there is no direct competition between either *P. annectens* or *C. moori* and *T. praeorbitalis.*

Furthermore, the data suggest that *T. praeorbitalis* shorter than 68 mm SL do not disturb the substrate sufficiently to attract other fishes. *Cyrtocara moori* and *P. annectens* shorter than 49 mm SL are usually observed in the rocks and vegetation (J.R.S., personal observation) and are probably too vulnerable to predators to follow *T. praeorbitalis* over the sand substrate.

Preying on benthic macroinvertebrates that are dislodged by other fishes has been described for other species. Rankin (1986) observed smallmouth bass *Micropterus dolomieu* foraging behind northern hog suckers *Hypentelium nigricans* that disturbed the substrate and presumably dislodged benthic macroinvertebrates. Other commensalistic associations of *C. moori* include one with *Fossorochromis rostratus* at Nkhata Bay (Fryer and Illes 1972). *Cyrtocara moori* and *P. annectens* both establish commensalistic relationships with *Taeniolethrinops furcicauda* and *Lethrinops furcifer* in the southeast arm of Lake Malaŵi (J.R.S., personal observation). Moreover, *P. annectens* has been observed feeding in association with *P. fenestratus,* which disturbs the benthos by expelling a stream of water from its mouth (videotape, PSU 3735.2). In 1992, we observed six *Nimbochromis polystigma* foraging behind a single *F. rostratus* near Domwe Island in southern Lake Malaŵi.

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