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DEFENSE OF HETEROSPECIFIC CICHLIDS BY *CYRTOCARA MOORII* IN LAKE MALAWI, AFRICA.—Many species of animals come together to feed in multispecific aggregations, to the benefit of one or both species. Insectivorous birds often associate with grazers to feed on insects flushed out by the grazing animal (North, 1944; Jackson, 1945; Willis, 1968; Rand, 1953; Smith, 1971). Several such associations are known between fish. Karplus (1978) has described a feeding association between the grouper (*Epinephelus fasciatus*) and the moray eel (*Gymnothorax griseus*). Individual groupers were observed feeding on fish flushed out of crevices by the eel. The leather bass (*Dermatolepis dermatolepis*) has been observed to follow schools of *Kyphosus analogus* and *Prionurus punctatus*, feeding on the small fish these herbivores disturbed (Montgomery, 1975). Pilotfish (*Naucrates ductor*) associate with whitetip sharks (*Carcharhinus longimanus*) in the Pacific, and may derive any of several benefits from the association (Magnuson, 1971). The pilotfish may be protected from predation, or may use the shark as breeding substrate. Association with the shark may also improve the energy balance of the pilotfish by providing nutrition (from ectoparasites of the shark or fragments of food missed by the shark) or by reducing the energy required for locomotion (because of boundary layer effects).

The cichlid fish *Cyrtocara moorii* in Lake Malawi, Africa, receives benefits from a similar interspecific association (Fryer and Iles, 1972). *C. moorii* follows individuals of several cichlid species which feed in the sandy lake bottom, plucking food from the cloud of detritus stirred up by these fish. *C. moorii* actively defends this resource, attacking other *C. moorii*, and *C. annectens*, a species which sometimes feeds in the same manner. This paper describes the ecology and behavior of *C. moorii* and *C. annectens*, and discusses related behaviors of the host, *Lethrinops praeorbitalis*, which they follow.

Study area and methods.—The study area was a long sandy beach near the tip of the Nankumba peninsula, a region called Cape Maclear (14°S, 35°E), southern Lake Malawi (McKaye, 1981: Fig. 1). The beach was 4 km long and sloped gently toward deeper water. The bottom was mostly fine gravel and sand, with a belt of finer deposits at 8–12 m depth, below wave action and seasonal lake level fluctuations. A few weeds (*Vallisneria* sp. and *Potamegeton* sp.) grew in this muddier region. Visibility at this site is good most of the year (5–20 m Secchi disk readings), and water temperature fluctuates from 22–29.5 C (McKaye, in press). Observations on the sandy shore fish community at Cape Maclear were begun in Oct. 1977. To quantify fish densities biweekly transects of 100 m^2, at 3 m depth contours, were conducted by SCUBA divers. Further observations were made for this study by following individual fish for periods of 15 min each. During these watches notes were made on the feeding, aggression and social behavior of the fish. Notes were transcribed from plastic slates after each dive. These observations were made between 17 June and 13 Aug. 1980. Stomachs and gonads were examined from 16 fish collected in block nets during this same period. Individual fish were tagged with plastic "T-tags." Sightings of tagged individuals were recorded during the course of all underwater work at the site.

Results.—*Cyrtocara moorii* is a relatively rare fish at this location and is found at depths down to 15 m (Table 1). It occurs at highest density in shallow water (3 m), possibly because of greater algal productivity in the shallows. *Lethrinops praeorbitalis*, the main host species, is somewhat more abundant than *C. moorii* and is seen down to 21 m. It is most frequent around 10 m. *Cyrtocara annectens*, an occasional follower, is most

TABLE 1. DENSITY OF FISH PER HECTARE (10,000 m²) AT VARIOUS DEPTHS.

Meters depth	3	6	9	12	15	18	21	24	27
Species									
C. moorii	25	9	8	4	4	0	0	0	0
C. annectens	194	56	322	180	105	0	5	0	0
L. praeorbitalis	31	31	66	33	14	0	14	0	0
N (100 m² transects)	16	32	27	27	22	14	14	10	14

abundant and also has a peak density near 10 m depth, where zooplankton densities are high (McKaye, in press). Eighteen individuals of *C. moorii* were tagged. Three were resighted within the study area. One tagged individual remained in the area for at least six weeks. We tagged 11 *C. annectens* and resighted four individuals, including one sighted two months after its tagging. Three were observed feeding on zooplankton in the lee of an experimental reef. Thirteen individuals of *L. praeorbitalis* were tagged. Seven were resighted, one 18 months later just 20 m from the spot where it was tagged. Though over 500 individuals of 30 species have been tagged since Oct. 1977, this is the only individual resighted more than one year after its tagging.

Lethrinops praeorbitalis feeds by plunging its elongate snout into the bottom and sifting through the sand for the larvae of *Chaoborus*, a lake-fly. While the *Lethrinops* is feeding in this way the follower species, *C. moori* and *C. annectens*, swim close behind and beneath the gills of the host, plucking food particles from the cloud of sediment stirred up by the plunging feeding motion of the larger fish. This is the dominant feeding mode for *C. moorii*, though we occasionally observed them alone feeding on filamentous algae and zooplankton in the water column. *C. annectens* is primarily a zooplankton feeder and becomes a follower only on occasion. The feeding rate is variable, ranging from 0–8.5 bites/min for *C. moorii* and 0–12 bites/min for *C. annectens*. The plunging rate of *L. praeorbitalis* varied from 0–19 per min. Stomach analysis by us and by Fryer and Iles (1972) indicate little dietary overlap between the host and follower species *Lethrinops praeorbitalis* feeds primarily on insect larvae, especially *Chaoborus*, whereas *C. moorii* consumes mostly filamentous algae and detritus. *C. annectens* is primarily a zooplankton feeder but feeds upon detritus when it follows *L. praeorbitalis*.

Only two species, *C. moorii* and *C. annectens*, were observed to follow the "host" species during observations. Usually only one "follower" accompanied a host, though on several occasions as many as four individuals were seen together with a single host. In these cases a hierarchy was formed among the followers, with the largest fish following the host most closely and progressively smaller fish following behind. The largest follower chased away conspecifics which had standard lengths less than 2 cm of its own length. *C. moorii* did not remain with the same host individual but switched hosts an average of 6.8 times per hour (n = 22 watches). *C. moorii* was not always with a host and spent a considerable amount of time (37.4%, 115 of 308 min) alone, searching for a new host. In only five watches out of 20 (25%) did *C. moorii* stay with the same host for the entire watch.

TABLE 2. NUMBER OF AGGRESSIVE ENCOUNTERS (ATTACKS AND THREATS) PER HOUR OF OBSERVATION.

	Attacks given to			Attacks received from		
	C. moorii	*C. annectens*	Other cichlid	*C. moorii*	*C. annectens*	Other cichlid
C. moorii (feeding) N = 21 watches (308 min)	15.2	5.8	0.6	6.0	0	1.7
C. annectens (feeding) N = 4 watches (60 min)	0	6.0	0	3.0	2.0	1.0
C. annectens (nesting) N = 3 watches (45 min)	0	10.7	37.3	0	4.0	28.0

Lethrinops praeorbitalis appears to be the major host of these followers at Cape Maclear. We also observed them following *C. lateristriga*, a fish which feeds in a manner similar to *L. praeorbitalis*.

Aggressive interactions between followers were frequently observed. *C. moorii* attacked conspecifics and *C. annectens* when they tried to follow the same host. *C. moorii* deters potential competitors by chasing, ramming and nipping other individuals. *C. annectens* was not territorial while following the host species. Non-breeding *C. annectens* were not as aggressive, and were easily driven away from hosts by *C. moorii*. *C. annectens* never attacked *C. moorii* during the course of our observations (Table 2). Most observations of aggression in *C. annectens* involved two territorial males defending their nests in the sand against intruding cichlids.

Cytocara moorii exhibits marked changes in coloration during its daily activity. When swimming alone *C. moorii* typically shows a pattern of three dark spots on a light blue background. When the fish joins a host the spots fade and the background intensifies to an even, vivid blue. When several *C. moorii* follow a single host the dominant individual assumes the vivid blue coloration and subordinate individuals show the three-spot pattern. The vivid blue coloration seems to signal dominance. *C. annectens* typically has a horizontal stripe along its body. When it is the dominant individual behind a host, however, it becomes dark blue, almost purple. When breeding, male *C. annectens* adopt a vivid blue color. Neither host species underwent marked color changes during our observations.

Cyrtocara annectens was observed breeding in the manner typical of many nest-building sandy shore Malawi cichlids. Males defended a mound of sand at about 8 m depth and chased intruders up to 3 m away. The males vigorously courted females when they came near the nest. Individuals of other species were driven away by the territorial males. No *C. moorii* were ever seen defending a substratum territory. Circling, typical of cichlid mating behavior, was observed when *C. moorii* males courted females over the open sand. This behavior is similar to that of other sandy shore species which do not defend a substratum spawning territory. The host species, *L. praeorbitalis* and *C. lateristriga*, were never seen breeding, but several individuals of *L. praeorbitalis* and *C. moorii* were found with large eggs in their gonads. It is probable that all four species were actively breeding during the study period.

Discussion.—The territories of animals usually center on a fixed point in space. Several examples are now known of animals which defend a moving territory. Though *C. moorii* frequently shifts from one host to another, its behavior might be considered territorial because of the "repulsion through overt defense" of other fishes from an exclusive area (Wilson, 1975). The observed interactions might also be interpreted as a dominance hierarchy. In either case, the aggressive interactions allow the dominant individual to maintain the most desirable feeding positions beneath the gills of the host. Because large hosts stir up a greater volume of sediment while feeding than do small hosts, the more desirable feeding areas may exist around the largest hosts. Second, the area is used for sexual display. Several times males were seen to court females after the females entered the male's feeding area. It is probable that females are attracted to the large hosts to feed. Males able to maintain dominance around such hosts might have a greater breeding success than other males, though we have not specifically tested this hypothesis.

The *C. moorii* we watched were not so closely associated with a specific host as were the fish studied by Fryer and Iles (1977) at Nkhata Bay. In our study area at Cape Maclear *C. moorii* frequently shifted to a new host, especially when its host ceased to feed. This was shown unequivocally by observation of tagged individuals. The primary host of *C. moorii* at Nkhata Bay was *C. rostratus* (Fryer and Iles, 1972), but we never observed *C. moorii* following *C. rostratus*, even though *C. rostratus* was common at Cape Maclear.

Several gaps still exist in our knowledge of the ecology of these fish. For example, only large individuals of each species were observed. We saw no individuals of *C. moorii* smaller than 65 mm, or of *C. annectens* smaller than 60 mm total length. The host species were always larger than 80 mm. After four years of study of the sand bottom community we still do not know where the younger individuals live. Second, in both feeding and breeding, dominant individuals of *C. moorii* and *C. annectens* adopt a darker color pattern. The value of such a color change is unclear, though it may reduce the number of attacks against these individuals by signalling

dominance. Finally, there are at least two hypotheses which may explain why individuals of similar size do not co-occur behind the same host fish. Fryer and Iles (1972) suggest that individuals may choose particles in proportion to their body size. Thus large individuals may tolerate smaller fish because they are not competing for the same food. It is also possible that sexual dominance precludes the coexistence of fish of similar size behind a single host. A large male may tolerate females and subdominant males as they do not threaten his mating success. Both of these hypotheses require rigorous testing.

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