The cichlid fish *Cynotilapia 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. anisitsi*, a species which sometimes feeds in the same manner. This paper describes the ecology and behavior of *C. moorii* and *C. anisitsi*, and discusses related behaviors of the host, *Lethrinus praenobilis*, 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 (McKay, 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 *Potamogeton* 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 (McKay, in press). Observations on the sandy shore fish community at Cape Maclear were begun in Oct. 1977. To quantify fish densities bivoltan transects of 100 m², 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 slides after each dive. These observations were made between 17 June and 13 Aug. 1980. Stomachs and gonads were examined from 16 fish collected in slack water during this same period. Individual fish were tagged with plastic “1-tags.” Sightings of tagged individuals were recorded during the course of all underwater work at the site.

**Results.**—*Cynotilapia 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 (5 m), possibly because of greater algal productivity in the shallows. *Lethrinus praenobilis*, 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. *Cynotilapia anisitsi*, an occasional follower, is most
TABLE 1. Density of Fish per Hectare (10,009 m²) at Various Depths.

<table>
<thead>
<tr>
<th>Species</th>
<th>3</th>
<th>6</th>
<th>9</th>
<th>12</th>
<th>15</th>
<th>18</th>
<th>21</th>
<th>24</th>
<th>27</th>
</tr>
</thead>
<tbody>
<tr>
<td>C. morii</td>
<td>25</td>
<td>9</td>
<td>8</td>
<td>4</td>
<td>4</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>0</td>
</tr>
<tr>
<td>C. annectens</td>
<td>104</td>
<td>56</td>
<td>322</td>
<td>180</td>
<td>165</td>
<td>0</td>
<td>5</td>
<td>0</td>
<td>0</td>
</tr>
<tr>
<td>L. praenotius</td>
<td>31</td>
<td>31</td>
<td>66</td>
<td>33</td>
<td>14</td>
<td>0</td>
<td>14</td>
<td>0</td>
<td>0</td>
</tr>
<tr>
<td>N (100 m² transects)</td>
<td>16</td>
<td>32</td>
<td>27</td>
<td>27</td>
<td>22</td>
<td>14</td>
<td>14</td>
<td>10</td>
<td>14</td>
</tr>
</tbody>
</table>

abundant and also has a peak density near 10 m depth, where zooplankton densities are high (McKay, in press). Eighteen individuals of C. morii 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. praenotius were tagged. Seven were resighted, one 12 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.

Leptcephalus praenotius feeds by plunging its elongate snout into the bottom and sifting through the sand for the larvae of Chadorus, a lake-fly. While the Leptcephalus is feeding in this way, the follower species, C. morii 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. morii, 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 to 8.5 bites/min for C. morii and 0.12 to 1.2 bites/min for C. annectens. The plunging rate of L. praenotius varied from 0.19 per min. Stomach analysis by us and by Fryer and Ils (1972) indicate little dietary overlap between the host and follower species Leptcephalus praenotius feeds primarily on insect larvae, especially Chadorus, whereas C. morii consumes mostly filamentous algae and detritus. C. annectens is primarily a zooplankton feeder but feeds upon detritus when it follows L. praenotius.

Only two species, C. morii 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. morii did not remain with the same host individual but switched hosts an average of 6.8 times per hour (n = 22 watches). C. morii 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. morii stay with the same host for the entire watch.

TABLE 2. Number of Aggressive Encounters (Attacks and Threats) per Hour of Observation.

<table>
<thead>
<tr>
<th>Attacks given to</th>
<th>C. morii</th>
<th>C. annectens</th>
<th>Other eel</th>
<th>Attacks received from</th>
<th>C. morii</th>
<th>C. annectens</th>
<th>Other eel</th>
</tr>
</thead>
<tbody>
<tr>
<td>C. morii (feeding)</td>
<td></td>
<td></td>
<td></td>
<td>N = 21 watches (308 min)</td>
<td>15.2</td>
<td>5.8</td>
<td>0.6</td>
</tr>
<tr>
<td>C. annectens (feeding)</td>
<td></td>
<td></td>
<td></td>
<td>N = 4 watches (60 min)</td>
<td>0</td>
<td>6.0</td>
<td>0</td>
</tr>
<tr>
<td>C. annectens (swimming)</td>
<td></td>
<td></td>
<td></td>
<td>N = 3 watches (65 min)</td>
<td>0</td>
<td>10.7</td>
<td>37.3</td>
</tr>
</tbody>
</table>
Lethrinaeus praebenthelis appears to be the major host of these followers at Cape Maclear. We also observed them following C. latericana, a fish which feeds in a manner similar to L. praebenthelis.

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

Cyprurus moseri exhibits marked changes in coloration during its daily activity. When swimming alone C. moseri 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. moseri follow a single host the dominant individual assumes the vivid blue coloration and subordinate individuals show the three-spotted pattern. The vivid blue coloration seems to signal dominance. C. amictus 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. amictus adopt a vivid blue color. Neither host species underwent marked color change during our observations.

Ctenopoma amictus was observed breeding in the manner typical of many nest-building sandy shore 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. moseri were ever seen defending a substratum territory. Circling, typical of cichlid mating behavior, was observed when C. moseri males coursed 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. praebenthelis and C. latericana, were never seen breeding, but several individuals of L. praebenthelis and C. moseri 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 known of animals which defend a moving territory. Though C. moseri 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. moseri 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. moseri frequently shifted to a new host, especially when the host ceased to feed. This was shown unequivocally by observation of tagged individuals. The primary host of C. moseri at Nkhata Bay was C. nitidus (Fryer and Iles, 1972), but we never observed C. moseri following C. nitidus, even though C. nitidus 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. moseri smaller than 65 mm, or of C. amictus 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. moseri and C. amictus 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 particular species 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 subordinate males as long as they do not threaten his mating success.

Both of these hypotheses require rigorous testing.

Acknowledgments.—We thank S. Louda, C. McKenzie, M. Oliver and P. Rienhal for reading this manuscript. This research was funded by NSF Grant DEB 79-12338 and a World Wildlife Fund Grant to KRM.

LITERATURE CITED


—. (In press). Ecology and breeding behavior of a cichlid fish, Cynotilapia acutirostrum, on a lake in Lake Malawi, Africa. ibid.


Thomas D. Kocher, Department of Environment