1976

Competition Between Color Morphs of the Midas Cichlid, Cichlasoma citrinellum, in Lake Jiloá, Nicaragua

Kenneth R. McKaye
University of California - Berkeley

George W. Barlow
University of California - Berkeley

Published in INVESTIGATIONS OF THE ICHTHYOFAUNA OF NICARAGUAN LAKES, ed. Thomas B. Thorson (University of Nebraska-Lincoln, 1976).

Competition Between Color Morphs of the Midas Cichlid, *Cichlasoma citrinellum*, in Lake Jiloá, Nicaragua

KENNETH R. MCKAYE AND GEORGE W. BARLOW

INTRODUCTION

Color polymorphism, or polychromatism, is a recurring phenomenon throughout the animal kingdom. In fishes one form, the goldfish, is particularly notable because of its conspicuousness and its occurrence in nature in such a large number of widely unrelated species; yet it is seldom common in any one species (Webber *et al.*, 1973). The Midas cichlid, *Cichlasoma citrinellum*, is unusual in this respect because in many of the lakes where it occurs in Nicaragua brilliantly colored morphs are relatively common. These morphs lack the species-typical dark markings, and individuals vary smoothly from white through yellow, orange, red, and mixtures of these. The most abundant morph, however, is golden orange, which we term gold and use collectively here for all the brilliantly colored fish; the cryptically patterned common grey morphs are called normals.

The occurrence of gold Midas cichlids is positively correlated with turbidity. While absent from some populations, they comprise about seven to ten percent of the adults of others. It is only in Lake Jiloá, with its intermediate visibility of usually three to four meters, that the golds are found where they can be observed. Their degree of development is slightly less than in other lakes, however, the morphs being paler and often having bits of normal coloration. (A comprehensive introductory treatment of the biology of *C. citrinellum* in Nicaragua can be found in Barlow, 1976.)

Laboratory studies have shown that when gold and normal morphs are put into competition the golds grow faster than the normals (Barlow, 1973). Direct observation revealed that golds tend to dominate normals, all else being equal (Barlow and Ballin, 1975), apparently because the gold coloration inhibits attack (Barlow and Wallach, 1975). Furthermore, the laboratory-raised adults prefer to mate with Midas cichlids of the same coloration, although all color crosses are easily carried out (Barlow, in prep.).

These laboratory findings pointed to a number of questions that needed exploring in the field. They suggested intensive intraspecific competition with the possibility that the two morphs could be evolving into separate species, or that one is replacing the other. But since the level of polymorphism apparently has not changed drastically in the last seventy years (*e.g.*, Meek, 1907), one is led to ask about the disadvantages of being a gold morph, such as susceptibility to predation (Barlow, 1976). The objective of this study, therefore, was to quantify the behavioral interactions of these color morphs in nature, guided by hypotheses about differences in distribution, aggression, reproduction, and predation.

MATERIALS AND METHODS

The field work was conducted in Lake Jiloá during the rainy seasons of two years, from 3 July to 15 August, 1972, and from 20 June to 3 September, 1973. Each year the start of the observations coincided with the onset of breeding activity, and observations had to be terminated at what seemed to be the peak of the breeding season.

All observations were done underwater with the use of a Self Contained Underwater Breathing Apparatus (SCUBA). Counts, measurements and general notes were made on writing slates and transcribed after each dive. The depth gauges were calibrated in feet, but the transect line in meters. This has resulted in a mixture of measurements which we regret but prefer to retain for neatness and simplicity of presentation, and in the knowledge that it is easy to convert from one system to the other.

Transects:

The occurrence of different types of Midas cichlids at different depths was estimated by counting the fish encountered by two divers swimming along a transect line. Successive samples were made at depth intervals of 10 feet from depths of 5 to 125 feet. For each sample, one diver set the 25 m line along a depth contour. He then returned to the starting point and the other diver, while staying at least 4 m away from the line. After five minutes, which proved sufficient for the fish to recover, the divers proceeded. They swam parallel to, and on opposite sides of the line, each recording Midas cichlids within 2 m of the line. Thus the area covered independently by each diver was 50 m^2.

The Midas cichlids were tallied separately in six categories as follows: (1) *Normal — nonbreeding*: grey with spots and/or weakly developed banding; supplementary observations had indicated that such fish are neither paired nor territorial. (2) *Normal — breeding*: grey with distinct black barring on a pale background; these are reproductively motivated fish that may or may not have been paired and were not clearly territorial. (3) *Normal — paired with territory*: pronounced barring, as in the preceding, but obviously territorial. (4) *Gold*: yellow-orange coloration and not holding a territory (since golds only intensify their colors a little when breeding, it was not possible to discriminate between nonbreeding and breeding golds without territories). (5) *Gold — paired with territory*. (6) *Gold-Normal — paired with territory*: one mate gold, the other normal (because counts had to be made quickly, only territorial pairs could be reliably recognized).

Some of the pairs had young. The estimated number, size, and age of such fry were recorded.

These transects were carried out at intervals of two to three weeks over rocky areas where breeding activity was high and are not meant to be representative of the entire lake. In the summer of 1972 the deepest transect sample was 90 feet, and the number of samples at each depth varied from five to eight. In 1973 there were twelve samples (six each, by two divers) at all depths down to 80 feet, but below 80 feet the number varied from six to twelve because it was difficult to work so deeply. The problem of nitrogen saturation limited the duration of the deeper dives, so transects in deep water had to be run over a period of two to three days. Below 80 feet underwater lamps were needed to distinguish the coloration of breeding and nonbreeding normal morphs.

Size of breeding fish:

Sleeping Midas cichlids were captured at night with a hand net. They were marked with color-coded Dennison T-tags, and their standard lengths were taken. When seen later, their standard lengths were estimated to test the error of such estimations. When the fish paused over suitable reference points on the bottom, the distance between reference points was measured. The entire procedure took three to five minutes per fish. Fifty percent of the estimates were within 4 mm of the actual measurement and none exceeded an error of 10 mm. Thus the error was roughly in the range of 3 to 8%. These estimates were done in 1973 in water between 20 to 50 feet deep.

Distribution of attacks:

Nonterritorial individuals or pairs of Midas cichlids occurring at depths of 20-50 feet were selected and surveyed for three minutes. Then their aggressive behavior was recorded for fifteen minutes, with the observer three meters away. All attacks and threats given and received were noted, with regard to the color type, as defined above. An attack was an accelerated swim, a charge, to within one body length of the target fish. A threat consisted of raising the dorsal fin or spreading the opercles, with or without an abbreviated charge that did not reach within one body length of the fish to whom the display was directed. The Midas cichlids followed were allocated to four categories: (1) *Normal — nonbreeding coloration*. (2) *Normal — breeding coloration*. (3) *Normal — paired*, but not territorial. (4) *Gold — paired*, but not territorial. Nonpaired golds were not followed because they were so infrequent at those depths. Interactions occurred with territorial Midas cichlids, and are so reported; details of the aggressive behavior of territorial pairs will be given in a subsequent report (McKaye, in prep.).

Survivorship of young:

The number of fry was visually estimated. Older fry were large and could be counted when there were fewer than 40 in the school. In the laboratory, estimates of the number of young fry were within 10% of the actual count. In the field two broods were estimated, then collected and counted, four days after they began to swim. The estimates were low by 9 and 14% of the counts. Since some fry inevitably escape or are lost, the estimates were rather worse than these figures indicate. Routine counting of fry was not feasible because the parents fled as the fry were caught and predators ate the unprotected fry when they were released. Most of the predators sleep at night; but it was not possible to collect and count all the fry then because they sleep dispersed among the crannies of their home cave — some out in the open at the mouth of the cave.

The number of fry was estimated every two to five days, starting with the first or second day of free swimming, and lasting as much as 30 days thereafter in one case. Twenty-two families were observed in water 20 to 40 feet deep, consisting of eighteen normal, three gold, and one gold male — normal female pair.

Results

Transects:

Distribution of all Midas cichlids. — *Cichlasoma citrinellum* was almost unique among the cichlids in Lake Jiloá in that it was the only species other than *Neetroplus nematopus* found at all depths. (The only other fish found from 0 to 130 feet was the predatory eleotrid fish *Gobiomorus dormitor*.) Midas cichlids were more abundant in the second year, 1973, but their pattern of occurrence by depth was much the same (Fig. 1). Below 50 feet their numbers began to drop off rapidly, although they became the dominant species there in the wet season (McKaye, in prep.). In 1972 the greatest number of Midas cichlids was found at depths of 20 to 50 feet. In 1973, however, the population peaked in 10 to 20 feet of water. In 0 to 10 feet of water the Midas cichlids were generally the smaller nonbreeding fish (McKaye, in prep.).

No golds were ever seen during the wet season between 0 to 10 feet and few were encountered between 10 to 20 feet. Below 20 feet, however, their percentage in the population steadily increased, reaching 60% between 100 to 130 feet (Fig. 2 and 3). The percentage of golds between 20 and 50 feet in 1973 was double that found in 1972.

The distribution of golds was clumped. They commonly congregated in groups of from three to twenty rather uniformly spaced fish. On the deeper transects both gold and normal Midas cichlids tended to gather in areas of 10 to 20 m^2, and few others were encountered. These areas were typically V-shaped canyons enclosed by large boulders and "walls" on two sides.

Distribution of breeding pairs. — In 1972 the density of breeding pairs of Midas cichlids was higher than in 1973 at all depths, and especially at 10 to 20 feet (Fig. 4). In both years the density of breeding fish was highest in water 10 to 20 feet deep, and in both there was a second peak between 30 and 40 feet. There was, nonetheless, a progressive decline, at depths below 20 feet, in the density of breeding pairs. Though pairs were observed defending territories below 60 feet, none there was ever observed with young.

In 1972 and in 1973 the density of breeding gold pairs was greatest between 31 and 40 feet (Fig. 5). Although the density of breeding pairs for the population as a whole was down in 1973 from 1972, the opposite was true for golds who were breeding at a greater density in 1973 than in 1972.

In both years, between 20 and 50 feet, the percent of gold pairs among pairs of *C. citrinellum* of all colors was greater than the percent of golds found there (Fig. 2 and 3). The percent of gold pairs, however, dropped off rapidly below 50 feet in contrast to the steadily increasing percent of golds at greater depths.

Distribution of schooling fish in breeding and nonbreeding color. — From 0 to 50 feet the proportion of fish in breeding color increased steadily, reaching a peak at 40 to 50 feet (Fig. 6). Below 50 feet the percent dropped off quickly. More than 80% of the fish in breeding color were between 20 and 60 feet.

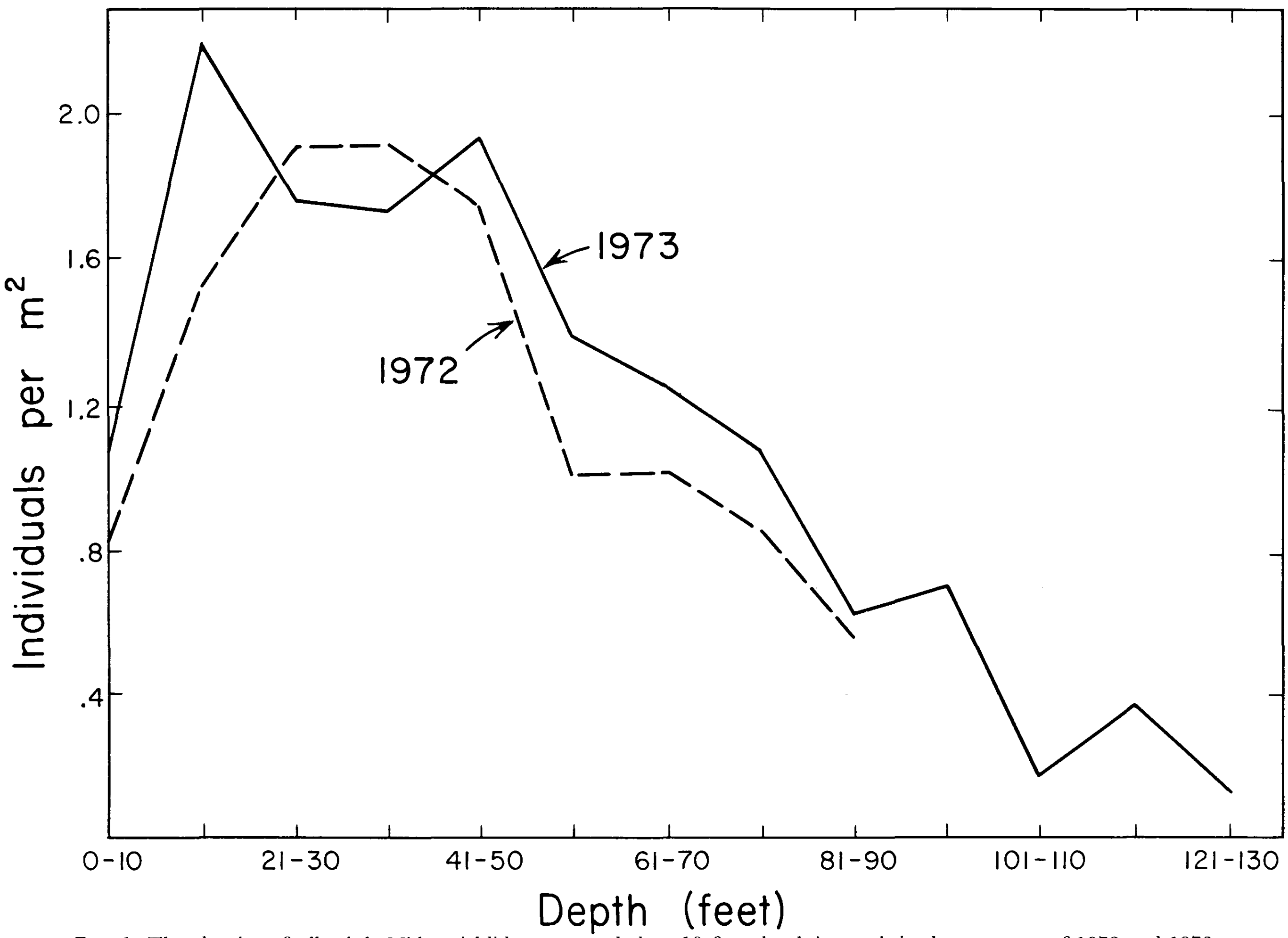

FIG. 1. The density of all adult Midas cichlids, as recorded at 10-foot depth intervals in the summers of 1972 and 1973.

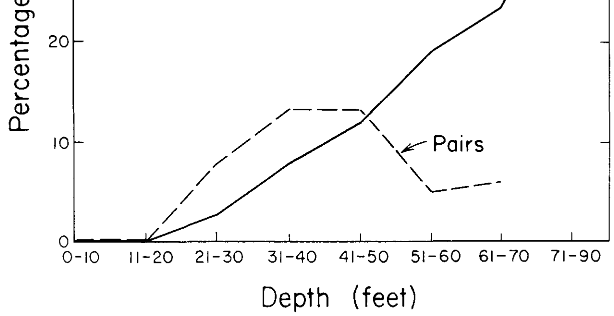

FIG. 2. The percent of gold morphs of the Midas cichlid at different depths in 1972. The solid line shows the percent of all nonbreeding fish present. The broken line shows the percent of gold breeding pairs, calculated from the total number of breeding pairs present.

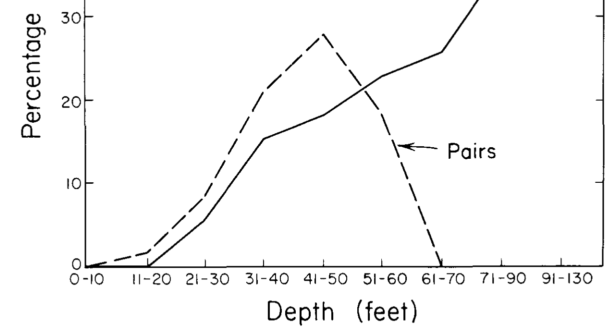

FIG. 3. The percent of gold morphs of the Midas cichlid at different depths in 1973. The solid line shows the percent of all nonbreeding fish present. The broken line shows the percent of gold breeding pairs, calculated from the total number of breeding pairs present.

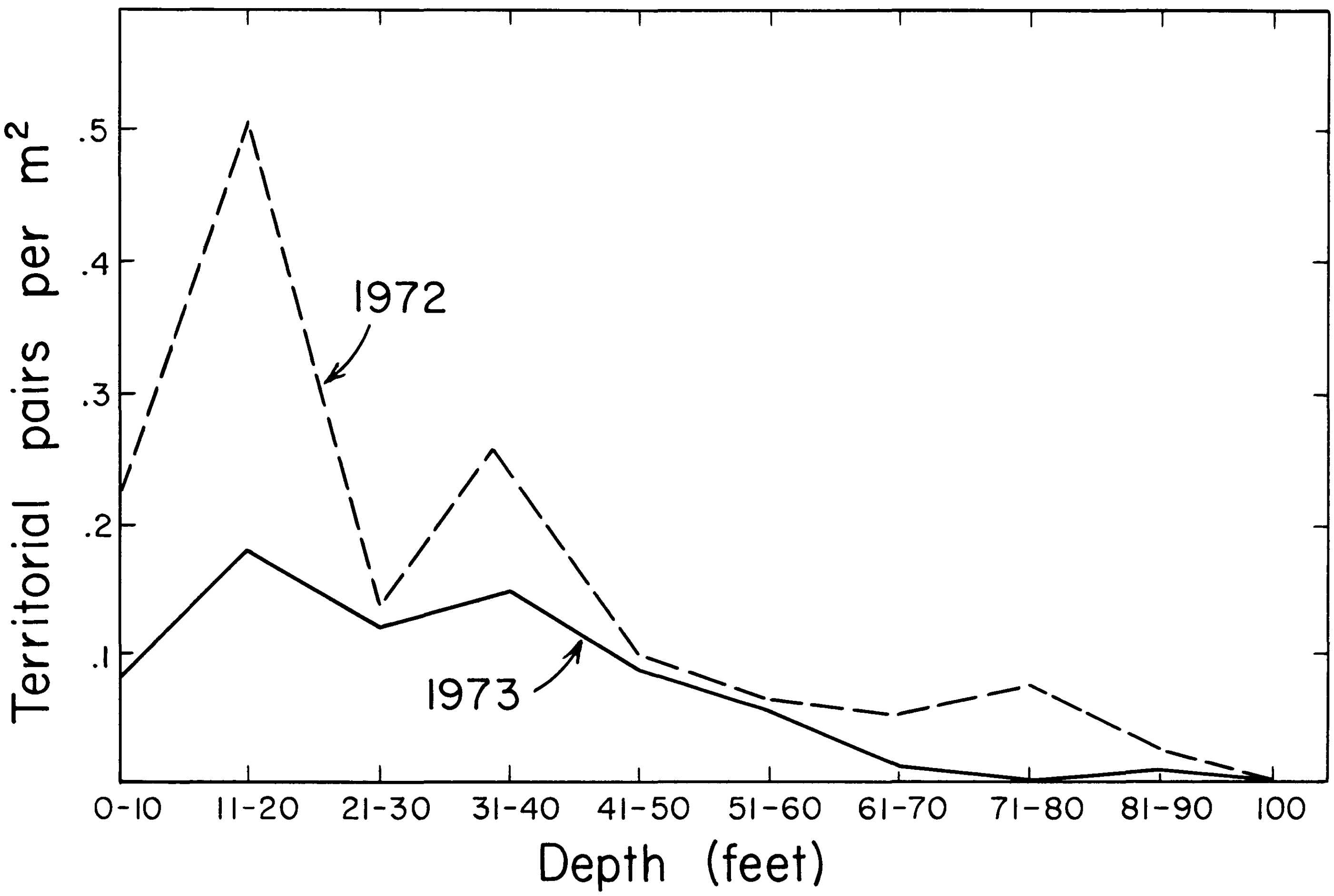

FIG. 4. The density of breeding pairs of all Midas cichlids, as recorded at 10-foot depth intervals in the summers of 1972 and 1973.

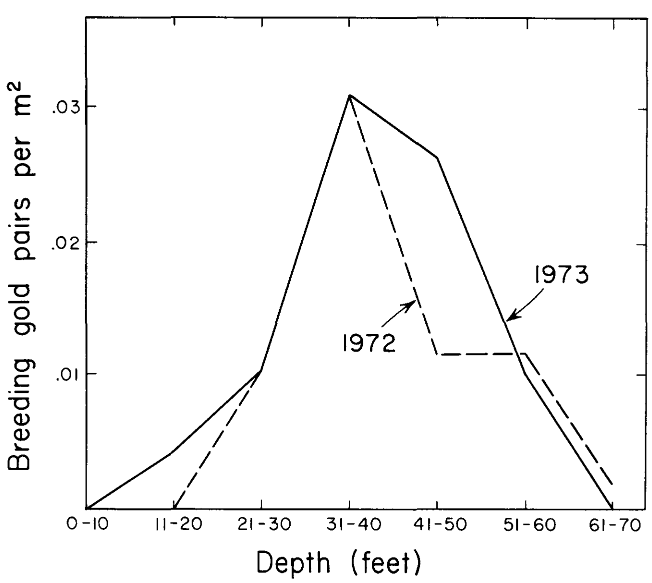

FIG. 5. The density of breeding gold pairs of Midas cichlids as recorded at 10-foot depth intervals in the summers of 1972 and 1973.

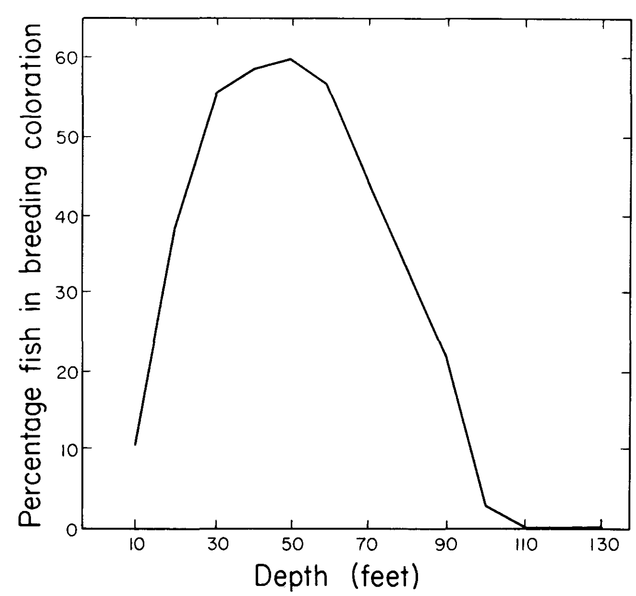

FIG. 6. The proportion of Midas cichlids in breeding coloration as recorded at 10-foot depth intervals in 1973.

TABLE 1. The frequency of occurrence of pairs of Midas cichlids, according to the coloration of the males and females. Expected frequencies are in parentheses.

1972

		Females: Normal	Females: Gold
Males	Normal	146 (131.2)	0 (14.8)
Males	Gold	8 (22.7)	17 (2.3)

1973

		Females: Normal	Females: Gold
Males	Normal	279 (236.5)	0 (42.5)
Males	Gold	1 (43.5)	50 (6.5)

Assortative mating (Table 1). — Normals and golds mated almost exclusively with fish of their own color. Of the nine mixed pairs tallied on the transects in two years, all the males were gold. Pairs with normal males and gold females were occasionally seen in the lake, but they were never encountered on a transect.

In 1972, when there were about 8% golds at depths of 20 to 50 feet, there were twice as many gold-gold pairs as gold-normal pairs (the convention here is to give the male's color first). In 1973, however, when the figure had risen to about 15%, 50 gold-gold pairs were seen as compared to one gold-normal pair. Thus an increase in the proportion of breeding gold individuals was accompanied by an increase in the proportion of exclusively gold pairs, climbing from 68% in 1972 to 98% in 1973.

Sizes of paired golds and normals. — The fish of the gold pairs were smaller than those of the normal pairs (Fig. 7). The mean standard length of gold males (129 mm) was significantly smaller than the value (150 mm) for normal males (t test, $p<.01$). The same holds for gold females compared to normals (means = 105 and 119 mm respectively; t test, $p<.01$). Unfortunately there were no accessible mixed-color pairs when these measurements were made.

The mean lengths (Fig. 7) of gold females averaged 81% of the lengths of their mates; lengths of normal females averaged 79% of those of their mates.

Distribution of attacks:

Although it was possible, while surveying normal fish, to determine whether they were paired, this was often not the case with the fish with whom they interacted. Therefore, interactions with paired and non-paired fish in breeding color were not separated in this analysis; they are simply referred to as "breeding," based on coloration. All interactions with territorial fish refer to normal pairs; territorial golds were present but in such small numbers that no interactions were seen during the sampling periods.

Normals in nonbreeding color. — Normals in nonbreeding color attacked only other nonbreeding fish, and those very infrequently (Fig. 8). They were never seen attacking breeding fish (Figs. 8, 9, 10 and 11). Nonbreeders were attacked, however, by territorial and nonterritorial breeders, but at a low level. This generally occurred when breeders were attacking several fish in close proximity, or when nonbreeders strayed into the territory of a pair.

Single normals in breeding color. — Nonpaired fish in breeding color attacked like-colored fish (breeders) at a rate of over 26/100 min., but never those that were territorial (Fig. 9). On the other hand they were attacked more by territorial fish than by any other type (Fig. 9); this is consistent with other observations showing that territorial fish selectively attack those with breeding coloration (McKaye, in prep.).

Single breeders, however, did threaten territorial fish (Table 2). When interacting with normals similarly in

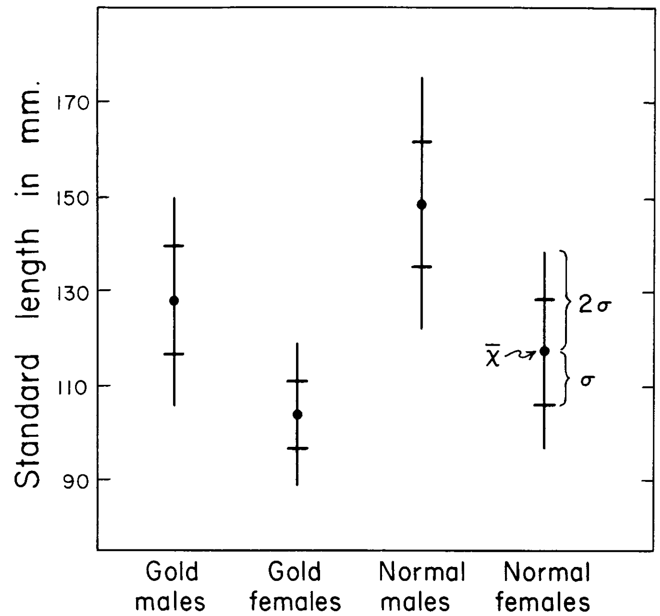

FIG. 7. The standard lengths of paired males and females of gold and normal pairs of Midas cichlids. For each category, the vertical line is marked with the mean value at the center and the values of the mean plus and minus one, then two, standard deviations.

TABLE 2. Ratio of threats and attacks given and received by *Cichlasoma citrinellum*

	Single fish in breeding color		Paired fish in breeding color		Gold pairs
Threats & attacks given to					
Nonbreeders	.50	**	.80		.25
Breeders	1.00		.48	**	.23
Territorial pairs	inf.		1.70		Never seen
Golds	3.00		3.00	**	1.50
Threat & attacks received from					
Nonbreeders	Never seen	**	Never seen		Never seen
Breeders	1.00		2.50	*	inf.
Territorial pairs	.50		.77		3.00
Golds	.57		inf.	*	1.50

[bracket **] Two values significantly different. χ^2, $p<.01$
[bracket *] Value at right significantly different from other two. χ^2, $p<.05$
[bracket **] Value at right significantly different from other two. χ^2, $p<.01$
inf. = no attacks; some threats observed
Never seen = no attacks or threats observed

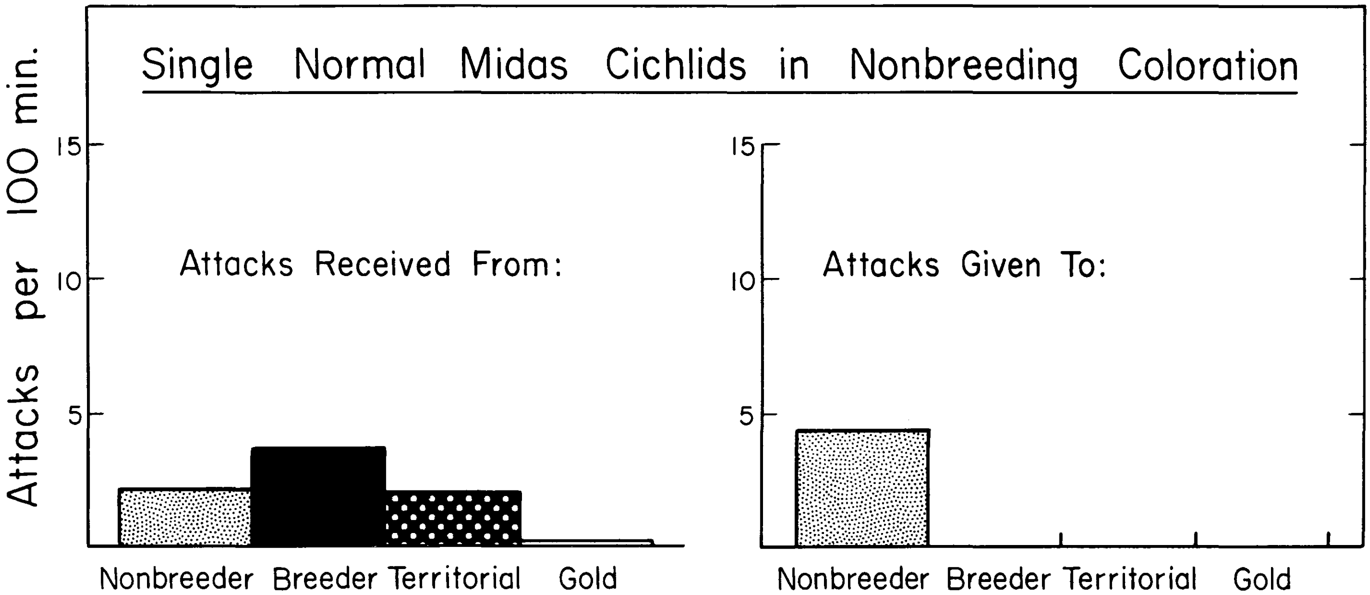

FIG. 8. Attacks received (left panel) and given (right panel) by single adult Midas cichlids in nonbreeding coloration. The categories For the histograms are explained in the text.

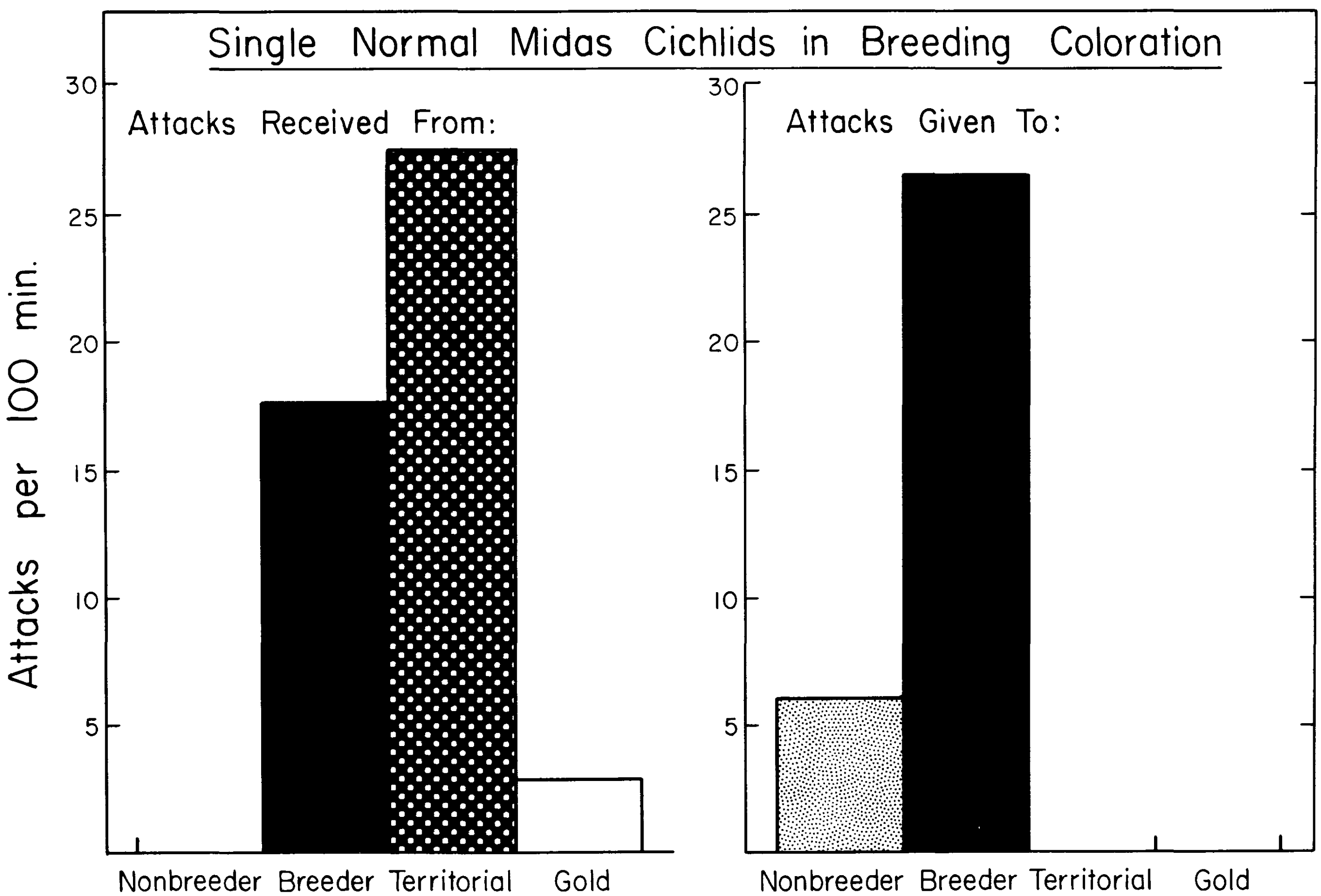

FIG. 9. Attacks received (left panel) and given (right panel) by single adult Midas cichlids in breeding coloration. The categories for the histograms are explained in the text.

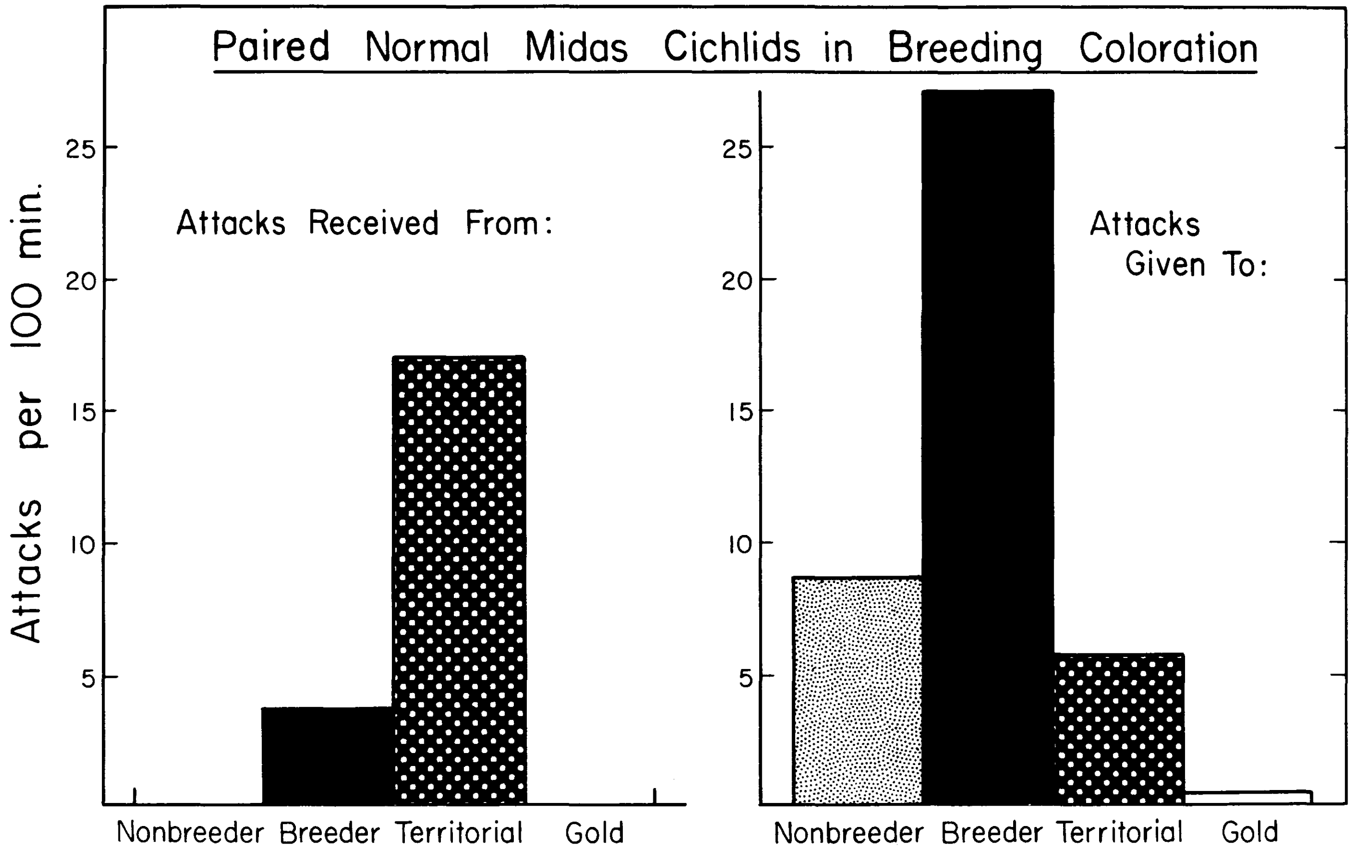

FIG. 10. Attacks received (left panel) and given (right panel) by paired normal Midas cichlids in breeding coloration. The categories for the histograms are explained in the text.

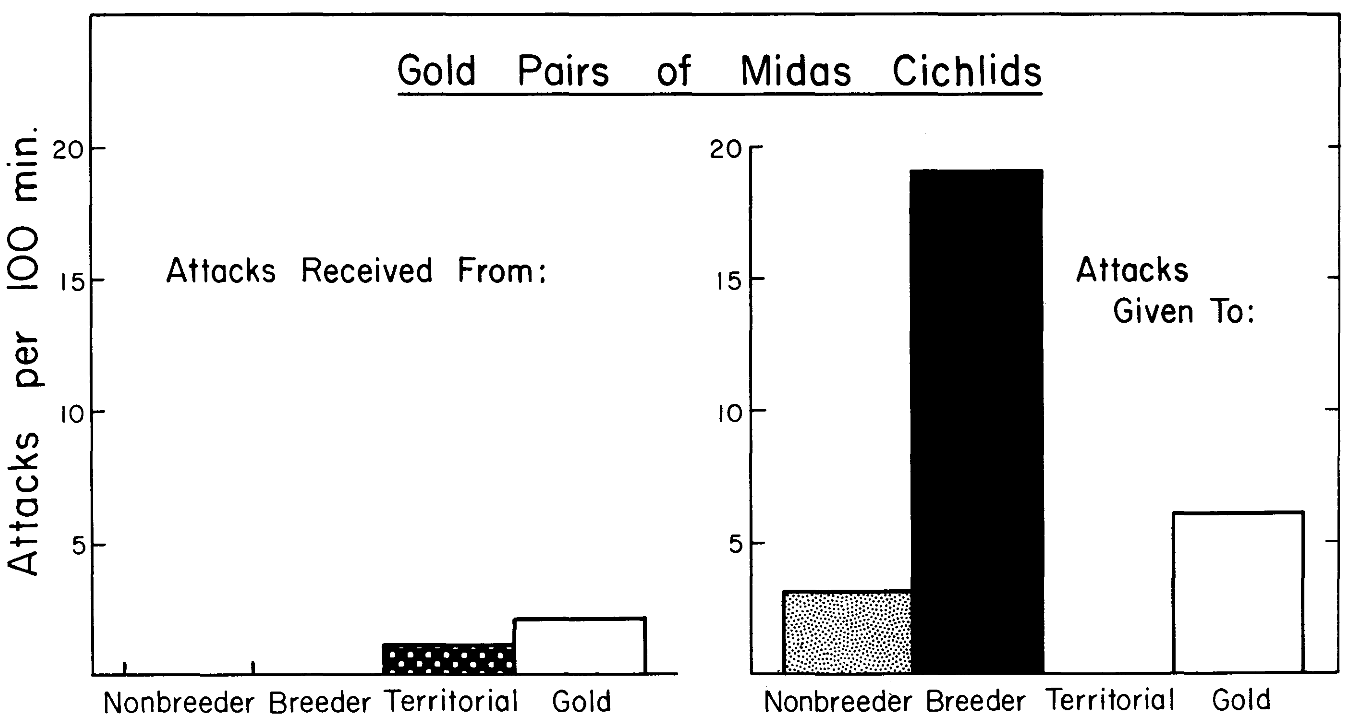

FIG. 11. Attacks received (left panel) and given (right panel) by pairs of gold Midas cichlids. The categories for the histograms are explained in the text.

breeding color, they threatened and attacked in equal amounts; but when engaging golds, they threatened three times as often as they attacked. Breeding fish were threatened about half as often as they were attacked by both territorial normal fish and nonterritorial gold pairs (Table 2).

Paired normals in breeding color. — Nonterritorial pairs attacked breeders at a rate equal to that of nonpaired breeders (compare Fig. 9 and Fig. 10). Though an insufficient number of fish were tagged to count attacks by and on individuals, it was apparent that many attacks by paired fish were directed to other paired fish. Often these were multiple attacks in which male attacked male and female attacked female. Such successions of attack were rarely seen among nonpaired fish.

Unlike single fish, paired fish did attack established territory holders (Fig. 10); once they were seen to attack a nonterritorial pair of golds. These paired nonterritorial breeders were also attacked significantly less (Mann-Whitney U, $p<.01$) by other nonterritorial breeders and by territorial pairs (Fig. 10) than were single breeders (Fig. 9).

When interacting with other breeding fish, paired fish threatened about half (.48) as often as they attacked (Table 2); this ratio is significantly less (χ^2, $p<.01$) than that (1.00) of single fish. Paired fish threatened territorial fish almost twice (1.70) as often as they attacked, and they threatened golds three times as often as they attacked them (Table 2).

Paired fish were threatened 2.5 times as often as they were attacked by breeders, which is significantly more (χ^2, $p<.01$) than the ratio (1.00) for breeders threatening single fish. Paired fish received a nonsignificantly greater proportion of threats from territorial fish (.77) than did solitary fish (.50). No attacks, and only four threats, by golds upon normal pairs were observed while watching the normal pairs.

Nonterritorial gold pairs. — Gold pairs attacked both nonterritorial breeders and territorial pairs significantly less than did normal pairs (Mann Whitney U, $p<.05$). But they attacked fellow gold pairs at a significantly higher rate than did normal pairs (Mann Whitney U, $p<.01$). Gold pairs were attacked significantly less by breeders and territorial pairs than were normal pairs (Mann Whitney U, $p<.01$; Figs. 10 and 11).

The ratio (.23) of threats to attacks by golds upon breeders was significantly lower than the ratio (1.00) for single fish upon breeders (χ^2, $p<.01$; Table 2). It was not, however, significantly lower than the ratio (.48) of threats to attacks by paired normals upon breeders.

Golds threatened each other less and were more likely to attack each other, given an aggressive interaction, than were single or paired normals (χ^2, $p<.05$).

When interacting aggressively, breeders and territorial normals were more apt to threaten and less likely to attack gold pairs than normal pairs (χ^2, $p<.05$).

Survivorship of young:

Only four of the 22 observed broods survived for as long as 16 days. The other 18 were devoured by predators and their parents lost their territories. Thus mortality was high (Fig. 12). The young were eaten primarily by other cichlids, notably *Neetroplus nematopus*, *Cichlasoma nigrofasciatum*, and fellow Midas cichlids, and by the eleotrid, *Gobiomorus dormitor*. A more detailed account of parental protection of young will appear elsewhere (McKaye, in prep.).

Of the four successful pairs (Fig. 13), three had at least one gold member: two were gold pairs, one a gold-normal pair, and the other a normal pair. The one gold pair that was not successful lost its brood on the first day when it became involved in a territorial battle with a pair of large normals; while fighting the normals for 10 to 15 minutes, their young were devoured by predators (for a detailed account, see McKaye and Hallacher, 1973).

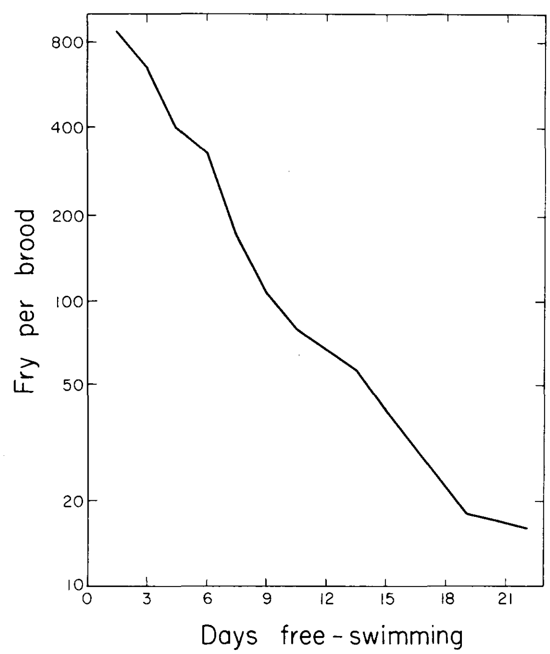

FIG. 12. The overall survivorship curve for schools of young Midas cichlids guarded by their parents.

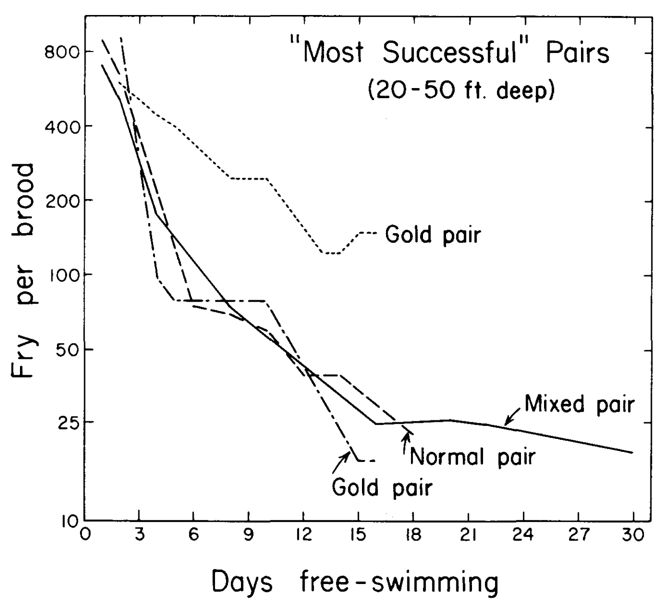

FIG. 13. Individual survivorship curves for the offspring of the four most successful pairs of Midas cichlids breeding at depths of 20 to 50 feet. The color types of the parents are shown.

In shallow water (0-20 feet), where golds do not usually breed, 50% of the normal pairs still had young after 16 days. Golds were not even seen in this area in 1972. In 1973, however, one gold pair bred in 13 feet of water, but lost all its young by the sixth day after the fry had become free swimming. (Data on survivorship of young in 1973, when the density of paired fish was less, have not yet been analysed.)

Discussion

Patterns of aggression play an important role in the success, or lack of it, in breeding pairs (see below). Differences in aggressive behavior also contribute to the different distributions of breeding gold and normal morphs.

The breeding adults at all depths directed most of their aggression toward normal adults in breeding coloration, especially those not already holding territories. The form the aggression took was also different: they were twice as likely to attack as to threaten nonterritorial normals showing breeding coloration. Such behavior could account in large part for the displacement toward deeper water of excess fish in breeding condition (see below).

Laboratory studies have shown that, size for size, golds tend to dominate normals (Barlow and Ballin, 1975). This superiority in aggressive interactions appears to derive from an inhibitory effect of the gold coloration on the other fish (Barlow and Wallach, 1975). The field data are in agreement. Both territorial and nonterritorial breeding normals directed fewer attacks toward golds than toward normals. Their aggressive behavior was also at a lower level, having a high ratio of threats to attacks. Golds manifested less aggressive behavior than did normals, but when they did they were more inclined to attack than to threaten. Golds were also relatively more aggressive toward golds then were normals. In summary, golds were attacked less and seemed to have less need to attack others, but when aggressive they tended to attack rather than threaten.

We now have direct observations and data verifying that there are too few suitable sites for the number of pairs trying to breed (McKaye, in prep.). One of the reasons so few pairs are able to complete a breeding cycle is that other pairs evict them from their territories prematurely.

Apparently the best sites are in shallow water, at depths of 10 to 20 feet. That is deep enough to be away from most land based predators, and it is below surface turbulence most of the time. The light there is sufficient to insure productivity: *Aufwuchs* is still plentiful at those depths, as are planktonic algae, but both decrease at greater depths. These provide a base for the microfauna on which the fry feed. The adults ingest the *Aufwuchs* and animals associated with it (Barlow, 1976).

In Lake Apoyo, when no *C. citrinellum* were breeding, they were most abundant at depths of 10 to 20 feet. Likewise, in 1973 in Lake Jiloá, when the density of breeding pairs was relatively low (one-third the 1972 level), but the population density high, the greatest density of Midas cichlids was found at this depth.

Most of the breeding pairs in Lake Jiloá first established territories in shallow water. They were *all* normal in color. They also seemed to be the largest individuals in the population. (Barlow 1976), observing at these depths, also commented that only the largest fish were able to breed.) Fighting over territories was seldom seen. Evidently the small adults did not contest with the few large territory holders. Midas cichlids somewhat smaller (120 - 160 mm S.L.) than the biggest ones moved to sites in deeper water (McKaye, in prep.). The nonterritorial Midas cichlids remaining in the shallows were yet smaller (90 - 130 mm), but the largest of these were probably reproductively mature, judging by the size at which breeding occurs in the laboratory. The breeding adults in the shallows rarely attacked them because they usually avoided the adults and their progeny. Close approach by small Midas cichlids, however, as when attempting to eat the fry, elicited immediate attack.

Both normal colored and gold morphs held territories in the zone just below the shallows. The competition for breeding sites was overt there. Fights were frequent and there was a steady turnover of territories with a consequent loss of eggs, larvae or fry. This was in contrast to the situation in the shallows where premature loss of territories was less common and therefore successful reproduction higher.

The striking phenomenon in the subshallow zone of 20 to 50 feet, apart from the greater contesting for territories, was the apparent supremacy of gold pairs. This was clearest at depths of 30 to 40 feet. There golds held territories in greater numbers than would have been predicted from their local abundance. Moreover, the gold pairs there were more successful in raising fry. This advantage derives from the ability of golds to dominate normals of similar and somewhat larger size.

This raises the question of fish size in relation to color polymorphism. In another population, in Lake Masaya, the larger the fish the higher the proportion that are gold. Thus golds are relatively more abundant in the largest size classes (Barlow, 1976). In Lake Jiloá a different situation appears to prevail (based on data collected by McKaye in the spring of 1974 and not yet fully analyzed). Golds are most numerous as middle sized adults (110-140 mm). This suggests either that they experience greater mortality than normals at larger sizes, or that their growth is retarded by an earlier involvement in energetically costly reproductive behavior. Barlow (1976) has presented evidence showing that the adults are relatively safe from predation, and an examination by McKaye of stomach contents of their predators in Lake Jiloá supports this conclusion. Observations suggest that gold adult Midas cichlids are, on the other hand, more susceptible to disease than are normal morphs in Lake Jiloá (McKaye, in prep.). This could account for the lack of gold morphs at the largest sizes. The golds in Lake Masaya, however, may be more resistant to disease than are the normal morphs there (Barlow, 1976).

The significant point is that the gold morphs in Lake Jiloá are able to breed at a smaller size than are the normals. In the subshallow zone they obtain and hold territories in competition with appreciably larger normal morphs. In the laboratory, golds generally defeat normals in matched-pair encounters; when the weight of the gold is about 87 ± 5% that of its normal rival, the probability is 50% that either will win (Barlow, in prep.). The field data suggest that a greater size disparity is possible. We reason, nonetheless, that the territorial normals in the shallows are too large for the breeding gold morphs. In turbid lakes, such as Masaya, golds breed in the shallows. Recall, however, that they also reach large sizes there.

Although the two morphs compete with one another, they do interbreed, even if at a much lower frequency than would be predicted from their numbers in the population. Also, a fish may breed as a normal, then later become a gold. If such fish breed with normals that remain normal in color, gene flow will have occurred, although this would favor fish that delay metamorphosis. Thus there is clearly genetic exchange between the color morphs, although at a relatively low level.

The early phases of this research program were guided by the hypothesis that this polymorphism is involved in population regulation (Barlow, 1976). During periods of overcrowding in a monomorphic population, all individuals would be equally disadvantaged in competition for food. If these conditions were severe, no fish would be able to harbor enough reserves to breed until the population declined or more food became available. Coupled with loss of recruitment, the population size would decline. The fry do not compete with the adults for food. Should any pair breed, their offspring would have an abundance of food due to the lack of competing fry. The inclusive fitness (Hamilton, 1971) of pairs that are able to breed during periods of overpopulation should therefore be high, and selection should favor such individuals.

Some of the observations in Lake Jiloá support this hypothesis. In 1973 the population of Midas cichlids was up, compared to 1972. Breeding, however, was down, apparently as a consequence, whether due to less food available per fish or to disruptive competition for breeding sites. In contrast, more gold pairs bred in 1973 than in 1972. Moreover, they paired more exclusively with golds. Both factors would lead to a greater genetic contribution by the golds during a period of increased population density.

Golds also seem to have a genetic advantage in terms of generation time. They bred at smaller sizes than did the normals and so were presumably younger. Perhaps they were even younger than their sizes would indicate, for in the laboratory golds grew faster than normals when they were raised together (Barlow, 1973). We assume that this holds in the field as well, so golds might reach reproductive size faster than normals.

It could be argued that, since the normals breed at a larger size than golds, they are able to lay more eggs. That is true, but the critical point is which morphs produce the most offspring surviving to a reproductive age. The data here suggest that the gold pairs are at least more successful in raising fry when compared to normals breeding at the same depth. But for the population as a whole this superiority of golds was apparent only in an area that seems to be suboptimal. Only normals bred in the best area, the shallows, where they were more successful in rearing young.

Given these differences, one wonders why the golds have not evolved into a separate species, breeding in deeper water, or replaced the normal morphs. The two morphs seem to be in rough equilibrium. There must be offsetting disadvantages to being gold in color, and these must depend on frequency of occurrence in combination with the physical environment (Barlow, 1976; Barlow *et al.*, 1975). We suspect, but have not proved, that the main selective pressure working against golds is predation. They can persist only in low numbers, at large sizes, and under special light conditions, such as deep or turbid water (see Barlow, 1976).

Acknowledgments

We would like to thank the many people who helped make this research possible. Leon Hallacher and Phil Sharkey assisted on dives and helped collect data on the distribution of golds and normals. Jeffry R. Baylis was responsible for much of the work in organizing the expedition in 1972 and conducted parallel research of his own in Lake Jiloá; discussions of research plans with him were of great help. Tom Hartwell lent us his truck and spent many hours helping us prepare equipment for Nicaragua. Mary Lou Pressick made available her air compressor, and Lloyd Austin, diving officer of the University of California, Berkeley, gave freely of his time to get our diving equipment in order. Alfonso Solórzano generously allowed us to live in his house and aided us in many ways. The Nicaraguan government, and especially Antonio Flores of INFONAC, were of great aid in minimizing procedural delays and in putting a laboratory at our disposal. Special thanks go to Katherine H. McKaye, who dived both summers on this project, and was involved in developing many of the ideas presented here.

This research was supported in part by grants to K.R. McKaye from the Center for Latin American Studies, University of California, Berkeley, and from Sigma Xi, and by NSF Grant GB 32192X to G. W. Barlow.

Gerta O. Barlow provided invaluable assistance in the preparation of the manuscript.

Summary

The distribution and behavior of gold and grey morphs of the Midas cichlid, *Cichlasoma citrinellum*, were examined in Lake Jiloá, Nicaragua. The two color morphs mated assortively there and had clumped distributions. Golds paired and bred at a smaller size than did greys. The percentage of golds increased with depth, and the golds bred most successfully at 30-50 feet; greys bred in highest numbers at 0-20 feet. Aggressive interactions between fish of the same color were higher than between fish of different colors. Color polymorphism is evidently maintained by an advantage that golds have in aggressive interactions, increasing their ability to capture and maintain territories. But the golds are probably disadvantaged by their enhanced visibility, and thus that of their offspring, to predators. This could explain their absence from depths of 0 to 20 feet, where the highest breeding density of *C. citrinellum* was recorded; it is also where light intensity was the greatest and consequently algal productivity the highest.

Resumen

Se estudió la distribución y el comportamiento de los morfos gris y dorado del cíclido Midas, *Cichlasoma citrinellum*, en el Lago Jiloá, Nicaragua. Los dos morfos se apareaban con individuos de su propio morfo y tenían distribuciones amontonadas. Los dorados se apareaban y se reproducían de un tamaño menor que los grises. El porcentaje de dorados aumentaba con la profundidad, y el apareamiento era óptimo entre 30 y 50 pies; los grises se reproducían en mayor número entre 0 y 20 pies. Las interacciones agresivas eran más frecuentes entre morfos del mismo color que entre los de color diferente. El polimorfismo de color evidentemente se mantiene por la ventaja que los dorados tienen en los encuentros agresivos, que aumenta su habilidad de capturar y mantener territorios. Sin embargo los dorados (y sus crías) tienen la desventaja de ser más visibles a sus depredadores. Esto puede explicar su ausencia en profundidades entre 0 y 20 pies, donde se encontró la máxima intensidad reproductiva de *C. citrinellum*; aquí es también donde la intensidad lumínica es máxima y, consecuentemente, es donde existe la mayor productividad de algas.

Literature Cited

Barlow, G. W. 1973. Competition between color morphs of the polychromatic Midas cichlid *Cichlasoma citrinellum*. Science 179:806–807.

Barlow, G. W. 1976. The Midas cichlid in Nicaragua. *In:* Investigations of the Ichthyofauna of Nicaraguan Lakes. T. B. Thorson, ed. School of Life Sciences, Univ. Nebr.–Lincoln.

Barlow, G. W. and P. J. Ballin. 1975. The influence of coloration on dominance in the polychromatic Midas cichlid. Anim. Behav. (in press).

Barlow, G. W., D. H. Bauer and K. R. McKaye. 1975. A comparison of feeding, spacing and aggression in color morphs of the Midas cichlid. I. Food continuously present. Behav. (in press).

Barlow, G. W. and S. J. Wallach. 1975. Color and levels of aggression in the Midas cichlid. Anim. Behav. (in press).

Hamilton, W. D. 1971. Selection of selfish and altruistic behavior in some extreme models. *In*: Man and beast: Comparative social behavior. J. F. Eisenberg and W. S. Dillon, eds. Smithsonian Institution Press, Washington, D. C.

McKaye, K. and L. Hallacher. 1973. The Midas cichlid of Nicaragua. Pacific Discovery 25(5):1–8.

Meek, S. E. 1907. Synopsis of the fishes of the Great Lakes of Nicaragua. Field Columb. Mus. Pub. 121, Zool. Ser. 7(4):97–132.

Webber, R., G. W. Barlow and A. H. Brush. 1973. Pigments of a color polymorphism in a cichlid fish. Comp. Biochem. Physiol. 44B:1127–1135.