A COMPARISON OF FEEDING, SPACING, AND AGGRESSION IN COLOR MORPHS OF THE MIDAS CICHLID. I. FOOD CONTINUOUSLY PRESENT

by

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INTRODUCTION

The Midas cichlid, Cichlasoma citrinellum, is a common fish in Nicaragua, inhabiting its many lakes. It is polychromatic — there is a wide but discontinuous range of color patterns. Fish that show the cryptic patterns typical of cichlid fishes are termed 'normal'. In some of the lakes, however, including the large lakes of Nicaragua and Managua, 7 to 10% of the adult population consists of individuals that lack the species-typical markings and are variously white, yellow, orange or red, some being mixtures of two or more colors; the most common color phase among these brilliant individuals is golden orange, which we refer to as 'gold'. This phenomenon and the natural history of the species are described in detail elsewhere (Barlow, 1975).

The relatively frequent occurrence in nature of these gold morphs raises questions about survival value in relation to communication. When a Midas cichlid becomes gold (all start life normal), it loses its species-identifying markings as well as the ability to change color patterns. Switching color patterns is an important part of communication among cichlids (BAERENDS & BAERENDS-VAN ROON, 1950; LEONG, 1969). The gold morphs, therefore, appear to be handicapped by their coloration in at least three ways: (1) They

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are not camouflaged and so may be more vulnerable to predation. (2) Lacking the species-typical markings could interfere with species recognition. (3) Being unable to change colors, they can communicate only one message through their coloration. There must be some advantages to being gold. Otherwise, natural selection would have reduced their occurrence to zero, or to a rare individual. In this report we concentrate on one aspect of the advantage enjoyed by the gold morph.

The normal morphs show yellow, orange, or red to varying degrees, especially in their eyes and on their throats. These markings appear to play a role in displays seen during aggressive interactions. We therefore suspected that being gold affects the dominance relationships between Midas cichlids. Preliminary observations indicated that such differences could be profitably investigated.

In the first experiment (Barlow & Ballin, 1976) we established that golds generally dominate normals. Furthermore, this dominance seems to confer an advantage in feeding, although the evidence here was less certain. A subsequent experiment (Barlow & Wallach, 1976) revealed that the gold fish are not inherently more aggressive than the normal ones. Rather, gold coloration appears to inhibit attack in gold and in normal fish.

A third experiment was done on rate of growth (Barlow, 1973). Golds grow faster than normals, but only when kept together with normals. Pure cultures of golds grew at about the same rate as pure cultures of normals. Thus golds have an edge here over normal colored fish of similar size, but that margin is manifested only when they are in mixed groups.

These are inferences, however, drawn mostly from experiments done in relatively small aquaria. In those small arenas the fish were forced to remain in close proximity to one another, doubtless elevating the level of aggressiveness. Furthermore, at each meal the fish were fed just enough to assure that most of the food was quickly eaten. When fed, all of them rushed to the food, irrespective of dominance relationships, and ate rapidly with almost no attacking (see also Magnuson, 1962). Any advantage of dominance in relation to feeding was apparent only in the fighting over scraps when much of the food was already eaten. It was desirable, therefore, to test the conclusions in a large arena and with food continuously available. This seemed a more reasonable approximation of natural conditions.

A number of considerations, including field observations and pilot experiments, led to an experiment that pitted one large fish against six small ones. The large fish resided in a shelter next to a feeder containing food all the time. The small fish had to approach the feeder and shelter at the apex of a V in order to eat.

We anticipated that the large fish would attack the normal morph more than the gold when both were present. It follows that the small gold fish should have been able to approach closer than the normal ones, and also to feed more. A further prediction was that small fish, irrespective of their own color, would attack the small normals more than the small golds. We also made predictions in relation to the various controls, but these will be stated further on.

Experiments are often full of surprises, and this one was no exception. The effects of experience figured in strongly. As a consequence, we sought further explanations to pull the results together while testing our original hypotheses.

MATERIALS AND METHODS

Hereafter the large gold colored fish are referred to as G and the large normal colored fish as N. Likewise, small golds are g, and small normals are n.

Pretreatment.

The animals were kept separately according to parentage in a heated pool. All fish were immature. Those termed large ranged from 29 to 88 g in weight, while the smalls ranged from 12 to 37 g. At least two weeks prior to an experiment they were transferred to large aquaria and housed separately by color, gold or normal, as well as by size.

Water conditions: tap water, plus 2.0 g/l marine salt, constantly filtered through glass wool; temperature $25^{\circ} \pm 0.5^{\circ}$ C, pH 7.0-7.4. Photoperiod: on at 0800 and off at 2000 hr, preceded and followed by 30 min. of low illumination. Feeding: twice daily; a variety of foods.

Experimental arena (Fig. 1).

Three wading pools were used, each 182 by 122 cm, filled to a depth of 22 cm. The bottoms and sides were flexible vinyl sheeting, light green in color. Dark green squares, 10 X 10 cm, were painted on the bottoms, creating a checkerboard pattern. Two plastic-screen fences were placed in each arena forming a V; at the apex lay a feeder, and a shelter (half of a terra-cotta flower pot) occupied by the large fish. Three additional terra-cotta shelters were situated at the opposite end of the arena. This arrangement simplified scoring and accentuated the interaction between the large fish and the small as they sought food.

Food was kept before the animals at all times. Live tubificid worms were added to the feeder through a tube from above. The worms entered the feeding dish through slots and radiated out into the gravel. The worms extended one end of their body above the gravel, as is their habit, and on through the fine screen cover that permitted the passage of just one worm per opening.

To assure an even distribution of temperature, water was pumped from one end to the other on both sides of the pool. Water conditions and photoperiod were as described under Pretreatment.

Television monitoring.

A large inclined mirror was placed above each arena, reflecting a top view of the arena into a television camera. A stop-motion video tape recorder and monitor were located in an adjacent room. An electronic recycling timer provided an audible signal every 30 sec.

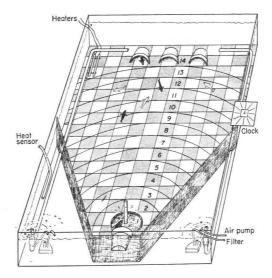


Fig. 1. The arena, showing the large fish just emerging from his shelter at the near end of the pool. He is partly in zone 1, which is co-extensive with the feeder. The pipes running the length of the pool on both sides transport water from the far to the near end by means of air lifts; the other objects in the near corners are air driven flow-through filters.

that was recorded at the time of filming. The checkerboard pattern on the bottom was useful in overcoming the background-matching response of the normal morphs. Over a monotone substrate they matched color and shade so well that they became difficult to see on the television screen. Moving over alternating dark and light surfaces, they adopted an intermediate shade that made them continuously visible.

Experiment.

The plan.

From pilot experiments, we were able to predict how the animals would respond when placed in the arena. We arranged the position of the main shelter and the feeder to manipulate the behavior of the animals. We knew the large fish would spend most of its time at the shelter with the food in Zone I, and that the smaller fish would approach the food or seek out the shelters in Zone I4.

The large fish was confronted with 6 small fish. These small fish were of about equal weight. The mean weight of the small fish was approximately half that of the large fish, or less. The 'mixed' or test group consisted of a large fish plus 3 g and 3 n (Table 1). Earlier studies led us to suspect that there would be behavioral differences when the animals were new to the situation as opposed to when the situation had become reasonably stable. Therefore, the fish were observed on Day 1 and Day 3.

We expected that a large fish might be less dominant if it were normal in color than if it were gold. So in half the trials we used G, and in half N, alternating colors randomly between trials.

With the small fish, it was possible that differences in their behavior might be due to the interactions of the 3 g and 3 n, rather than to their interaction with the large fish. We needed two control groups (Table 1). One of these consisted of 6 fish of equal size,

TABLE I
Summary of experiments

Color test	Large fish	Small fish	Trials	Day
mixed	1 Gold	3 gold + 3 normal	5	1 + 3
mixed	1 Normal	3 gold + 3 normal	5	1 + 3
pure	I Gold	6 gold	5	1 + 3
pure	1 Normal	6 gold	5	1 + 3
pure	1 Gold	6 normal	5	1 + 3
pure	1 Normal	6 normal	5	1 + 3

all n, termed a 'pure' group. The other pure group had 6 fish of equal size, but all of them g.

There were also slight differences in the lighting of the three arenas, as well as in their proximity to doors into the room. To cancel out possible differences between the three arenas, each experimental and control group was assigned to each of the arenas an equal number of times on a semi-random schedule.

Execution of the experiment.

Initially each fish was weighed and its standard length measured. The animals were assigned to three groups, each having one large fish and 6 small fish. They were placed in the arenas between 1600 and 1700 hr on Day 0. The day that followed was termed Day 1, and the third day thereafter became Day 3.

Each observation period lasted 20 min. The first was made near midday on Day 1. (Pilot studies had shown that maximum activity occurred through the morning hours and into midday, but fell off near 1600 hr.) On Day 3 the fish were again so observed.

When ready to record, the camera was positioned and switched on, and the observer departed. The fish quickly resumed normal activity, so recording commenced 15 min. after leaving the room. After the last recording, the fish were removed, weighed and measured again, and then kept apart from unused fish. Five such trials were carried out for each combination.

Criteria for measurements.

The behavior of all 7 fish was recorded. But the data are treated in four categories, to wit, G, N, g, and n.

Position.

The position of all seven fish was tallied by zone every 30 sec. If the fish was on a boundary, it was considered to be in the zone in which more than half of it lay. If it was precisely half and half, the assignment was determined by tossing a coin; in practice, this was rarely needed.

Forage.

Forage was recorded each time a fish bit at the food dish.

Attack.

An attack is an accelerated swim by one fish toward another, approaching to within one or less body lengths. It could culminate in a butt or a nip. It could repeat, *i.e.* one fish could pursue, making several separate accelerated rushes, each of which was tallied as a separate attack. Attacks were recorded with regard to who made the attack, to whom it was directed, and where it occurred.

Mouth-lock.

Two fish face one another and each bites the other on its upper or lower jaw and holds on. Sometimes this position was maintained for several minutes, but rarely so after Day o. It was recorded as but one occurrence of mouth-lock in each 30 sec. sampling interval in which it occurred, regardless of its duration. Again, both position and type of each individual was recorded.

This behavior became so infrequent that the data were combined with 'attacks' although there are good reasons to consider it separately (see Barlow & Ballin, 1976). Tailbeat and lateral display were not tallied because they were not reliably distinguishable on the television screen.

Bob-out.

The large fish swims forward one-third to one-half out of its shelter, but brakes suddenly and backs into the shelter. It was done in a continuous motion, as though the fish were on a rubber band. It was elicited by, and aimed at, an approaching small fish. Its effect generally was that the small fish moved away.

Statistical analysis.

Nonparametric techniques were used throughout (SIEGEL, 1965). As appropriate, these were the Sign Test, Mann-Whitney U Test, Wilcoxon Matched-Pairs Sign-Ranks Test, and the Friedman Two-Way Analysis of Variance. Unless otherwise specified, a 5% critical value was set for determining significance.

RESULTS

General account.

The large fish were secretive. They spent most of their time out of view in the main shelter next to the food. Occasionally, however, they ventured forth. A few individuals alternated residency between the three small shelters in Zone 14 with that in Zone 1, but these shifts were transient and did not influence the data.

The 6 small fish spaced themselves out in the large arena. Usually one or two took up residence in a shelter in Zone 14. A few could commonly be seen in the middle of the arena, while one or two would be closer to the feeder.

When approaching the feeder, signs of hesitancy, such as stopping and starting, could usually be detected in Zones 5 to 8. Nearer to the feeder, about Zone 4, an acute approach-avoid conflict became evident. The small fish would often stand still but repeatedly open and close their fins or show other incomplete starting and stopping, backing, or turning movements. Commonly, they would then either move quickly toward the feeder or swim away.

Another situation that sometimes arose was for one of the small fish to assume a subdominant status close to the feeder. In a given trial this was not always the same fish. The occurrence of subdominance was irregular and did not alter the major patterns.

As the trials progressed it became obvious that our original hypotheses

were inadequate to account for all that we were observing. Apparently one of the most important rules of the game derived from the color of the small fish in relation to that of the large one. Consequently, in examining data for difference between colors, we were guided by an additional hypothesis which stemmed from a set of opposite and same-color rules. The nature of this relationship will become clear as the analysis proceeds.

Inter-observer agreement.

It is always valuable to have an estimate of error. An imperfect but useful gauge of error can be obtained by having two observers gather data from the same behavior. Two of us tallied data for distribution, attacks and forages from the same television tape of a 20 min. observation session. The comparisons were mainly confined to the behavior of the small fish.

For the distribution, the correlation between two observers was calculated from the sums of occurrences of the 6 small fish in the 14 zones. The agreement was nearly perfect, and the correlation coefficient r = 0.988.

The attack scores for the small fish were more difficult to analyze because relatively few attacks occurred, and they were spread across 14 zones. While the correlation coefficient was not calculated, the pattern was clear. Each observer recorded nearly the same number of attacks (29 and 31), and mostly in the same zones. The few disagreements arose from difficult cases in which the attack occurred at the boundary of two zones. In the definitive analysis, zones were pooled (see further on), minimizing such boundary decisions.

Only the large fish foraged in this session. About the same number was reported (10 versus 9). And, with one exception, the scores by 30 sec. intervals were identical.

Our results were thus consistent between observers, and should be reproducible by others insofar as criteria are involved. However, the two observers probably took pains to be accurate on this trial because they knew their errors would be exposed. On the other hand, this comparison was made early in the analysis. Each observer became more proficient with time; this helped balance out the inevitably lower attentiveness during routine data gathering. We therefore conclude that observer error in this study was of the order indicated by this comparison and that this is a tolerable level.

Feeding behavior.

Large fish.

Because there was only one large fish per arena, and because the absolute frequency of feeding was low, the number of conclusions that can be drawn from these data are limited. However, a few things are clear. For one, G fed much more often than did N (U test, p = .001).

A comparison of their mean rates of feeding per hour with that of the small fish is also informative. Over all trials, the mean rate for G was 9.7/hr. This was about twice the mean rate for small fish, although the rates for some combinations of small fish almost reached that level. The rate of feeding for N was only 0.7/hr, or about 1/4 to 1/6 that of the mean for small fish.

Thus there was a pronounced difference in feeding behavior of G as compared to N. Whereas G fed at a higher rate than either N or the small fish, N fed at a much lower rate than any of the other fish.

Small fish.

Having 3 to 6 small fish of a given color per trial, there were more data to work with. It could be shown, for instance, that the small fish fed more on Day 3 than on Day 1 (Wilcoxen, p = .025). Apparently the small fish were not feeding up to their potential on Day 1, probably because some learning was involved in taking worms from the new feeder, and because aggressive relationships had not stabilized (see below).

Our initial hypothesis about the advantage of being gold led us to predict that g would be able to feed more often than n. However, over all the experiments, g and n fed at nearly the same rate.

Our original hypothesis also predicted that there would be more feeding in the presence of N than in the presence of G, but no significant differences emerged.

We turned to a comparison of feeding in the presence of large fish who were either of the other or of the same color. Thus we contrasted the feeding behavior of g when with G, and n when with N (same color) to that for feeding by g when with N, and n when with G (other). Combining the data for Days I and 3, the differences just missed significance (U test, p = .057). But since feeding was significantly higher on Day 3, and probably a better indicator of the relationships, the data for Day 3 were analyzed alone (Table 2). Here the differences were clearly significant (U test, p = .014). Thus,

TABLE 2

Feeding on Day 3 by small fish, according to their color and that of the large fish

Forages per small fish per hour Color of large fish Small fish Same Other 6g 2.3 9.1 6n 2.4 7.5 3g 7.0 3n2.0 7.0

on Day 3, small fish fed less in the presence of large fish whose color they shared. This difference may have been due to differences in the behavior of the large fish rather than of the small one.

Changes in weight.

An analysis of the initial and final weights shed little light on the problem at hand, which is to be expected in such a short period. These findings, however, are of some general interest.

The 6 small fish in each trial were selected so as to be nearly equal in weight. The range of weights in each trial was around 8-10% of the mean weight (minimum and maximum = 1.7-25.2%). After four days in the arena, the spread in weights increased 1.4 to 2.4-fold. This increase in spread to around 15-20% was noted in all trials.

A number of papers have pointed out that when one starts with a group of fish about equal in size, a spread in their weights rapidly develops. Brown (1957) reviewed the literature on this problem, called growth depensation, and suggested dominance relationships as one possible factor causing depensation. Our observations indicate that differences in aggressiveness between the individuals in competition for food led to a rapid spread in weights, as Magnuson (1962) has shown so clearly for a cyprinodontid fish.

Distribution of small fish.

We made the assumption that proximity to food could be equated to an advantage in obtaining food. We resorted to this argument because so few acts of feeding were seen.

A zone-by-zone analysis proved to be too fine since the fish often moved rapidly across three or four 10 cm zones. Therefore, we lumped the zones into three regions. Zones 1-4 were critical to fish approaching the feeder; it was called the Near Region (3,074 cm²). Zones 5-8 also lay within the V and was a marshalling area for fish approaching the feeder; we designated this the Mid Region (4,177 cm²). The remainder of the arena, Zones 9-14 seemed a neutral ground and also contained the three shelters; this we called the Far Region (8,230 cm²).

Since the position of each fish was recorded every 30 sec., we had 240 entries for the 6 small fish during each 20 min. of observation. For ease of comparison, we calculated the mean number of occurrences per 30 sec. sampling interval per fish per hour.

We also had to adjust for the areas of the three regions. Whether the fish were distributed uniformly or at random the chance of a given fish being in a particular region was directly proportional to its area. Therefore, frequency of occurrence was further divided by the area of the region and scaled to yield mean occurrence per square meter.

Then we made predictions at two levels. The first of these, the specific, related to the color of the fish. And this consisted of two hypotheses: The

first hypothesis followed from the original work and declared that the advantage should accrue to gold, whether G or g. This meant that in comparing the effects of G and N, the small fish should be further from the feeder when with G than with N (Fig. 2). On Day I there were no significant differences in this respect. Likewise, on Day 3 we were again able to reject the hypothesis that the fish would approach more closely to N than to G.

Then we tested the hypothesis that the small fish would come closer to the feeder when the large fish was of the opposite color rather than the same. Our analysis of the feeding data, especially for Day 3, led us to expect that the fish would approach the fish of the opposite color more often than the same, and particularly on Day 3. The hypothesis might hold but only on Day 1 (p = .057).

Additional analyses were performed to see if there were differences between the three regions by color of fish. In no case were any of these differences significant. Even though we had abundant data, and trends seemed obvious, we encountered considerable variation; this made it difficult to achieve statistical significance.

As a consequence, we analyzed the data at a different level. We combined

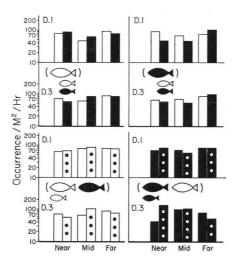


Fig. 2. The vertical bars portray the frequency of occurrence of small fish, per m² per hr., in the three regions, Near, Mid, and Far, of the arena. In the upper two rows are data from experiments employing mixed color groups, coded black for n and white for g; to the left the large fish was G, to the right, N; D.1 indicates Day I, and D.3, Day 3. The bottom two rows depict the distribution of small fish in the pure-color control groups. To the left, the occurrence of g in the presence of G (coded white) is compared by region with that in the presence of N (black discs on white). On the right the distribution of n with N (black) is juxtaposed to that of n with G (white discs on black).

the data for Days I and 3 and pooled the scores for the fishes irrespective of color, looking for overall differences between the Near, Mid and Far Regions. The mean occurrence of all small fish in the three regions, adjusted for differences in area, was 71.1 for Near, 71.8 for Mid, and 82.9 for Far (Friedman nonparametric analysis of variance, .05>p>.02).

We were frankly surprised at this. On the one hand, the few differences we found with regard to color just border on being significant. On the other, the analysis of distribution based on pooled groups, that is without regard to color, suggests that the fish were uniformly distributed through the arena. The fish were slightly more abundant in the Far Region, which we had anticipated because of the shelters there. However, we thought the fish would show pronounced differences between the Mid and Near Regions, either being particularly abundant close to the feeder, or scarce there because of the defending large fish.

The conclusion from this analysis is that, on average, the fish occurred about as often per unit area in the Near Region as in the Mid one. If we are to detect any potential differences in access to the feeder, we have to turn to the analysis of aggressive interactions.

Aggressive behavior.

Large fish.

The large fish seldom attacked, providing few data to analyze. Nonetheless, G attacked more than did N (Wilcoxon, .01>p>.005). There were no significant differences in their aggressive behavior with regard to the color of the small fish.

Small fish.

There were pronounced differences in the attack behavior of the small fish, depending on the conditions (Fig. 3 and 4). Many questions could be asked because of the complex interactions. There were six different conditions for determining who attacks whom (2 colors), where (3 regions). In each case there are different data according to the type of large fish (2 colors) and whether on Day 1 or Day 3.

Calculations.

The attack data were processed to make them more readily comparable. We adjusted the data to the mean number of attacks per fish per square meter per hour. We further adjusted the scores for the number of other fish in the enclosure available to attack. Take, for example, the mean attacks by g in the interaction of 3 g plus 3 n. Each g had 3 n to attack, but only 2 g

because it cannot attack itself. Therefore, the mean rate per fish was calculated (on a single trial basis) by dividing by 2 the number of attacks by g on g, but by 3 for the number of attacks by g on n. The same procedure was carried out for n. For the pure color groups, consisting of 6 fish, the scores were divided by 5, the number of fish each could attack.

In presenting the results of the statistical analysis, we will proceed from the more general to the more specific questions.

Day 1 vs 3.

The total number of attacks was about the same on Day 1 and Day 3.

Regions.

The first analysis asked whether there was a general trend for the occurrence of attacks across the three regions, irrespective of the color of the small fish and the large fish. We pooled the data for all the small fish and calculated grand means for the Near, Mid, and Far Regions, which were respectively 9.06, 19.4, and 14.7/m²/hr (Friedman, p≪.001). The attacks therefore were distributed across the Near, Mid, and Far Regions in a ratio of about 1:2:1.5. This was in contrast to the nearly uniform presence of the small fish in those regions.

We then asked the first questions about the effect of color, and here initially with regard to the color of the large fish. We predicted there would be fewer attacks among the small fish, in total, when the large fish was G than when the large fish was N; however, there was no significant difference. We asked, further, whether sharing the color of the large fish or not had an effect on the total aggressive behavior shown; it did not. Thus there were no significant differences in aggressiveness, all groups and regions taken together, in relation to the color of the large fish.

We posed another question about the effect of the color of the large fish. Did the small fish attack other small fish *less* if those small fish were the same color as the large fish? That answer is yes (Wilcoxon, p = .003). Evidently the small fish learned to suppress their own attacking, however produced, in response to the color of the large fish; they generalized this response to the small fish they met.

But the distribution of attacks across the three regions also suggested that g were attacked less than were n by other small fish, irrespective of the color of the large fish. This seemed particularly true for the mixed groups (Fig. 3). Therefore was asked, were g attacked less than n in mixed groups? Again the answer was yes (Wilcoxon .05>p>.025).

The forgoing analysis was done without regard to the color of the fish

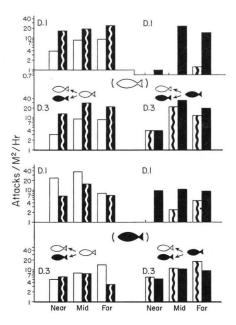


Fig. 3. The vertical bars reveal the frequency of attacks, per m² per hr., by region in the mixed color groups of small fish. The upper two rows are for Days 1 and 3 with G, the lower two with N. The left half of the figure shows the attacks by g on g (coded white) and on n (white on black). The right half shows the attacks by n on g (black on white) and on n (black).

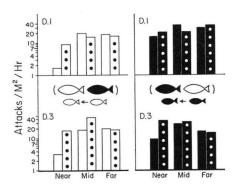


Fig. 4. The vertical bars indicate the attacks by small fish per m² per hr. and by region in the pure-color control groups. In the left half of the figure, attacks by g on g in the presence of G (coded white) are juxtaposed to those that occurred when with N (black discs on white). The right half shows the attacks by n on n when with N (black) as contrasted to when with G (white discs on black). The upper row is for Day 1, the lower of Day 3.

doing the attacking, but merely with respect to the color being attacked, regardless of the particular experiment. Now we turn to the analysis of differences across the three major regions, but within each of the test groups.

For each of the mixed color groups, on Day 1 and Day 3, we asked who attacked whom more over the three regions (Fig. 3, Table 3)? Of the eight comparisons (2 small fish colors \times 2 large fish colors \times 2 days), five were significant. In all five cases g was attacked less than n. But four of these five significant values occurred when the large fish was G. Thus (1) sharing

TABLE 3
Small p values for differences in attacks on g and n across three regions

Large	Day	g attacks		n attacks		
		g > n	n > g	g > n	n > g	
G	I		< .005		< .005	
G	3		< .005		< .005	
N	I	(n	.s.)		.005	
N	3	(n	.s.)	(n	.s.)	

the color of the large fish, and (2) the small fish being gold, appeared to summate, increasing the magnitude of the differences. On the other hand, when the large fish was N the effect of sharing the color of the large fish was cancelled by the gold color of the small fish. But the effect of g can be pronounced at first: n attacked n more than g on Day 1, even in the presence of N. By Day 3, however, they 'corrected' their responses and attacked g and n about equally.

A similar analysis of attacks across the three regions was carried out for the pure color groups (Fig. 4). Since there was only one color of small fish, we could only ask about the effect of the color of the large fish. We predicted that when 6 g were with G, attacking would be less than when with N. However, there were no significant differences when the comparison was across all three regions.

We asked the same question about the behavior of n, now anticipating that there would be less aggressive behavior when they shared the color of the large fish. Again, there were no significant differences.

Having examined the differences across all three regions, we turned to an analysis of the differences within regions (Fig. 3 and 4). Because the feeder was in the Near Region, we expected differences to emerge there. For statistical sensitivity, we now took advantage of the data that had been gathered at 30 sec. intervals. Within each interval, we compared the attacks on g and n, by g and also by n, treating each of the regions separately. For

the pure-color groups, we matched data contrasting attacks in the presence of G or N. These values were small, commonly ranging from about 0 to 5 attacks per interval. Therefore we employed the Sign Test, which tests how often one value is greater than the other (the difficulty here is that there was no way to assure independence from one interval to the next).

Within the mixed color groups, significant values exist in 50% of the comparisons (Table 4). In the pure-color groups, significant values likewise occurred in almost 50% (5 of 12) of the cases (Table 5).

TABLE 4

Small p values for differences in attacks on g and n within the three regions,
for mixed color groups (Figure 3)

			Attacked					
Large At	Attacker	r Day	Near		Mid		Far	
			g > n	n > g	g > n	n > g	g > n	n > g
G G	3g 3g	1 3		.010 ** .006 **		.007 ** .002 **		<.003 ** .002 **
G G	3n 3n	1 3	_	_		<.001 ** .203		<.002 ** .020 *
N N	3g 3g	3	<.002 **	.090 +	.132	.212	_	.003 **
N N	3n 3n	3	-	.002 **	_	.059 + —		.092 + .132
+ p <	.10							

⁺ p < .10

TABLE 5

Small p values for differences in attacks in the presence of G versus N, within the three regions, for pure-color groups (Figure 4)

Attacker	Day	Near		Mid		Far	
		G	N	G	N	G	N
6g	I		.002 **	.168			-
6g 6g	3	<	<.005 **		<.005 **		-
6n	I	.162			+ 001.	.019 *	
6n	3	<.005 **		+ 001.		_	_

⁺ P < .10

^{*} p < .05

^{**} p < .01

^{*} P < .05

^{**} P < .01

Again we detect the interaction of the small fish being gold and of sharing the color of the large fish. In mixed color groups, g were attacked less than n in 11 of 12 cases in which significant p values were found. But 9 of these 11 values occurred when the large fish was G. When the large fish was N, the advantage of sharing its color was neutralised by the small fish being gold. Consequently only one third as many comparisons were significant in the mixed groups when the large fish was N.

Within the pure-color groups we could, of course, compare only whether aggressiveness increased or decreased in relation to the color of the large fish. Here sharing the color of the large fish appears to have inhibited attack in many instances. There were 5 cases of significant differences, and in all of these there were fewer attacks in the presence of a large fish of the same color (Table 5). Furthermore, 3 of those 5 differences were in the Near Region.

In summary, attack was less likely when the small fish encountered was (1) gold in color, and (2) the same color as the large fish. Furthermore, there were differences between the regions. Attacks were fewest in the Near Region, which contained the feeder and the large fish. Fear of the large fish, not the presence of the feeder and its food, most likely accounts for the reduction in attacking. This interpretation is consistent with Heiligenberg's (1965) finding, using another species of cichlid fish, that frightening stimuli suppress attack.

Chance of attack.

It was possible that the forgoing analysis had led to false conclusions because attack rates were compared without regard to the availability of small fish to attack. Therefore, we calculated the chance of attack per 100 opportunities. For each trial we divided the number of attacks on each color category of small fish by the occurrence of fish of that color in that region, then multiplied the quotient by 100 (Fig. 5). The distribution of the fish was recorded at 30 sec. intervals; one consequence was the occasional pairing of some attacks when zero occurrence of fish at the moment they were mapped. Therefore, only the more general questions were tested statistically, using the means of the data.

As already reported, the combined mean occurrence, over all experiments and days, showed little difference between regions. If this were universally true, the patterns of attack would be little changed by dividing them by the number of occurrences. But the distributions in the different recordings often differed from the overall means. It seemed reasonable to enquire, then,

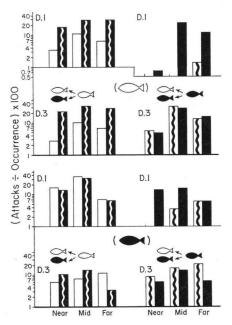


Fig. 5. The vertical bars convey the attacks by small fish by region, per m² per hr., but now adjusted to mean rate per individual per opportunity to attack. Attacks by g on g (coded white) and on n (white on black) are carried on the left half of the figure. To the right are the attacks by n on g (black on white) and on n (black). The upper half is for attacks in the presence of G, and the lower half for when in the presence of N. D.1 and D.3 indicate Days 1 and 3 respectively.

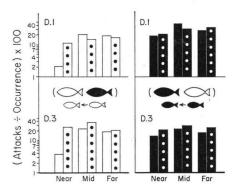


Fig. 6. The vertical bars represent the attacks per m² per hr., by small fish in the purecolor control groups. Attacks here have been adjusted to mean rate per individual per opportunity to attack. Attacks by g on g in the presence of G (coded white) are paired by region with those in the presence of N (black discs on white) on the left half of the figure. On the right are attacks by n on n when with N (black) as compared to when with G (white discs on black). D.1 and D.3 identify Days 1 and 3, respectively.

whether the chance of attack was in some way related to the distribution of the fish

The first question, nonetheless, was the general one which asked simply whether the chance of attack in the three regions differed when all groups were combined over all days. The mean chance of attack per 100 opportunities in the Near, Mid, and Far Regions were 10.5, 22.4, and 15.0/m²/hr., or a ratio of approximately 1:2:1.5 (p \ll .001). Thus the pattern of mean chance of attack across the three regions was essentially the same as that for attacks, a reassuring finding.

The decrease in chance of attack in the Near Region probably stemmed from inhibition of attacking brought about by fear of the large fish. If so, there should have been in the Near Region a greater suppression of attack on the small fish that shared the color of the large. This was clearly the case in the groups of pure-color (4 of 4, Fig. 6), and it was generally true of the mixed color groups, although there were exceptions (Fig. 5).

The decrease in chance of attack in the Far Region was probably due to the presence of shelters. These allowed the small fish to get out of view and thereby avoid aggressive interaction. In a sense, the opaque walls of the shelters added space to the Far Region.

The difference in patterns that resulted from correcting number of attacks for the distribution of the fish were small (compare Fig. 3 to Fig. 5, and Fig. 4 to 6). One important change, however, was that seen for the group of 3 g and 3 n with N on Day 1: The g attacked other g more than n (Fig. 3), although the difference was not significant. But with attacks adjusted for the occurrence of fish, the chances of g attacking another g or an n were unambiguously equal (Fig. 5).

Changes in attacking through time.

The small fish modified their attack behavior during the course of the experiment. This was clearest for n in mixed color groups. They demonstrated a marked suppression of attack on g on Day 1, the more so when the large fish was G rather than N. Later, on Day 3, there was little difference, n attacking g and other n about equally. In contrast, g showed almost no change through time. Judging from Fig. 3 and 5, however, they became more discriminating by Day 3, directing a slightly larger proportion of their attacks to n than to g.

DISCUSSION

It was not necessary to analyze the data to conclude that the large fish exerted almost absolute control over the feeder. While the small fish were able to approach and snatch food, their wariness indicated fear of the large

fish in its lair behind the feeder. The large fish seldom needed to actually attack to maintain its dominance. By Day I a relatively stable situation had developed. The large fish could even swim to the opposite end of the arena without relinquishing control over the feeder; the small fish showed the same hesitancy approaching the feeder when the large fish was away. Within 24 hr., then, the small fish associated the region of the feeder with possible attack by the large fish.

We have made a model (Fig. 7), for the likelihood of attack by a small fish, to structure the discussion. It depicts the decision making processes of a small fish meeting another of the same size. The fish assesses the other by

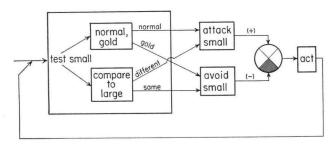


Fig. 7. A flow diagram portraying the decision making process in one small Midas cichlid when it meets another. See text for explanation.

color, determining whether it is gold or normal, and whether it is of the same or different color as the dominant fish.

We assume that factors increasing the chance of attack simultaneously decrease the likelihood of avoiding, and vice versa. This assumption is based on Heiligenberg's (1965) analysis of the interaction of attack and fright behavior in another cichlid fish. In the model, incremental factors for attack are the normal color and a color differing from that of the large fish. Decremental factors are gold and sharing the color of the large fish. These factors summate in an integrator, and the fish acts. If these were the only factors, the results would be highly predictable because there are only three possible states, summing across the outputs: +2, o, and -2.

Obviously other factors enter in, some of which seem almost stochastic, to produce a continuous gradation of responses. For one, it is almost a biological given that there are differences between individuals. For another, individuals vary through time; the threshold of attack fluctuates in no clear relation to external events (Heiligenberg, 1963, 1965). Such differences should average out with repeated tests. They contribute to the variability and gradation in responsiveness, but they should not result in differences between groups.

A number of deterministic parameters have not been incorporated into the model. One is proximity to the large fish. This would input on a sliding scale, and in two ways. First, coming closer to the large fish decreases the probability that a small fish will attack at all (Fig. 3, 4, 5, and 6). Second, this suppression of attacking is more pronounced if the small fish that is met shares the color of the large fish, as indicated in the model. The mechanism is thought by us to be the same, fear (see Heiligenberg, 1965) of the large fish. This subsystem could easily be incorporated into the model, as could one that deals with the relative size of the other fish.

A potentially more significant parameter is the role of experience. It is not easily incorporated because its contribution is so dynamic and because it enters the model at so many places. It is implicit, for example, in the test compartment 'compare to large' in which the decision is based on having learned the color of the large fish. The response to the color of the large fish, however, is not a simple matter. This can be seen by comparing the attack behavior of the small fish in mixed groups on Days 1 and 3. On Day 1 the effect of sharing the color of the large fish was clear, even though there was also an interaction with gold color and proximity to the large fish. But by Day 3 the effect of color-sharing among n had diminished to the point that there was almost no difference between the g and n. Apparently the small fish learned first the color associated with dominance, which they generalized to the small fish. But learning continued, and by Day 3 the small fish, especially n, had become more sophisticated, distinguishing better between small and large fish of the same color. Thus the plus and minus outputs from 'compare to large' are subject to continuous modification depending on recent experience.

Experience bears on the model in other ways that are certain to prove important. These can be classified into three types: parentage, siblings, and pretreatment. An understanding of these factors might account for some of the differences in aggressive behavior of g and n. One of the more general of these differences was that g observed the 'rules' better than n. Perhaps early experience was instrumental here.

The parents of most of the g had both been gold, while those of most n were both normal. Some groups of g and of n, however, were bred from $G \times N$ crosses. The design of this experiment, unfortunately, does not permit sorting out the effects of parentage. We suspect that the color of the father may have had a quantitatively different effect from that of the mother: Fry feed from mucus on the parents' body, and they prefer the male to the female (NOAKES & BARLOW, 1973).

Experience with siblings may be more important than that with parents.

All fry, irrespective of the color of the parents, are first normal in color (Barlow, 1975). Those whose parents were both normal remain normal throughout their lives. Thus the first encounter of most n with g took place in the experimental arena.

At an age of three to twelve months the first few offspring of a $G \times G$ cross metamorphose to gold. The timing of this metamorphosis varies greatly between pairs and among siblings, ranging from about three months to three years or more. Over time there is a continuous increase in the proportion of gold fish in a given group of siblings. As a consequence of this rate of change, g experienced n throughout their lives, and they were accustomed to them before meeting in the experimental arena. Since g grew faster than n in the holding tanks, they tended to become the largest, dominant fish. Therefore fish in mixed color groups probably had a more deeply engrained 'respect' for gold color.

The pretreament consisted of holding the animals in pure-color groups. That would have had little effect on $\hat{\mathbf{n}}$ but could have moderated the previous learning in g, perhaps reducing the differences between them.

Many other aspects of the experiences of these fish doubtless modified their behavior. But those experiences must have been comparable for the various groups and are thus not of central importance here.

Previous work, for example on growth differences (Barlow, 1973), dominance hierarchies (Barlow & Ballin, 1976), levels of aggression (Barlow & Wallach, 1976), and studies in progress, indicate that in spite of the adjustment n made in time in the experiment just reported, the advantage of being gold is persistent and is not due exclusively to some novelty effect. Note particularly that g also adjusted its behavior through time in the presence of N, coming to attack n more than g (Fig. 3 and 5).

This general finding, nonetheless, raises an intriguing point about the adaptive significance of the gold morphs. It suggests that at least part of the effectiveness of gold derives from novelty. If so, then the gold morphs could lose some of their advantage in social interactions if they became common. At some point, the summating disadvantages of being gold might start outweighing the advantages. For example, as they became more common gold morphs might find it increasingly difficult to dominate normal ones and to avoid predation.

Also relevant to the field situation is whether having food continuously available at one spot with a large fish lurking there was a fair test. In nature Midas cichlids were seen to dig for and to expose food; smaller fish approached and attempted to feed but were driven away (Barlow, 1975). While there is a resemblance to the situation and to the behavior as seen under

natural conditions, a better test might have been to have the food patchily or sporadically, rather than continuously, available. But the previous technique, of feeding the fish twice daily only as much as they could eat immediately, is surely unnatural.

There is the problem of efficiency as well. Among the small fish, it might not be profitable for one to keep the others continuously away from the food. Once it has eaten, it might be better off moving away. This would be particularly true if the other fish became increasingly aggressive with hunger and willing to fight, not just display. Little more can be said, however, without knowledge of the metabolic costs of maintaining a position close to the feeder by means of aggressive behavior.

Perhaps in our experiment g or n were capable of dominating at the feeder but did so only when hungry. That is, the effect of gold, or of color-sharing with the large fish, may have fluctuated with hunger. Our suspicion is that the effect of gold would have prevailed over the effect of sharing the color of the large fish if the small fish had been consistently hungrier, forcing more feeding and fighting. It is known that hunger stimulates fish to fight over food (Magnuson, 1962, and references therein). Also, under these circumstances, the large fish would probably have become more interactive. We are now testing this proposition (Barlow & McKaye, in prep.). Food is witheld from mixed color groups for 24 hr. The interactions are then observed following the return of the feeder. When the effect of hunger is better understood it should be possible to incorporate that information into the model.

SUMMARY

The Midas cichlid (Cichlasoma citrincllum) is an abundant fish in the lakes of Nicaragua. Many populations are polychromatic, about 7 to 10% of the adults being variously white, yellow, orange, or red, and without the species-typical markings. These are termed 'golds' because the most frequent color is yellow-orange. The common cryptically colored morphs are called 'normals'.

In the experiment, 6 equal sized small fish had to approach a feeder guarded by a Midas cichlid twice their mean weight. In the experimental groups, 3 of the small Midas cichlids were gold and 3 were normal (mixed color groups). The control groups were of two types, one with all 6 small fish gold, the other with all 6 normal (pure-color groups). In half of all trials, the large fish was gold, and in the other half normal in color. Data were gathered on Days 1 and 3.

- 1) Differences in the behavior of large fish toward the small ones were not statistically significant. However, the large gold attacked the small fish more often than did the large normal, although the rate of attacking was remarkably low. The large gold fish also fed on average much more often (9.7/hr.) than did the large normal (0.7/hr.), whose mean rate was about half that for all small fish.
- 2) There was little difference in rate of feeding among the small fish. However, on Day 3, only, the small fish fed significantly less in the presence of a large fish whose color they shared.
- 3) The spread in weights within each group of small fish increased 1.4 to 2.4-fold during the four days of the experiment (growth depensation).

- 4) The distribution of the fish within the arena was recorded at 30-sec. intervals, and analyzed with regard to Near (to the feeder), Mid, and Far Regions, adjusting the data to fish per m² per hr. There were no significant differences in distribution in relation to fish coloration. The small fish occurred at about the same rate in the Near and Mid Regions, but more frequently in the Far. The shelters in the Far Region had an effect equivalent to adding more space.
- 5) Across all experiments and groups of small fish, the rate of attacking was, in the Near, Mid, and Far Regions, respectively, 9.1, 19.4, and 14.7 per m² per hr. When these data were modified to take into consideration the fish available for attack in the same region, the scores became 10.5, 22.4, and 15.0 per m² per hr., respectively. Small fish, therefore, were about half as likely to attack in the Near Region, with the feeder and the large fish, as in the Mid Region.
- 6) The small fish attacked significantly less those small fish that shared the color of the large fish.
 - 7) Small golds, in mixed color groups, were attacked less than were small normals.
- 8) Attacks by golds on normals were compared to those on golds by region and by day. Likewise, the attacks by normals on golds were compared to their attacks on fellow normals. In total, there were 24 such pairs of comparisons for the mixed color groups. Of these, 50% were significantly different. In 11 of these 12 cases, golds were attacked less than were normals. And 9 of these 11 cases had the large fish gold. Thus sharing the color of the large fish conferred some immunity from attack. When both the small and large fish were gold the effects summated in the favor of small golds to produce significant differences. Conversely, when the large fish was normal the effects of gold coloration and that of not sharing the color of the large fish cancelled one another.
- 9) All the small golds had had prior experience with normal colored siblings, but most of the small normals had never been with golds before. The attack suppressing effect of gold color on normals was pronounced on Day 1 but weak on Day 3. This suggests that the effect of gold coloration is enhanced by infrequent exposure. If so, golds should experience a lessened advantage in aggressive interactions in direct proportion to their abundance in a population.
- 10) We hypothesize that gold coloration decreases the readiness to attack in the perceiver by stimulating incompatible fear responses.

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ZUSAMMENFASSUNG

Der Midas-Buntbarsch (*Cichlasoma citrinellum*) ist einer der zahlreichsten Buntbarsche in den Seen Nicaraguas. Viele Bevölkerungen sind polychromatisch. 7 bis 10% der Art können entweder weiss, gelb, rot oder orangefarben sein, ohne die arttypischen Muster aufzuweisen. Wir nennen sie "golden", weil die häufigste Farbe gelb-orangefarben ist. Die üblichen grauschwarz arttypisch gemusterten Fische nennen wir "normal".

In den Versuchen mussten 6 kleine Fische derselben Grösse sich einem Futterbehälter nähern, welcher von einem Artgenossen bewacht wurde, der doppelt soviel wog als der mittlere kleine Fisch. Die Versuchsgruppen setzen sich aus 3 kleinen "goldenen" und 3 "normalen" Fischen zusammen, (gemischte Farbgruppen). Die Kontollgruppen enthielten entweder nur goldene oder nur normale Fische (reine Farbgruppen). In 50% der Versuche war der grosse Fisch goldgefärbt und in der anderen Hälfte normal. Daten wurden am ersten und dritten Tage gesammelt.

- 1. Die Unterschiede im Verhalten des grossen Fisches gegenüber den kleinen Artgenossen waren statistisch nicht gesichert. Der grosse goldene Fisch griff im Vergleich mit dem normalgefärbten Fisch die kleinen Fische öfter an, obgleich die Angriffsrate auffallend niedrig war. Der grosse goldene Fisch frass auch viel öfter (9.7/Stunde) als der normale Fisch (0.7/Stunde), dessen durchschnittliche Rate wiederum ungefähr halb so gross war als für alle kleinen Fische.
- 2. Der Unterschied in der Fressrate der kleinen Fische war klein. Nur am dritten Tage, in der Gegenwart eines grossen Fisches der dieselbe Farbe besass als die kleinen Fische, frassen letztere bedeutend weniger.
- 3. Die Gewichtsspanne innerhalb jeder Sechsergruppe vergrösserte sich 1.4 bis 2.4-fältig während des viertägigen Versuches.
- 4. Die Verbreitung der Fische innerhalb der Arena wurde in 30-Sekundenintervallen protokolliert, und in Beziehung zu Nah-, (am Futterbehälter), Mittel- und Ferngebiet analysiert. Die Daten wurden auf Fische pro m² pro Stunde umgerechnet. Keine bedeutenden Unterschiede in der Verbreitung bezüglich der Farbe der Fische wurden gefunden. Die Fische kamen vor in gleicher Anzahl in dem Nah- und Mittelgebiet, aber in grösserer Anzahl in dem Ferngebiet. Die Unterschlupfstellen des Ferngebietes wirkten raumerweiternd.
- 5. In allen Versuchen und Gruppen kleiner Fische war die Angriffsrate in dem Nah-, Mittel- und Ferngebiet bzw. 9.1, 19.4 und 14.7 pro m² pro Stunde. Wenn man in diese Daten die Zahl der Fische einbezieht, die im selben Gebiete angegriffen werden konnten, so ändern sich die Ergebnisse zu 10.5, 22.4 und 15.0 pro m² pro Stunde, d.h. die kleinen Fische würden halbsowenig in dem Nahgebiet, wo sich der Futterbehälter und der grosse Fisch befand, angriffsbereit sein als in dem Mittelgebiet.
- 6. Die kleinen Fische griffen die anderen kleinen Fische, welche dieselbe Färbung hatten als der grosse Artgenosse, bedeutend weniger an.
- 7. In gemischten Farbgruppen wurden kleine goldene Varianten weniger angegriffen als normale Artgenossen.
- 8. Die Angriffe kleiner goldener Fische auf kleine normale und andere goldene Artgenossen wurden miteinander verglichen, und zwar in bezug auf Gebiet und Tag. Die Angriffe der normalen Fische auf goldene und andere normale Artgenossen wurden gleichfalls verglichen. Im ganzen haben wir 24 solcher Vergleichspaare für die gemischten