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Dummy-Elicited Aggressive Behavior in the Polychromatic Midas Cichlid

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RESUME

Comportement agressif de *Cichlasoma citrinellum* face à un leurre.

Les réponses agressives de 12 individus du Cichlidé Midas, *Cichlasoma citrinellum*, espèce polymorphe, envers cinq leurres simulant un congénère, de taille différente et de coloris neutre (livrée tachetée) ont été examinées. Les leurres ont été présentés quotidiennement pendant six jours durant une minute et selon un schéma équilibré. La couleur (dorée ou normale) et le sexe des sujets variaient indépendamment. Les attaques se sont trouvées être en corrélation positive avec les menaces si bien que les unes et les autres ont été cumulées pour donner une mesure globale de l'agressivité. Les attaques menées par les sujets à l'encontre des poissons-cibles (jeunes individus conspécifiques aveuglés) cinq minutes avant et après la présentation d'un leurre ont été analysées pour déterminer l'apparition d'effets résiduels dus à l'exhibition des leurres.

Le sexe du sujet n'a eu aucun effet significatif. Que le sujet soit doré ou normal n'a eu également aucun effet. Aucune différence n'est apparue dans les attaques envers les poissons cibles aveuglés, qu'ils soient dorés ou normaux. L'agressivité provoquée directement à l'encontre du leurre a augmenté de la même façon, mais a diminué en face du plus grand des leurres. La méthode directe s'est avérée supérieure à l'indirecte, basée sur les effets résiduels : les données étaient moins variables et plus cohérentes pour mettre en lumière la tendance fondamentale ; celle-ci a été vérifiée par l'analyse indépendante du comportement des individus les plus agressifs. Il est apparu que les deux plus petits leurres ont entraîné la chute du niveau d'agressivité résiduelle au-dessous du seuil de base. Un modèle de cette dépression est présenté et comparé avec les données extraites alors.

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SUMMARY

Aggressive responses of 12 individuals of the polychromatic Midas cichlid *Cichlasoma citrinellum* were tested with five different sizes of neutrally colored (spot pattern) life-like dummies. The dummies were presented daily over six days, for one minute apiece, in a balanced design. Color (gold or normal morph) and sex of the subjects were varied independently. The attacks and threats at the dummies were positively correlated in their occurrence so they were combined to yield an aggregate measure of aggression. Attacks on blinded juveniles, five minutes before and five minutes after viewing a dummy, were analyzed to test for the occurrence of residual effects of exposure to the dummies.

Sex of subject had no significant effect. Whether the subject was a gold or normal morph was also without effect. There was no difference in attacks on blinded gold and normal juveniles. Residual aggression increased linearly with size of dummy. Aggression that was evoked directly also increased with size but decreased at the largest dummy. The direct method proved superior to the residual one : the data were less variable and more consistent in revealing a pattern ; and the same pattern was verified using only the most aggressive subjects. The two smallest dummies appeared to cause residual aggression to fall below the baseline level ; a model for this depression is presented and compared with the data that were then extracted.

INTRODUCTION

Earlier experiments, done mostly with juveniles, indicated that gold colored morphs of the Midas cichlid *(Cichlasoma citrinellum)* dominate and grow faster than normal ones when the two morphs compete for food (Barlow, 1973 ; Barlow and Ballin, 1976 ; Barlow *et al.*, 1975 ; Barlow and McKaye, 1982). When adults of the same sex and size are matched in combat, golds usually defeat normals (Barlow, 1983 b). Golds and normals seem to be about equally aggressive, at least as juveniles (Barlow and Wallach, 1976), however, suggesting that golds enjoy their advantage over normals because the gold coloration inhibits aggression, rather than because melanin deficiency and aggressiveness are somehow genetically coupled. Because the areas of gold coloration on the normals are appropriately situated to enhance threat displays, Barlow (1976, 1983 a) suggested that an all-gold morph acts as a supernormal releaser of fearful behavior (e.g. hesitation, avoidance, immobility). Fear responses are known to diminish aggressiveness in a cichlid fish (Heiligenberg, 1965) and could provide the basis for the gold advantage in aggressive encounters.

To test the inhibition hypothesis directly, however, requires that one be able to separate the effect of coloration as such from any dispositional effects that might be coupled with it, either genetically or as a consequence of repeated experience. Since this was clearly impossible in experiments involving staged encounters between live fish, we decided to employ dummies as stimuli to elicit aggression. For this first stage in the resarch, we used only gray (normal) dummies, and varied systematically the color and sex of the adult subject fish; this was done to determine whether the morphs are, in fact, equally aggressive and whether there are reliable sex differences in aggressiveness. To establish optimal size of dummy for future experiments, we examined the effect of a range of dummy sizes that bracketed the size of the subject.

Investigators have traditionally recorded aggressive behavior directed to the dummy itself. However, Heiligenberg (1965) and Leong (1969) employed as their measure the induced change in the level of aggression toward juvenile conspecifics. By comparing attacks before and after presenting the dummy they were able to compensate for fluctuations in the subject's readiness to attack. To compare the utility of the two approaches, we recorded the subject's behavior toward the dummy, as well as that toward conspecific juveniles before, during, and after presenting the dummy.

An advantage of using the Heiligenberg and Leong design was that it allowed us to test, additionally, whether the level of aggression exhibited toward the juvenile fish was influenced by their color. If gold does inhibit attack in the perceiver, the color of the small fish ought to make a difference. Barlow and McKaye (1982) reported that a large fish attacked small gold individuals more, not less, than it did small individuals of the normal morph; but they were not able to distinguish between the effects of coloration *per se* and the effects of correlated differences in frequency of feeding or aggressive interactions among the small fish. The juveniles in the present experiment, called target fish, were blinded, ruling out differences in their aggressive and feeding behavior. Any difference in attacks directed to gold or normal target fish by the subject would necessarily be due to coloration.

There is no generally accepted method of testing with dummies, and the effects or differences in position, movement, and resemblance to live fish appear to vary considerably across species. In addition, because dummies are generally less effective than live opponents in eliciting aggression, their use requires complex controls and a balanced statistical design to maintain satisfactory and unbiased levels of responding. A substantial component of this report therefore, is concerned with the development of a suitable methodology for the maintenance of reactivity in the subject, presentation of maximally effective dummy stimuli, and quantification of aggressive responses.

MATERIALS AND METHODS

SUBJECTS

The Midas cichlid displays a stable polychromatism in several Nicaraguan lakes (Barlow, 1976). The cryptic morph, which we call "normal", is primarily gray with black bars or spots; in nature, they display varying amounts of yellow or orange coloration on the throat and in the eyes. Normals have functional melanophores and can quickly change their markings. About 8 % of the individuals of this species are amelanic and cannot change colors. Most of these morphs are some shade of yellow or orange; we call them "golds". White morphs also occur in nature and in captive-reared populations, but they are infrequent.

All of the fish employed in this study were raised in the laboratory, as first- or second-generation descendants of fish caught in Lake Masaya, Nicaragua. When the young fish reached or exceeded about 75 mm SL they were transferred to a heated outdoor pool where they completed their maturation among large groups of conspecifics of both morphs. The experimental subjects were six adult males and six females, half of them gold and half normal in color, ranging from 220 to 250 g and 170 to 190 mm SL.

Pre-treatment

It is difficult to maintain a high level of aggressive responding in isolated cichlid fish. When they are kept alone they become progressively less reactive and less mobile until finally they simply retreat into a corner (see Fernö, 1978; Heiligenberg, 1965; Reyer, 1975). We evolved a procedure of pre-treatment and handling that alleviated the problem. At least three to four weeks before the experiment, the subjects were brought into the laboratory from the holding pool and assigned to compartments in large tanks with adult fish of the same size and sex, one of each color on each side, separated by screening. Each week the fish were netted and moved to a new compartment. That accustomed them to handling. It also continually exposed them to novel rivals, which maintained reactivity.

Maintenance conditions

Throughout the course of the experimental observations, the subject and target fish were confined in a large aquarium (90 × 60 × 46 cm deep). The front, left, and right walls of the tank were clear glass; the long rear wall was opaque. A hide was provided against the lower center of the rear wall. Fine gravel and sand covered the bottom.

The fish were fed twice daily, at 0 900 and 1 600 hr, mostly on commercially available "dry" food supplemented by our own "fish fudge" (Barlow and Capetto, 1974) and live adult brine shrimp, *Artemia salina.* Light (0 730 to 1 930 hr) was provided by a 30-watt warm-white fluorescent tube suspended just over the water surface. The water in the aquarium (carbonate hardness ca. 16 gm/1; pH 7.0-7.8) was slowly and continuously replaced with pre-heated tapwater (30 % turnover/day) and was kept at 28 degrees ± 1 degree C.

Apparatus

Dummies

Preserved fish were cast in plaster of Paris, from which detailed latex models were made. The dummies were painted the gray color with median-spot pattern that characterizes normal colored, nonterritorial fish (Barlow, 1976) and were provided with realistic glass taxidermy eyes. We employed five sizes of dummies that embraced the size of the subject. The standard lengths of the dummies were 120, 140, 160, 180 and 200 mm (respectively 70, 80, 90, 100 and 110 % of the length of the median subject). All the subjects were within 10 mm of the 180 mm (100 %) dummy, and most were much closer in length.

The literature provides few usable guidelines for dummy presentation. Some researchers have placed the dummy in the water with the subject (e.g. Rowland, 1975), while others have put it just outside the aquarium (e.g. Figler, 1972). Some researchers have used a moving dummy (Thompson and Sturm, 1965), but others have kept it stationary (Heiligenberg, 1965). Moving dummies appear to be more effective stimuli (Rhoad *et al.*, 1975 ; Stringer and Hoar, 1955).

Our presentation involved suspending the dummy by two fine wires from a motor-driven pulley system, positioned outside the left wall of the observation tank *(fig. 1)*. The dummy was propelled slowly into the subject's view, moving parallel to the glass and toward the front of the tank at about 1 cm/s. The movement was interrupted by two pauses, during which the dummy rocked back and forth slightly. It out of view of the subject one minute after the presentation was initiated.

Target fish

The target fish were juveniles, selected to be 2 to 4 % of the weight of the subject (around 10 g). Of the 10 target fish with each subject, half were gold and half normal, about equal in size. Each target fish was blinded by cutting the optic nerves to prevent it from responding to visual stimuli from other target fish, from the subject, or from the dummy (Leong, 1969).

Priming

Beyond the right wall of the observation tank, at a distance of 23 cm, was a smaller aquarium (60 × 60 × 30 cm deep) containing two "primer" fish, who were separated from each other by a transparent screen *(fig. 1)*. The primer fish were adult males, selected to be around 85 to 90 % the weight of the experimental subject. In each trial, one primer was gold and the other normal. Their role in the experiment was to provide aggressive stimulation for the subject fish during periods when observations were not being made and thereby prevent the loss of reactivity that would otherwise have been associated with solitary confinement.

Visual access to the primer fish by the subject was controlled with a removable one-way mirror. The primer fish were maintained in weaker light than prevailed in the observation tank so that when the mirror was in place the subject could not see them. The primer fish always had a clear view of the observation tank, however, which allowed the subject and targets to serve as stimulation ("dither", Barlow, 1968), keeping the primer fish mobile and reactive.

The mirror was constructed of two sheets of flexible plastic (Mylar). Each sheet was bent into a long "U". The two troughs were then joined to form a "W" with the middle point of intersection directed horizontally toward the primer fish ; that design prevents the subject from seeing its own reflection (Lott and Woll, 1966). During the course of an experiment, the mirror was removed once daily, at 1 630 hr. The subject was then allowed four 10-minute sessions of interacting with the primer fish, alternating sessions between the two color morphs by occluding the view of first one primer fish then the other, after which the mirror was replaced. Pilot studies raised the possibility that if only two sessions were used, the subject might direct more attacks, on the following day, to target fish of the same color as that of the last primer to which it had been exposed.

PROCEDURE

On Friday afternoon, a subject, two primers, and a set of juvenile target fish were weighed and measured and placed in the aquaria without the one-way mirror in place. The following Monday morning the mirror was inserted between the two tanks. Testing was performed once daily, between 1 000 and 1 300 hr, for six successive days, each test involving a single presentation of each of the five dummies and a blank control in which the driver motor was run, but no dummy appeared. The presentation sequence was semi-random within days, but fully balanced across days, each treatment occurring once in each sequential position

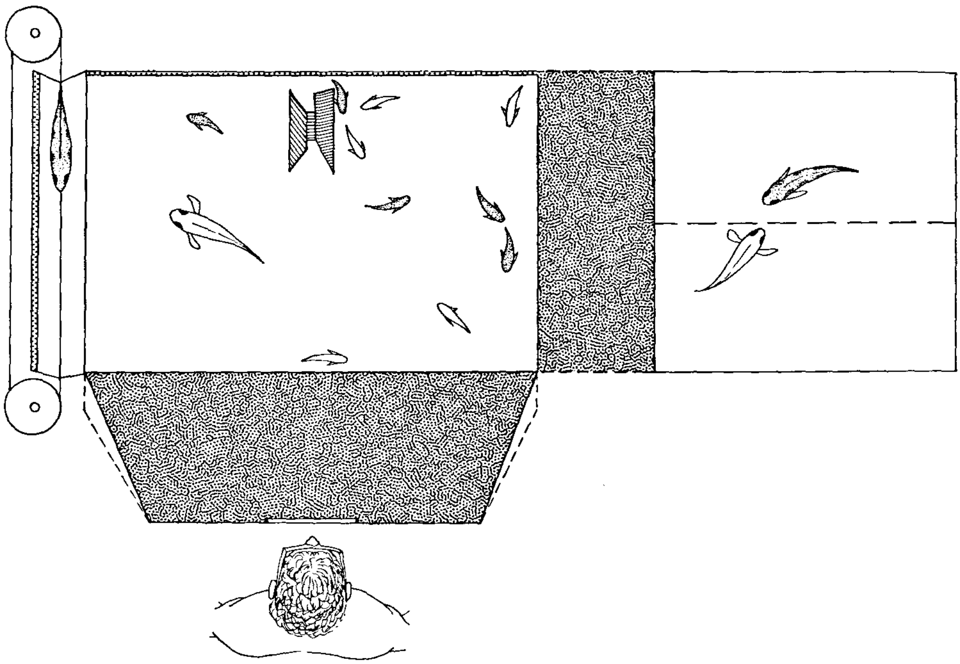

Fig. 1 : *A top view of the experimental situation. The two primer fish are in the tank to the observer's right, separated by a screen ; a bowed one-way mirror lies between them and the main tank with the subject and 10 target fish ; a shelter is situated in the rear center portion of the tank. The subject is responding to a pully-transported dummy that has just entered a small theatre. The observer watches through a thin slit fitted with a piece of shiny brass, fine-mesh screen.*

Fig. 1 : *Vue plongeante du dispositif expérimental. Les deux poissons-amorceurs sont maintenus dans le bac de droite, séparés par un écran ; un miroir courbe à sens unique est placé entre eux et le bac principal, qui contient le poisson-sujet et les dix poissons-cibles. Un abri est situé dans la partie centrale arrière du bac. Le sujet réagit au leurre tiré automatiquement par une poulie dès qu'il est entré en opération. L'observateur surveille à travers une étroite fente munie d'un écran de fines mailles en laiton.*

over the series of tests on a single subject. The six one-minute presentations, termed " stimulus periods ", alternated with seven 15-minute intertrial intervals, termed " nonstimulus periods ". The behavior of the subject fish was recorded continuously for the full duration of the test.

The observer sat in a darkened area behind a black cloth curtain and watched the fish through a screened slit. The behavior of the subject was coded on magnetic tape, with a real-time base, by means of a keyboard, thus permitting direct input of the data into a large central computer. For some events, two keys were pressed : one was for the behavioral action, e.g. bite, and the other was for a modifier, e.g. at the glass or at a target fish of a particular color.

Measures of behavior

The aggressive behaviors recorded were, in order of increasing intensity (Losey, 1982) :

1) *Flare :* Extending the gillcovers while the mouth remained closed. The body was often bent into a lateral S-shape. The subject faced the dummy and frequently

moved forward and backward. This behavior, a threat display, was not shown to target fish.
2) *Charge:* An accelerated swim toward a dummy or target fish.
3) *Butt:* Swimming or charging culminating in actual contact by the subject's head with the glass or the target fish, but without biting.
4) *Bite:* With its mouth open, the subject raked or bit a target fish or raked the glass between itself and the dummy.

Objects of aggression were almost always the dummy during the stimulus period and the target fish during the nonstimulus period. During the blank (control) stimulus period, aggression was also directed to the target fish.

Analysis

The basic experiment was designed for repeated-measures Anova. That model was not used because of the high incidence of zero cells, and because of the consistent large differences between individuals: some were regularly highly aggressive while others were hardly aggressive at all, with a range of intermediate subjects. Therefore, we elected to use nonparametric models in which the ranking of scores within each individual's behavior normalized the data.

The data utilized were the means from each individual. For example, when analyzing the effects of different sizes of dummies, each subject provided five scores, the mean values for six days for each of the five dummies. The control data merely showed that the blank runs did not differ from baseline data, so data from the control presentations were left out of the analysis.

Tests across dummies employed the Friedman two-way Anova. Correlation coefficients were tested against the null hypothesis using the Spearman method. Mean scores for individuals, comparing subjects, were analyzed with the Mann-Whitney U test. Any reference to variance is $\pm$ 2 S.E.M.

RESULTS

Choice of measure

Butt and bite proved difficult to separate because they grade insensibly into one another; they appear to be two extremes in the expression of one motor event. Hence, butt and bite were combined and are called *attacks* here. Flare and charge occurred together so commonly that we pooled them and called their occurrence *threat,* in keeping with earlier observations on interacting Midas cichlids.

We wanted a composite measure to take advantage of all the data on aggressive behavior, to avoid losing information. Attack and threat seemed to occur together. Using the total scores for attack and for threat from each subject, $r_s = 0.68$ ($.01 > p > .005$). Because the overall attacks and threats were highly positively correlated, they were combined and called simply *aggression* for the analysis of responses to dummies.

Responses in the presence of different sizes of dummies

Frequency of aggression varied significantly in accordance with the size of the dummy (4df, Chi Square = 13.8, $p \simeq .01$). Proceeding

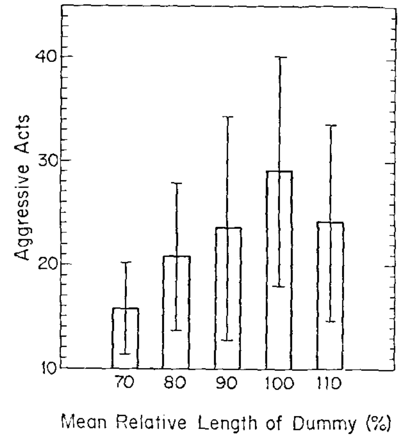

Fig. 2 : *The mean number of total aggressive acts (± 2 S.E.M.), per subject shown to each dummy across all six days.*

Fig. 2 : *Nombres moyens de tous les actes agressifs par sujet (± 2 écarts-types de la moyenne) dirigés à l'encontre de chaque leurre pendant les 6 jours d'expérience.*

from smallest to largest dummy, aggressiveness increased to a maximum at the dummy about equal in size to the subject, then fell off symmetrically at the next larger size *(fig. 2)*.

The subjects varied greatly in their rates of aggression toward the dummies. The least reactive fish had a mean score of only 1.03/min while the most reactive had a mean of 7.93, the scores of the other 10 fish falling on a continuum between these two extremes. As a research strategy, one might be tempted to reject data from relatively non-reactive subjects, as Heiligenberg (personal communication) has done. The more reactive fish produce more data and could, within the time limits of observation, provide a clearer picture of the pattern of responses to dummies. Such a research strategy, however, presumes that the pattern of responses is the same across all fish, irrespective of individual differences in levels of aggression, and that might not be the case.

To test this, we divided the 12 subjects according to levels of aggression into three groups, the highest, middle, and lowest four fish *(table I)*. (It is important to note here that this analysis is based on the rankings of mean responses by each individual to the five dummies. Thus while low responders produced few data, they contribute precisely the same number of values of ranks to the analysis as do the other groups.) The high group showed the same pattern of ranks as did the entire group (the same shape as in *(fig. 2)*, and produced an even larger Chi Square value *(table I)*. The patterns of ranks for the middle and low groups was roughly the same as in *figure 2*, but both failed to achieve significance. Progressively adding the other groups to the high group did not change the pattern and had only a slight effects on the Chi Square values *(table I)*.

One could ask the question the other way round : What would be the effect of removing the high group ? When that was done, the pattern was less clear, showing only a general trend for more aggression

Table I : *Comparison of statistical tests when the fish are divided into three groups according to levels of aggressiveness, and when the groups are then progressively combined (Accumulative Scores) from highest to lowest levels of aggression.*

Tableau I : *Comparaison des résultats des épreuves statistiques quand les poissons-sujets sont divisés en trois groupes d'après leur niveau d'agressivité et quand les groupes sont progressivement combinés (valeurs cumulatives), allant du niveau le plus élevé jusqu'à celui le moins élevé.*

Level of aggression	$\overline{X}$ aggression per min	Chi square	Probability	Chi square accum. scores	Probability
4 highest fish	6.3	14.2	$.01 > p > .001$	—	—
4 middle fish	3.5	4.6	$p \simeq .50$	14.4	$.01 > p > .001$
4 lowest fish	1.8	3.8	$p \simeq .50$	13.8	$p \simeq .01$

toward larger dummies, and the differences were not significant (Chi Square = 5.4, $p \simeq .20$).

We conclude that it was mainly the high responders who set the pattern. The middle and low groups would probably have shown the same pattern, and almost did, but one must allow for the possibility that they would not. To avoid bias, we draw our conclusion from the randomly drawn sample of all 12 fish, a conclusion we would have arrived at if only the high responders had been used.

Do responses change with time ?

We noticed that the aggressive responses were often highest on the first day. Was that really the case ? If so, did the pattern of response change with the level of aggression ?

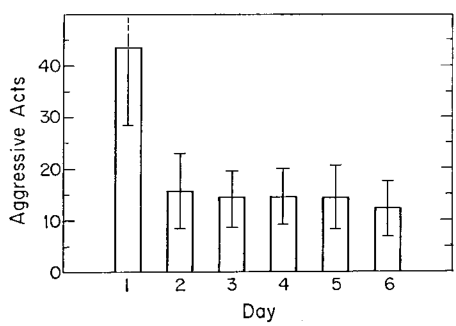

Fig. 3 : *The mean number of total aggressive acts (± 2 S.E.M.), per subject shown on each day to all five dummies.*

Fig. 3 : *Nombres moyens de tous les actes agressifs par sujet (± 2 écarts-types de la moyenne) dirigés à l'encontre des 5 leurres chaque jour.*

Aggression was especially high the first day then sank to a stable level on succeeding days *(fig. 3* ; 5 df, Chi Square = 24.4 $p < .005$). When the pattern of aggression toward the five dummies was examined on Day 1, it was the same as across all days. However, the differences between dummies just escaped significance (2 tails, 4 df, Chi Square = 7.62, $p = .10$). And when the fish were analyzed in three separate groups, the highest, middle and lowest four fish, no group showed significant differences.

One might assume that the failure to show significant differences on Day 1 was due to the greater variation and that the more stable period, Days 2 to 6, would be statistically more sensitive. That was not the case, although the Chi Square value for Days 2 to 6 was slightly higher (8.87), and the pattern for each day was again as in *figure 2.* The four most aggressive fish did show significant effects of dummy size (4 df, Chi Square = 13.85, $p \sim .01$), and the pattern was as in *figure 2.* Thus the level of aggression does change with time, but the pattern of responses apparently does not.

Effects of dummies on attacks toward target fish

For each fish, we compared the attacks on target fish preceding and following the presentation of the dummy. The attacks in the following five minutes were subtracted from those in the preceding five minutes. The difference was the residual effect of having seen the dummy.

The pattern was simple and clear *(fig. 4) :* The difference in attacks increased with size of dummy, though the two smallest dummies appear

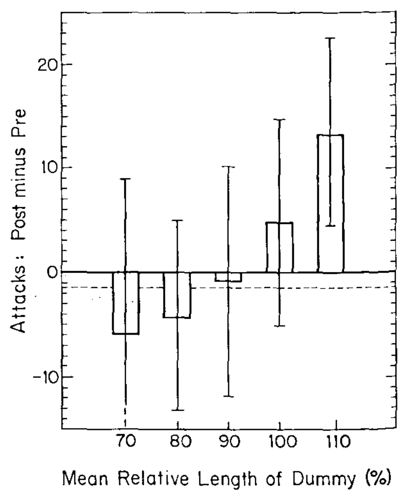

Fig. 4 : *The mean change in attacks (post 5-min exposure minus pre 5-min exposure to dummy ; ± 2 S.E.M.) as a result of having been exposed to a dummy. The horizontal dashed line, at — 1.4, represents the mean for all blank (control) presentations.*

Fig. 4 : *Variations moyennes des attaques dirigées à l'encontre des poissons-cibles comme conséquence de l'exhibition du leurre (différence entre les attaques effectuées pendant 5 mn après l'exhibition du leurre et celles effectuées pendant 5 mn avant ; ± 2 écarts-types de la moyenne). La ligne pointillée horizontale représente la valeur moyenne pour toutes les présentations-témoins.*

to have caused a decrease. The pattern, however, was not statistically significant (4 df, Chi Square = 3.82, $.50 > p > .30$) because no two subjects showed the same pattern. When the group means are analyzed with regard to Spearman correlation, instead of Friedman Anova, then $r_s = 1.0$ ($p = .01$).

Were males more aggressive than females ?

It is commonly believed that males are more aggressive than females. Here, no significant differences were found, whether examining aggression toward dummies ($p = .9$) or toward target fish ($p = .29$) (see also Barlow, 1983 b). Differences were greater between individuals than between the sexes.

Were gold subjects more aggressive than normal ones ?

Gold and normal morphs have been said not to differ in aggressivity (e.g., Barlow and Wallach, 1976). The same conclusion was reached here. There were no significant differences between the two color morphs for aggression toward dummies ($p = .29$) or for attacks on target fish ($p = .16$).

Were normal target fish attacked more than gold ones ?

The hypothesis that gold inhibits attack predicted that the small normal colored target fish would be attacked more than the small gold ones. They were, but not significantly so ($p = .29$). The means of total attacks per subject were 255 ± 72 toward normal and 222 ± 45 toward gold target fish. When the analysis was done separately by sex or by color of subject, there were still no significant differences.

DISCUSSION

There were two major objectives of this study. The first was to establish the optimal relative size of dummy to elicit aggression from Midas cichlids. The second was to determine which is the more effective method for revealing the influence of dummies, observing while the dummy is present (the direct method), or calculating the change in level of attacks on target fish [the indirect or residual method of Heiligenberg (1965) and of Leong (1969)] ? The second objective needs addressing before the first can be satisfactorily answered.

Direct versus indirect methods

The data from the direct method were more consistent in their pattern. The major difference between subjects was in the level of aggressiveness (the large ± 2 S.E.M. in *figure 2* reflects the differences between individuals). The Friedman Anova, however, eliminates differences in levels because it ranks the aggression toward dummies for each subject.

The residual method failed to produce a significant difference for size of dummy. There were again large difference in levels of aggression between individuals. In addition, the patterns varied erratically between individuals. Ranking the responses to dummies retained the variation in pattern. Nonetheless, the combined means, for all subjects, yielded a perfect correlation of increasing attacks from small to large dummies. The effect may be real but the method would have failed if the pattern had not been rectilinear.

We conclude that the direct method is superior because it is more efficient. The pattern of response is more consistent across individuals. Consequently data from fewer individuals suffice to test hypotheses. Nonetheless, the indirect method may yield different, or additional, information about the behavioral mechanisms of aggression (see below).

Optimal size of dummy

The data indicated that in order to evoke the highest level of aggression the dummy ought to be about the same size as the subject. Further, the variation observed in response to the dummies suggests that a close match to the subject's size is not critical. Rowland (1975) tested the aggressive responses of an African cichlid fish, *Hemichromis bimaculatus*, to dummies of five different sizes ; the variation in pattern of response of the five male subjects was too great to permit a general conclusion.

If we could have anticipated the outcome, we would have employed a dummy in the category of 120 %, or even 130 %. Then we could have seen if there is a symmetrical decline as larger dummies are presented, as compared to the small dummies *(fig. 2)*.

The general outcome is reasonable. Size is an important determinant of winning a fight in the Midas cichlid (Barlow, 1983). A territory holder need not invest heavily in aggression toward small Midas cichlids, and it ought to avoid hostile interactions with damaging larger ones. The most aggressive behavior should be shown to a Midas cichlid of about the same size.

Consistency of pattern of response

We were gratified to find that the pattern of aggression toward the dummies was so consistent. Only the very low responders showed no discernible pattern, and that may have been just a matter of too few data from them for the pattern to emerge. In effect, the pattern was set by the preponderance of data from the more aggressive fish. If just the most aggressive fish had been used, the same general conclusion would have been reached as when all the fish were employed. And though the fish were more aggressive on the first day, that did not affect the outcome, nor did sex or color of subject have an effect.

Gold morphs were no more aggressive than normal ones. Females did not differ from males. We would not advocate using females when there is a choice, however, because they sometimes spawn in the middle of an experiment, and that greatly alters their behavior.

Attacks on gold and normal target fish

This experiment provided an opportunity to test the hypothesis that gold coloration inhibits attack (Barlow and Wallach, 1976 ; Barlow, 1983). As mentioned in the Introduction, Barlow and McKaye (1982) obtained contradictory evidence when a large Midas cichlid was confronted by six juveniles, each about half the weight of the large fish. The large fish have attacked the gold juveniles more than the normal ones because the gold juveniles fed from the feeder more often and did more attacking among the small fish than did the normal juveniles.

In the present experiment there could be no difference between the small target fish because they were blind. In that condition, they were attacked about equally by the large fish. The prediction was that the normal target fish would be attacked more. The target fish, at 2 to 4 % the weight of the large fish, may have been too small to evoke a differential response, based on color, from the large fish.

Dynamics of the residual effect

In the belief that it is as important to discover problems as it is to solve them, we offer the following. The most remarkable effect of dummy size may have been the depression of aggression below the control level for the smallest dummies in the 5-minute interval after the dummy had been presented.

We can suggest an intuitive but testable model *(fig. 5)* to account for the difference in responses to the dummies. The model flows from a consideration of *figure 2,* showing at least some elevation of attacks when the small dummies were present, and *figure 4,* in which aggression was depressed below baseline after the small dummies disappeared. The model also owes some inspiration to the dynamics of the action potential of a neuron and earlier formulations of reaction specific energy (e.g., Lorenz, 1950) ; it is similar, as well, to the dual-process theory of habituation (Groves and Thompson, 1970).

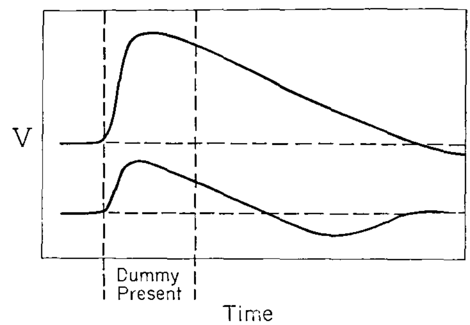

Fig. 5 : *Fluctuations in the variable V, which reflects a readiness to respond aggressively. The upper curve portrays the change in V in response to large dummies, the lower curve in response to small dummies.*

Fig. 5 : *Fluctuations de la variable V qui reflète l'état de préparation pour répondre agressivement. La courbe inférieure indique la variation en V en réponse aux grands leurres et l'inférieure, la variation en réponse aux petits.*

The model assumes that exposure to a dummy increases the value of some variable, V, which produces a change in the readiness to respond aggressively. The increment in V over the resting level is proportional to the size of the dummy, as in *figure 4.* The subject responds initially with a rise in V above the baseline level *(fig. 5)* and begins to behave aggressively. Performance of aggression results in a decrement in V, however, generating a lag and a tendency to overshoot the baseline level before rising back to it.

Because the increase in V is small when the dummy is small, the depression in V occurs quickly and lies within the post-stimulus interval. But when the dummy is large, V rises much higher and remains above the baseline level after the dummy stimulus has been withdrawn ; as a consequence, the subject directs its aggression toward the otherwise less evocative target fish.

After we conceived of the model and drew *figure 5,* we decided to examine the data to see if the model is reasonable. Because the sample size is relatively small, we combined the data for overt attack toward the two largest dummies, and toward the two smallest ones. Attacks were examined in successive 20-second intervals ; running means for successive pairs of intervals were calculated *(fig. 6).* No statistical testing was done, but the resulting curves show a modest correspondence to the model, good enough to suggest an interesting problem for future study. The curves also reveal that the subject's aggressiveness returns to baseline levels within 10 minutes after seeing a dummy.

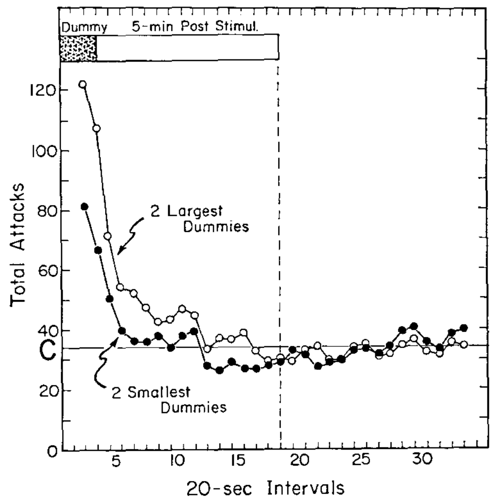

Fig. 6 : *Total attacks to the large dummies (means of the 2 largest) and to small dummies (means of the 2 smallest) in 20-sec intervals. Each data point represents the running mean of successive pairs of 20-sec intervals ; to convert to attacks per fish, divide each data point by 24. The letter C, on the ordinate, indicates the mean of the two blank control intervals during the same time span.*

Fig. 6 : *Nombres totaux d'attaques envers les grands leurres (moyennes des 2 plus grands) et envers les petits (moyennes des 2 plus petits) pendant des intervalles de 20 secondes. Chaque point représente la moyenne mobile pour deux intervalles successifs de 20 secondes ; pour convertir ces chiffres en attaques par poisson, divisez la valeur de chaque point par 24. La lettre C, sur l'ordonnée, indique la valeur moyenne obtenue pour deux intervalles-témoins pendant le même laps de temps.*

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