THE RELATIONSHIP BETWEEN COLOR CHANGE AND SOCIAL BEHAVIOR IN THE GREEN SUNFISH, LEPOMIS CYANELLUS (RAF.)

Thesis for the Degree of Ph. D.

MICHIGAN STATE UNIVERSITY
DIANE MERLE FABRY

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ABSTRACT

THE RELATIONSHIP BETWEEN COLOR CHANGE AND SOCIAL BEHAVIOR IN THE GREEN SUNFISH, *LEPOMIS CYANELLUS* (RAF.)

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Green sunfish show a wide range of coloration, from pale, translucent green to alternating bars of jet black and silvery gray. Since the most striking coloration appears to be directly related to the hierarchies which these fish form in a laboratory environment, the purpose of this study was to determine the relationship between coloration and social behavior.

Fish were observed both in the laboratory and in a natural lake environment. General observations were made on coloration as it relates to dominance, subordination, territoriality, and breeding.

Seventeen hierarchies of four fish each were maintained in 10-gallon tanks, and the coloration of individuals holding different social position was compared, as well as the coloration of fish engaged in behavior of different intensity levels. Each group was observed for 60 minutes.

Experiments with clay models were conducted to determine whether particular colorations elicited specific behavior patterns. The models represented alpha, submissive, and omega (extremely submissive) fish. An unpainted model and two painted uniformly black or white served as controls. The models were held stationary or were advanced toward the fish for a two-minute period. A total of 20 alpha fish were tested in their home tanks (10-gallon). Subordinates were removed prior to the test and were later returned.

A dominant green sunfish showed light or intermediate ground color, no barring or light barring, and red (or sometimes white) iris. A submissive individual showed dark ground color, heavy barring, and black iris. Individuals in the lake environment were colored like dominant laboratory fish except when resting over a dark substrate. Even then, they retained their red iris color. The dark coloration characteristic of submissive laboratory fish was not noted among lake fish, except in breeding females.

Territorial fish showed dominant coloration.

During spawning, both sexes often showed intensified barring, and males were sometimes indistinguishable from females except for iris color. In males the iris was bright red. In females, it was black.

Iris color was considered a more certain indicator of dominance than either ground color or barring.

The social position held by a fish was apparently more closely related to its coloration than was its actual behavior. High-ranking fish tended to retain their light coloration and red iris during submissive actions. Low-ranking individuals tended to retain their dark coloration and black iris during dominant behavior. A tendency was noted for dominant fish to become lighter in color as the intensity level of their behavior increased. No corresponding darkening was noted for increasing intensity levels of aubmissive activity, since submissive fish are generally always extremely dark.

The results of the experiments with models were not definite enough to serve as the basis for conclusions at this time, although some tendencies were suggested by the data. The naturally colored models elicited more dominant behavior than did the black and white control models, which elicited more submissive behavior. The former were probably recognized as rivals, while the latter were feared because of their unnatural coloration. More specific experiments are needed to determine the aspects of coloration to which the fish actually respond, and their relative significance.

THE RELATIONSHIP BETWEEN COLOR CHANGE AND SOCIAL BEHAVIOR IN THE GREEN SUNFISH, *LEPOMIS CYANELLUS* (RAF.)

By

Diane Merle Fabry

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LIST OF SYMBOLS AND ABBREVIATIONS

dom.: Dominant actions

subm.: Submissive actions

L: Light ground color

I: Intermediate ground color

D: Dark ground color

N: No barring

Lt: Light barring

H: Heavy barring

R: Red iris

W: White iris (includes colorless, yellowish-white, and light gray)

B: Black iris (includes dark gray)

Σ: Sum

$P\{\chi^2 \geqslant \ldots\} < \ldots$: The probability that chi-square is greater than or equal to . . . is less than . . .

df: Degrees of freedom

α: Alpha fish

β: Beta fish

γ: Gamma fish

δ: Delta (omega) fish

α-I: Alpha-I model

S: Submissive model

ω: Omega model

C: Unpainted control model

α-II: Alpha-II model

Bk: Black model

W: White model

INTRODUCTION

Coloration among Vertebrates

Green sunfish in a laboratory environment display a wide range of color variations, extending from pale translucent green to alternating bars of jet black and silvery gray. The most striking colorations are related to the social hierarchies that develop in the aquaria, and the fish can change color at times in a matter of seconds. In observing these fish, I became interested in the role that coloration might have in their social activities. The purpose of this study was to determine the relationship between social activity and particular colorations.

Coloration in fishes has long been of interest to researchers. The naturalist, Abbott (1894), noted color changes in relation to sexual attraction and behavior and an apparent correlation between bright coloration in fishes and their supposed lack of ability to produce sounds. Among vertebrates, rapid color changes occur in amphibians and reptiles as well as in fishes, and have been investigated with particular regard to the types, controlling mechanisms, and the effect of various environmental factors and chemicals.

Ando (1960) stated that there are three basic types of color change in fishes: (1) the "*Fundulus* type," in which there is little hormonal effect and the changes are produced mainly through the nervous system; (2) the "*Anguilla* type," mainly controlled by hormones and not by the nervous system; and (3) the "*Ameiurus* type," in which both the nervous and endocrine systems effect control. In a general review of fish coloration, Pincher (1946) noted three categories: one in which the changes take place within seconds and apparently are entirely under nervous control; one in which they occur within a few hours and are brought about by hormones; and a third, taking place over a period of several months, in which the number of pigment cells increases or decreases.

Coloration in fishes may be due to biochromes, or pigments, or to schemacrhomes, that is, structural configurations (Lagler, Bardach and Miller, 1962). Originally, carotenoids were thought to be responsible for all red, yellow and orange coloration. It is now known that several pigments are involved. The original names of the chromatophores, however, are still used: red chromatophores are known as erythrophores, and yellow ones as xanthophores. Black and brown colors in fish skin are due to melanin, found in melanophores (also called melanocytes). Crystalline guanin, stored in guanophores as an excretory product, produces chalky white, silvery, and iridescent colors. Various combinations of the three basic kinds of chromatophores will produce other colors.

Because black and shades of brown are the colors involved in the darkening of green sunfish, melanophores are of greater interest in this study than are the other types of pigment cells. Also, since rapid color changes are probably the most important with regard to the social behavior of the fish, this study concentrates on those changes that are under nervous control, although hormonally controlled changes are also known to occur in these fish.

Melanophores are generally regarded as having a double innervation where they are under nervous control. The nerves are connected with the spinal cord and the sympathetic chain (Wyman, 1924). The melanophores themselves are believed to be of nervous origin (Lerner, 1961) and have the general shape of a neuron, with radiating processes. Melanin occurs within these cells in the form of minute granules which disperse by moving outward in an orderly fashion into the radiating processes of the cell, until they are more or less evenly distributed. When the melanin has dispersed in many dermal melanin corpuscles, the result is a darker appearance of the skin. When aggregating, the granules move toward the center of the cell until they are contracted into a tiny dot. The pigment is thus contained within a very small area, and the overall appearance of the skin is light.

The major hormones known to affect melanophores are MSH (melanocyte-stimulating hormone), of which there are two types, alpha-MSH and beta-MSH, both causing a dispersion of melanin granules; and melatonin, which causes the granules to aggregate (Lerner, 1961). MSH of both types is of pituitary origin, and melatonin is of pineal origin. Other hormones and hormone-like substances, as well as many chemical agents, have also been studied (Wright and Lerner, 1960; Thurmond, 1961, 1962, 1967; Abbott, 1968). Some agents may act directly on the melanophores, while others may act through the nervous system, affecting the melanophores indirectly (Wyman, 1924).

Most of the work on hormonal control has been done with amphibians, and especially with the leopard frog, *Rana pipiens* (Sawyer, 1947; Wright, 1955; Zimmerman and Dalton, 1961; Khazan and Sulman, 1961; Bagnara, 1961; Novales and Novales, 1962; Thurmond, 1961, 1962, 1967; Martin and Snell, 1968). Amphibians, however, have no nervous control of melanophores, and thus their reactions cannot be equated entirely to those of fishes.

With regard to the actual mechanisms of dispersion and aggregation, studies of different animals have produced various results. Adrenalin is believed to act as the transmitter between nerve and melanophore for the aggregation of melanin granules. It affects the melanophores directly (Fujii, 1959, 1961; Abbott, 1968). Ishibashi (1960) and

Fujii (1959) both found the potassium ion to be important in this process in teleost fishes. The ion is thought to cause the secretion of the neurohumor, which in turn brings about the concentration of pigment.

Acetylcholine has generally been thought to be the transmitter in melanin disperion. Green (1968), working with isolated scales of *Fundulus heteroclitus*, reported that dispersion can be elicited by acetylcholine. Abbott (1968), on the other hand, working with both live *Fundulus heteroclitus* and isolated scales, found no evidence for a cholinergic dispersing mechanism.

In teleost fishes, acetylcholine is thought to disperse melanin granules by increasing the sodium ion permeability of the cell membrane, followed by "some kind of mechanico-excitation coupling and cytoplasmic solation." (Novales, 1961). Novales thought that MSH may disperse melanin in the same way. The effect of various agents is probably brought about by affecting the passage of sodium ions. In the amphibia that he studied, Novales (1961) found an absolute sodium ion requirement. No such requirement, however, was found for the dogfish(Novales and Novales, 1966), although MSH action was reversibly inhibited in a sodium-free medium. A definite requirement for cations was found.

The importance of vision in fishes is not to be overlooked as a factor affecting color change. The vision of at least some fishes is acute, as demonstrated by a study by Hager (1938), in which *Phoxinus laevis* learned to discriminate between optical signals showing very minor differences. Sumner (1937) stated that fishes respond more to visual stimuli than to any other kind. Whether fishes are capable of seeing colors has been a matter of great debate in the past. Warner (1931) reviewed several experiments on color vision in fishes in which most of the criticism centered on whether the animals respond to light intensity or to color itself. Brown (1937) concluded that largemouth bass do see colors, preceiving them somewhat in the way a human with normal color vision looking through a yellowish filter would see them. Behre (1933) and Morrow (1948) decided that probably not all fishes are capable of distinguishing between different wave-lengths of light, but that some definitely can. Morrow believed that color could be considered an active influence on the social behavior of fishes.

Sumner (1937, 1939) was certain that fishes respond to the albedo of light, the ratio of incident to reflected light. If this is the case, the intensity of the light source would not be as important a factor as the reflecting capacity of the background. Certainly many observations have been made and experiments conducted which show that fishes of various kinds do react to the background, by adapting their coloration to it. Some examples are given by Brown and Thompson (1937), Miller and Kennedy (1946), Pavan (1946), Breder and Campbell (1948), and Armitage (1953). The albedo would therefore appear to be very important. Other experiments, however, show that fish respond to intensity as well (Breder and Rasquin, 1955; Woodhead, 1956; and Jones, 1956).

Other environmental factors known to affect melanophore activity are oxygen lack (Robertson, 1951; Rahn, 1956) and temperature (Pye, 1964). Food apparently has little effect on the external coloration of fishes as long as the diet is nutritionally adequate,[1] although it is known in some cases to affect the coloration of the flesh. Xanthophyll and/or carotene may be important. Brown (1937) stated that there is a yellow pigment present in the retina of the largemouth black bass. Sumner (1937), however, believed that the amount of xanthophyll present in a fish is not closely related to its visible coloration. Carotene and xanthophyll are obtained by fish from plants in the food chain. If experimental fish are kept over the winter months, it would be necessary to see that they receive an adequate

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[1]Personal comment by Dr. James C. Braddock, Department of Zoology, Michigan State University, July 30, 1968.

supply of these pigments. At other times, food consisting of whole animals such as immature or adult aquatic insects would provide the nutrients required to keep the animals healthy.

Behavior of the Green Sunfish

Aggressiveness and territoriality have been studied in various animals, particularly in fishes, birds, and mammals, and are definitely characteristic of the green sunfish. The social behavior of the green sunfish, including its spawning and nesting behavior, seems to be centered around these two traits.

Under laboratory conditions, these fish establish well-defined hierarchies, usually of the straight-line type, although there may be modifications. In a small tank, a particularly aggressive alpha fish may become a despot, claiming the entire tank for its territory and so severely persecuting the other fish that they do not develop any ranking among themselves. In other situations, "partial territories" may form (Greenberg, 1947), in which the alpha fish is dominant throughout the tank and the beta fish defends a part of the tank against all except the alpha. Occasionally each of the fish may claim a territory, and a relative peace reigns unless one fish ventures too close to the boundary of another's preserve. The omega fish usually has no territory, but may find some spot in the tank where it is less susceptible to attack by others and will tend to remain there. Greenberg (1947) reported that even when there are no territories, each fish tends to remain in a given area.

Whether or not green sunfish form hierarchies in their natural environment is unknown, but probably they do not. Erickson (1967), working with pumpkinseeds (Lepomis gibbosus L.), thought that the hierarchical behavior he saw among his laboratory fish was a function of their close confinement in tanks. Hall[2] suggested that the aggressiveness shown by fish under laboratory conditions may be the end of a continuum, and definitely related to lack of space. Hunter (1963) reported frequent fighting among males on crowded spawning grounds, but none among males in a smaller pond with more widely spaced nests.

Apparently, a green sunfish is able to recognize other fish at various levels of the hierarchy. Another possibility, of course, is that a fish does not recognize anything of the social arrangement except its own immediate position when it confronts another fish. Whether it shows dominance (aggression) or submissiveness (fear) will depend on several factors. Greenberg (1947) reported that sex and size are important. Males tend to outrank females and

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[2]Personal communication by Dr. Donald J. Hall, Department of Zoology, Michigan State Univestity, July 7, 1970.

larger fish tend to outrank smaller ones, although exceptions occur. Whether a fish is in its home area or territory can also be a critical factor. Although the relationship of prior residence to territoriality was not certain, Braddock (1949) found that prior residence in an area did give *Platypoecilus maculatus* a greater potential for dominance.

The level of aggression of the fish is another factor determining dominance, and can account for a smaller fish outranking a larger one. The fact that males tend to outrank females is perhaps due to the greater testosterone levels of the male as well as to a difference in size. Beeman (1947) showed that in mice, an increase in testosterone level caused a definite increase in aggression. This could be true of green sunfish as well.

Various studies have shown the importance of previous conditioning (Allee, 1942; Beeman and Allee, 1945; Guhl, Collias and Allee, 1945; Beeman, 1947a; Greenberg, 1947; McDonald et al., 1968). As a result of its encounters with others, an animal will become conditioned to dominance or to subordination and will tend to maintain this behavior in future encounters, unless it meets a fish that greatly differs from itself in terms of size or level of aggressiveness.

General health is also relevant to hierarchical position. A sick or injured fish will tend to avoid all encounters, and usually ends up at the bottom of the hierarchy. There may be other factors as well, quite unknown at present. McDonald et al. (1968) suggested the possibility that an olfactory stimulus similar to an alarm substance might be given off by low-ranking fish which have been injured by their superiors, and that this substance might have an effect in eliciting attacks. Also, they suggest that the dark coloration of a subordinate fish might possibly elicit attack.

Among green sunfish, any sign of fear[3] of submission on the part of any individual generally evokes aggression from the others present. Even the omega may attack a higher-ranking fish that loses a fight. The hierarchy of green sunfish presents an extremely tense social situation in which each fish is constantly trying, by every means possible, to advance its social position, or if it is already the alpha, to maintain it.

Any newcomer is "sized up" very quickly. If it shows any sign of fear (such as avoidance behavior, for example), its place at the bottom of the hierarchy is assured. Depending on the factors given above, however, it may or may not stay there. If the newcomer is an alpha from another group, all of the preliminaries may be omitted, and the

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[3]For the sake of brevity, the terms "fear" and "frightened" as used here and hereafter in this paper refer to behavior similar to that which, in humans, is usually attributable to adrenalin release.

stranger will confront or be confronted by the resident alpha. Whichever is the more aggressive at the moment (usually the resident) will challenge the other; if the stranger is not intimidated, a fight ensues. The loser goes to the bottom of the social ladder and begins again.

If two male green sunfish that are matched in size, level of aggressiveness, and previous conditioning to dominance are placed in a tank which is new to both of them, they may develop territories, dividing the space fairly evenly with some visual marker (inside or outside the tank) for a boundary. In such a case, the activity level remains very low, with each fish staying in its own resting place for long periods of time. From time to time, one may approach the boundary. The other also approaches the boundary immediately, and both fish present repeated frontal displays consisting of a short, rapid approach, spreading of the opercula, backing up, reapproaching, etc. Rarely will either fish cross the boundary, as though an invisible wall were keeping them apart.

The reproductive behavior of green sunfish has been described by Hunter (1963). Territoriality is a prominent feature, with nests constructed and defended only by males. If the nests are closely spaced, a high level of aggression may be maintained, especially during the actual spawning period. Males defending nests drive away all intruders, and in this study, were observed to leave the nest every few seconds. They would swim out half a meter or so and then return, as if "looking" for possible intruders even when none were present.

Females are very submissive during spawning, although in approaching an occupied nest, they withstand the often violent attacks of the male. An approaching female may be driven away several times, but usually returns and eventually enters the nest. The spawning behavior itself is typical of that of Centrarchidae in general. Occasionally males will spawn with more than one female at a time. When the gametes have been released, the female is vigorously driven away. The male then fans the eggs with sweeping movements of his caudal peduncle and caudal fin. He defends the eggs and also the young for a short period of time after hatching.

Tranquilli (unpublished) has presented the major components of aggressive behavior in the green sunfish. The individual elements appear in many cases to be similar to those shown by various other fishes that have been studied (Neil, 1964; Miller, 1964). The dominant and submissive actions shown by the fish observed in the present study are listed and briefly described below.

<u>Dominant Actions</u>

1. <u>Approach</u>.--One fish swims in the direction of another, usually slowly, although the approach may be more rapid. The fish approached may react in several ways, but does not flee.

2. <u>Drive</u>.--One fish chases another, usually rapidly. A drive may appear to begin as a rapid approach, but differs from that action in that the second fish flees and is pursued.

3. <u>Turning toward</u>.--A fish may turn in the direction of another fish without actually approaching it, but merely pivoting on its axis while remaining in place.

4. <u>Nip</u>.--One fish bites another. The nips may be directed at any part of the body, but are most frequently given on the fins or caudal peduncle. Repeated nipping usually results in ragged fins and may even dislodge scales and cause open wounds.

5. <u>Opercle spread</u>.--With a short, rapid approach, the fish extends its opercula laterally. A short backing up usually follows. The purpose of this action is apparently to attempt to intimidate the opponent by making the head appear larger and bringing the prominent black opercular tabs into view.

6. <u>Fight</u>.--Greenberg (1947) and Hunter (1963) both described the fighting behavior of the green sunfish. Here, the total pattern will be divided into two major components,

with the term "fight" applying only to the actual contact between the two fish. One of the fish seizes the mouth of the other in its jaws, and the pair circle in this position. The fins are fully extended and the caudal peduncle is arched to the side, giving evidence of the extreme tension of the body. Little damage is apparently done to either fish in this type of contact. Conceivably, a large fish might be able to injure a much smaller one, but if there were such a size discrepancy, the two fish would most likely not be fighting. The smaller would have shown submission. The significance of mouth fighting seems to be intimidation.

7. Challenge.--This constitutes the other major component of the fighting pattern. One fish approaches another, stops short, and with fins fully extended and body tense, tilts its dorsum away from the opponent and rocks from side to side on its long axis. The rocking motion very closely resembles tail-beating as reported for other species (Neil, 1964; Miller, 1964), in which waves of water are directed at the opponent's head. The challenge appears to be an invitation to fight, since if the opponent responds with the same behavior, mouth-fighting usually follows immediately. A challenge is not always followed by a fight, however. The second fish may ignore repeated challenges. In a typical situation, if a dominant fish is placed in a strange tank having an established hierarchy, the resident alpha will soon challenge the newcomer, and if ignored, will

challenge repeatedly until the newcomer finally responds either by submission or by returning the challenge. In the latter case, the dominance relationship is then settled by mouth-fighting.

8. Ram.--One fish swims rapidly toward another and violently bumps into it, frequently nipping at the same time. This behavior is usually directed at the caudal peduncle, although it may be directed at any part of the body. Scales are frequently dislodged by ramming, and breaks in the skin may also result. The omega fish is the usual object of ramming, and may sustain injuries serious enough to contribute to or cause its death. (Stress may also be considered a factor in the death of an omega.)

9. Raking side.--One fish swims past another, scraping its jaws against the side of the second as it passes. This behavior seldom occurs.

10. Fin raise.--The dorsal fin is raised in direct response to the action of another fish. This differs from a raised fin as a warning signal in that it is in response to a specific act and is not usually maintained. The raised fin as a warning signal appears to be a general fear response and is usually maintained for a long period.

11. Swimming over.--One fish swims over another, brushing its ventral side against the lowered dorsal fin of the second.

12. Swimming under.--One fish swims under another, brushing its lowered dorsal fin against the venter of the second. Swimming over and under are not frequently noted. Perhaps they are a means of harassing a subordinate.

13. Shove.--One fish pushes another out of the way.

The following actions were seen in connection with the experiments using models, described later.

14. Backing up.--The fish backs up slowly while facing the model (or conceivably, an opponent). This could be considered a semi-dominant action, since the retreat does indicate fear to some degree, but the maintenance of visual contact indicates aggression. If the fish were genuinely afraid, it would turn and flee.

15. Maintaining the body in a position perpendicular to the model (or opponent).--A challenge sometimes follows such an action.

16. Maintaining the body in a position parallel to the model (or opponent).--A challenge sometimes follows this action also.

17. Tilting away.--This appears to be the start of a challenge, but goes no farther than the original tilting. Fins are fully extended.

Submissive Actions

1. Fleeing.--One fish swims rapidly away from another. Fleeing is always the response given to a drive, but may be the response to other dominant actions also.

2. Moving away.--One fish moves out of the way at the approach of another. Usually the movement is not hurried, and the distance moved is only a few centimeters.

3. Avoiding.--A fish does not allow another to come near it, but rather moves away before the approacher gets close.

4. Tilt.--A fish tilts its dorsum toward (or sometimes away from) another which is approaching it, swimming over it, or swimming under it. All fins are folded. This activity was observed fairly often as a response of lower-ranking to higher-ranking fish, but infrequently of higher-ranking toward lower-ranking fish. For this reason, it is believed to be an indicator of submission.

5. Hiding.--One fish eludes another by concealing itself.

6. Retiring to corner.--The submissive fish retreats to a corner, usually the one customarily occupied. This behavior may be shown by an otherwise dominant fish, but since it essentially represents a retreat to familiar territory, it is categorized as submissive.

7. Head up.--With all fins folded, the submissive fish assumes a position at an angle with the horizontal.

The extent of the angle assumed appears to increase with the degree of persecution suffered by the fish. An extremely frightened and battered omega may be completely vertical, and often occupies a very small space in a corner.

8. Head down.--As in head up, this action denotes extreme submission, and the degree of the angle appears to increase with the degree of submissiveness, ranging from a very slight inclination to vertical. Head down occurs less frequently than head up.

9. Jerking.--In response to a nip or some other dominant action, the submissive fish moves a few millimeters out of place. The movement is rapid, and the fish usually returns immediately to the former position.

The following actions were observed in connection with the experiments with models.

10. Moving ahead of.--This differs from fleeing only in that the retreat is not rapid.

11. Passively being pushed by the model.

In addition to the above is the category of no response, where a fish gives no visible response to the action directed toward it by another.

Coloration in the Green Sunfish

Coloration in the green sunfish is, in some respects, difficult to classify. Instead of distinct patterns that are readily distinguishable from each other, these fish display a continuum of coloration ranging from pale to dark, with each phase grading into the next. Tranquilli (unpublished) and McDonald et al. (1968) dealt with this problem by using categories of light, intermediate, and dark. An effort is made here to be more specific. It must be kept in mind, however, that any attempt to classify completely the coloration of green sunfish will be arbitrary to some extent due to the intergrading phases. In Table 1, the whole range of coloration is divided into nine phases, based upon four aspects: ground color, iris color, and the presence or absence of vertical barring and of fin spots.

The lightest ground color is pale, translucent green, which then begins to grade into brown. The brown becomes gradually darker with each phase, finally ending with black in Phase 9.

Iris color may be red, black, colorless, white, yellowish-white, or gray. In red iris, which is associated with dominance (Greenberg, 1947), an inverted triangle of black appears at the top. The red grows increasingly distinct and vivid as aggression increases, often becoming brilliant in a fish that is, for example, winning a fight. Black iris is associated with submissiveness. As submissiveness increases, the iris becomes darker; and finally the entire eye appears to be solid black. At some stage before this extreme is reached, a distinct ring of white may appear around the pupil. Colorless, white, yellowish-white, and gray seem to be a continuum that falls between red and

Table 1. The range of coloration in the green sunfish.

	Phase	Ground color (including fins, except for pectorals)	Iris Color	Barring	Fin Spots
Light	1	Pale translucent green	Always red	None	None
	2	Very light brown (or pinkish brown); may have greenish cast	Nearly always red	None	None, or dorsal fin spot
	3	Medium to golden brown; may have greenish cast	Usually red	None	None, or dorsal fin spot; may have anal fin spot also
Intermediate	4	Medium brown	Usually red, or colorless or white	Light	Usually with dorsal fin spot; may have anal fin spot also
	5	Medium brown	Usually red or black	Distinct, but not heavy	Usually with dorsal fin spot; may have anal fin spot also
	6	Dark brown, gray, or gray-brown	Usually red	None, or indistinct or partial barring, merging with ground color	Usually with dorsal fin spot; may have anal fin spot also
Dark	7	Medium to dark brown; may have olive cast	Nearly always black	Heavy	Usually with dorsal and anal fin spots
	8	Dark brown	Nearly always black	Heavy black bars alternating with yellowish bars	Usually with dorsal and anal fin spots
	9	Black	Nearly always black	Jet black bars alternating with silver gray bars; rarely with none	Usually with dorsal and anal fin spots

black. The lighter colors are associated with dominance and gray, which grades into black, with submissiveness.

Absence of barring is characteristic of the lighter color phases (1, 2 and 3), but sometimes occurs in the intermediate phases (4, 5 and 6) also. Barring is characteristic of the intermediate and dark phases, and is present in the latter with one exception: Phase 9 may consist of solid black. Barring first appears in Phase 4, where it is usually very light and often indistinct. The bars gradually grow heavier and darker, culminating in jet black. In the intermediate phases and in Phase 7, the interstitial bars are the same color as the ground. In Phase 8, the melanin granules in these interstitial bars begin to aggregate, and a yellowish color appears which is probably due to xanthophores. This aggregation continues as Phase 8 grades into Phase 9, until the melanin is completely contracted. Coloration due to other chromatophores also diminishes, and the silvery appearance (sometimes with a purple iridescence) of the interstitial bars is then due to guanophores. The number of vertical black bars varies among individuals, but usually from six to eight are present, each approximately three to five millimeters wide. The interstitial bars may be of similar width or narrower.

Two fin spots may occur in the green sunfish. One appears on the soft-rayed portion of the dorsal fin, while the other is on the anal fin. Both are directly adjacent to the body. Both may appear and disappear quickly, first showing as indistinct black marks which become darker as melanin granules disperse. The dorsal fin spot is directly associated with social activity. The anal fin spot may or may not be present in the darker phases, and in this study, did not seem to be related to sociality.

The above color characteristics are evidently under nervous control in green sunfish, since they may change very quickly. In their natural environment, for example, fish were observed to change from Phase 4 to Phase 6, or vice versa, within 15 seconds.

Some color characteristics of the fish do not change. At all times, the pectoral fins remain transparent, pale greenish-brown--almost colorless. Also, there are permanent jagged blue lines on the side of the head. The opercular tabs are black with a posterior edging of salmon pink.

Since each phase grades into the next, arbitrariness cannot be altogether avoided. Nevertheless, there are certain features which serve to separate the different phases. Translucence is found only in Phase 1. Phases 2 and 3 are similar, but the latter is characterized by a darker ground. Phase 4 includes the same ground color as Phase 3, but light barring is present. In Phase 5, the ground is still intermediate, and barring becomes heavier and distinct. Phase 6 was seen only in the field, usually in fish that were resting over a dark substrate. In Phase 7, heavy black bars alternate with dark brown bars. The alternate bars are yellowish in Phase 8 and silvery in Phase 9.

Almost any combination of iris color and fin spots may occur in the various phases. In Phase 1, the iris is always red and fin spots are always absent. Otherwise, fin spots are usually absent in the lighter phases, while the dorsal fin spot is usually present in the intermediate and dark phases. Iris color is usually red in the lighter and intermediate phases and is usually black in the darker. The colorless-to-gray continuum begins to appear in Phase 2, becomes more frequent in the intermediate range, and disappears by Phase 8.

The dark coloration associated with submissiveness may also be shown by fish that are sick, injured, frightened, or in any way disturbed. A dominant, healthy fish that is undisturbed by its surroundings is characteristically light or intermediate in color.

During the breeding season, adult male green sunfish show white or yellowish-white borders on the dorsal, caudal, anal, and pelvic fins. In a large fish (e.g. 15-18 centimeters), these borders may be three to four millimeters wide. Among fish kept in the laboratory for this study, the fin borders began to appear in mid-January, becoming more distinct as spring approached. They persisted until mid-October, gradually fading. Sexually immature fish (under approximately eight centimeters) may also show white fin borders, but never to the extent found in adult males. Aside from the above, there is no difference in coloration between males and females.

Coloration and Social Behavior

Until recently, there has been little specific information in the literature on the social significance of coloration in green sunfish, although some work has been done with other species. Breder and Coates (1935) and Tavolga (1956) reported that coloration plays no part in sex recognition in, respectively, the guppy, *Lebistes reticulatis*, and the goby, *Bathygobius soporator*. Barlow (1967) noted colorations associated with spawning in the South American leaf fish, *Polycentrus schomburgkii*. In 1959, he observed that *Badis badis* showed particular colorations associated with fright, aggression, territoriality, and the parental state. Braddock and Braddock (1955) observed color changes related to fighting in *Betta splendens*, and Allee (1952) noted that fighting behavior in fish may be accompanied by intensified pigmentation. For the yearling kamloops trout, *Salmo gairdneri kamloops*, dark colors have a stronger releasing value for aggressive attack than do bright colors, although spotting of fins and color patterns do not seem to be involved. (Stringer and Hoar, 1955). According to Clark (1950), *Cantherus pullus* shows color

Figure 1. A green sunfish in Lawrence Lake, Phase 4

Figure 2. A laboratory fish, almost black, with white fin borders

changes related to the psychological and physiological state of the fish. Robins, Phillips and Phillips (1959) reported color changes in the pike blenny, *Chaenopsis ocellata*, in connection with "being disturbed." Newman (1956) reported that in the brook trout, *Salvelinus fontinalis*, and in the coastal rainbow trout, *Salmo gairdneri*, dominant fish are light and subordinate fish are dark in color. Greenberg (1947) reported the same for green sunfish. According to Neil (1964), the opposite is true for *Tilapia mossambica*. In a study of the pumpkinseed, *Lepomis gibbosus* (*Eupomotis gibbosus*), Noble (1934) observed that the bright colors of the male are primarily intimidating devices designed to scare away other males and, perhaps, to attract females.

It is important to emphasize that, with the exception of Neil's work, none of the studies cited above specifically concerned the coloration of fishes. Rather, the observations on color were recorded as minor or even incidental information.

Greenberg (1947) has provided the most explicit information to date on the coloration of green sunfish as correlated with their behavior. According to his observations, the dorsal fin spot darkens and lightens with apparent excitation or lack of it. An active fighter almost always has fin spots, but loses them quickly if he loses a fight. Greenberg also noted that the iris of the fish became more prominently red during an encounter, and was generally the sign of a dominant fish. A black iris, on the other hand, was reported to be the sign of a submissive fish. Females and subordinates showed vertical barring.

More recently, data have been gathered which basically support Greenberg's findings. Hunter (1963) reported that an extremely frightened green sunfish shows vertical barring. McDonald and Kessle (1968) and McDonald et al. (1968) found dark and light coloration associated with submissiveness and dominance, respectively. Tranquilli (unpublished) found the same. None of Tranquilli's dominant fish, however, showed red iris. Instead, the iris was yellowish-white.

Many questions have arisen in the studies cited above and in others, as well as from my own observations. The work reported here was designed to provide answers to those listed below.

1. Evidence suggests a correlation between dominance and light coloration and between submissiveness and dark coloration. Does this relationship hold true for specific actions? Certain actions, for example, can be designated as more aggressive than others. Is a dominant fish more brightly colored for the more highly aggressive ones?

2. What is the specific relationship between color and position in the social hierarchy? Is an alpha fish

always brightly colored and an omega always dark? What coloration is associated with intermediate positions?

3. How does color relate to territoriality?

4. How does color related to breeding activity?

5. What might be considered the coloration of an "undisturbed" green sunfish--one in its natural environment, unaffected by social interactions?

6. Coloration in other fishes has been shown to have signal value. Is this also true for coloration in green sunfish? If so, what is the signal value? What is the significance and relative importance of ground color, iris color, barring, and fin spots?

While at least partial answers are suggested by the findings reported here, many other questions remain unanswered. Each should be the basis of a future study.

MATERIALS AND METHODS

Laboratory observations and experiments were conducted at two locations: (1) Gull Lake Laboratory, Kellogg Biological Station (Michigan State University), Hickory Corners, Michigan, during the summers of 1968, 1969, and 1970; and (2) Michigan State University, East Lansing, Michigan, during the period of October, 1971 through March, 1972. Each is described separately below.

1. The general procedure was the same for each of the three summers at Gull Lake Laboratory. Two or three 20-gallon aquaria were prepared with marl, sediment, and plant material from Lawrence Lake, the site of field observations (see below). Each tank held three to five centimeters of marl and sediment plus assorted macrophytes. Small clumps of spike rush (*Eleocharis sp*.), bulrush (*Scirpus acutus*), pondweed (*Potamogeton illinoiensis*), and stonewort (*Chara vulgaris*) were used. In addition, each tank was provided with an outside charcoal filter, an air supply, and a hardware cloth cover. Water for the tanks came from Gull Lake, which, like Lawrence Lake, is alkaline and contains much marl.

Adult green sunfish 13.8 to 17.7 cm. long, mostly males, were obtained from Lawrence Lake and maintained in groups of three or, occasionally, in groups of two. The fish were fed several times per week on freshly caught insects (mostly mayflies and orthopterans) and on earthworms.

The water temperature in the tanks usually varied between 19 and 26 degrees C., the same range generally found in the field observation area. In 1970, however, extremely hot weather caused the water temperature at both laboratory and field observation areas to rise to 30 degrees C. for a period of several days. This coincided with an outbreak of fungus disease which killed all of the laboratory fish. All materials that had come into contact with the diseased fish were then discarded, sterilized with a strong bleach solution, or autoclaved, and the tanks were prepared again. New fish, all adult males, were obtained from a farm pond in Barry County, Michigan. There was no further difficulty with the disease.

In 1968, brown paper coverings were kept over the tanks during non-observation periods to minimize disturbances from people entering and leaving the laboratory. This practice was discontinued after a few weeks, when there were fewer people using the area. It then became apparent that the fish were not disturbed by passers-by, and the paper covers were not used at all thereafter except during the experiments with models described below.

The purpose of the preliminary observations was to suggest hypotheses, while that of the general observations was to provide as much information as possible concerning the general social behavior and coloration of the fish. In order to stimulate activity, the hierarchies that developed were frequently manipulated by reorganizing the groups, removing fish, or adding new fish brought in from the field.

Observations were made in the morning, late afternoon, and early evening, during which the observer sat at a distance of three to four meters from the tanks and recorded data in a notebook. Observation periods varied in length from 14 to 66 minutes.

2. Observations and experiments conducted in East Lansing used fish from two sources, which will be referred to as Groups A and B. The fish of Group A, obtained from the Limnological Research Laboratory at the university, varied in length from 8.2 to 8.5 cm., and were of undetermined sex. They had been seined from a pond in East Lansing and maintained in a holding tank with other green sunfish of assorted sizes for some time prior to this study, and were presumably well-adapted to laboratory conditions. Those of Group B, mostly males and ranging in length from 12.5 to 18.0 cm., were obtained from a dealer in Norman, Oklahoma. Unfortunately, fish of the same size as those in Group A had been expected, and the tanks that had been prepared were thus too small. Larger ones, however, were

not available, and Group B fish were maintained in 10-gallon tanks. This, together with the probable disturbance caused by transportation, undoubtedly contributed to the fact that the fish of Group B never did adapt to the laboratory as well as did those of Group A. They required a longer time to "settle down" and to establish hierarchies (16 days, for some, as opposed to two days for Group A fish), and most of them remained generally dark in color throughout the period of observation.

Aside from the difference in the size of the tanks relative to the size of the fish, both groups were maintained under similar conditions, and at no time were fish of the two groups intermingled. Stock fish were kept in 20-gallon holding tanks, and fish under observation were kept in groups of four in 10-gallon tanks. All tanks had a slate bottom except one (glass bottom), which was placed on a black surface. Each tank was filled with dechlorinated tap water and was supplied with air, an outside charcoal filter, and a glass cover. Broken flower pots, rocks, and pieces of slate provided hiding places in the holding tanks. No structures were provided in the observation tanks. Visual barriers were placed between adjacent tanks to prevent fish from responding to others not in their own groups. Fish in tanks on both sides of an aisle, however, could see each other. These were watched carefully to determine whether any interactions occurred across the aisle. Apparently they did not. The fish were fed daily on mealworms; beef heart; or trout chow, a balanced, dry food.

Due to poor natural lighting in the laboratory, an artificial photoperiod of 15 hours of light and 9 hours of darkness was provided by five 100-watt incandescent lamps. Water temperature in the tanks varied between 19 and 24 degrees C.

A. Hierarchical groups of four fish each.--Ten hierarchies using fish of Group A and 10 using fish of Group B were maintained in 10-gallon tanks. Each was observed for 60 minutes. Data were recorded in a notebook by the experimenter, who sat at a distance of one to three meters from the tank. The longer distance was used wherever possible, but could not be used for tanks adjoining the aisle. Fortunately, green sunfish are usually more interested in each other than in a human observer, and the proximity of the observer did not seem to disturb them.

The hierarchical position of each fish was determined as follows: the number of dominant actions received plus the number of submissive actions given were subtracted from the number of dominant actions given, and the resulting scores were compared. The fish having the highest score was designated as the alpha fish, the one with the next highest score as the beta fish, etc. In cases where scores were identical or nearly so (i.e., one to two points difference), the fish involved were given identical ratings. One fish, which did not enter into the hierarchical relationship of its group (neither gave nor received any actions), was not rated. Only those groups which showed a distinct hierarchy with four social positions were included in the statistical analysis.

B. Territories.--Only a few observations on territoriality and coloration could be obtained, since green sunfish prefer to establish territories behind and under things, which makes it nearly impossible to observe their coloration accurately. In bare tanks without any obscuring structure, the fish can be easily seen, but do not readily form territories.

On four occasions, two fish in a hierarchy were seen to be territorial. In each case, after the hierarchy had been observed, the other fish were removed and the remaining ones, still territorial, were observed for 60 minutes. Also, pairs of fish of equal size (or nearly so) were placed in separate tanks (10-gallon) in the hope that they might become territorial. Of eight such attempts, two were successful. In all, six territorial pairs were observed. Other territorial situations occurred only when an alpha fish became despot and claimed the entire tank as a territory.

Along with the results of the above observations, notes will also be included on a territorial pair observed for 30 minutes in a laboratory at Evergreen Park, Illinois. These fish, 8.0 and 8.4 cm. long and of undetermined sex, were obtained from a slough in the Palos Woods Division of the Cook County Illinois Forest Preserve and were maintained in an eight-gallon, slate-bottom tank with air supply and glass cover. One case of territoriality not connected with breeding was observed at Lawrence Lake, and is also described.

C. Experiments with models.--Models were used to determine whether particular colorations elicited specific behavior patterns, possibly to learn aspects of the signal value of these colorations. A fish from Group A was used to make a plaster mold, from which clay models were then made. After firing, each model was fitted with a handle of coathanger wire approximately .5 meter in length, and was painted (except as noted) with non-gloss enamel. The finished models, 8.5 cm. long, were as follows:

1. Unpainted control: Uniformly pinkish-brown.

2. Black control: Uniformly black.

3. White control: Uniformly white.

4. Alpha-I: Light golden brown all over with black dorsal fin spot, red iris, and black pupil.

5. Alpha-II: Uniformly pinkish-brown (unpainted) except for black dorsal fin spot, red iris, and black pupil.

6. Submissive: Dark brown all over, superimposed with six black vertical bars on each side, and with black pupil.

7. Omega: Black all over, superimposed with five silver vertical bars on each side.

Figure 3 shows the seven models.

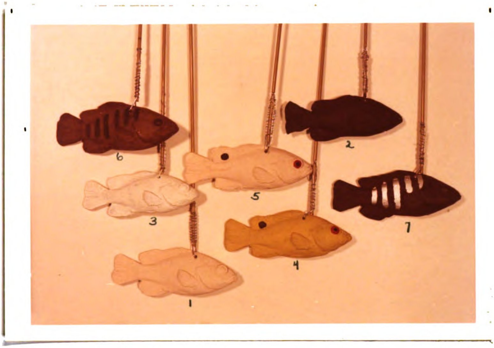

Figure 3. Models

Three experiments were conducted with the alpha fish of 20 hierarchies.

<u>Experiment I</u>: Sixteen animals from Group A, 8.2 to 8.5 cm. long, were assembled into four groups of four and placed in the experimental tanks (10-gallon). Each group had at least one fish of 8.5 cm. length, so that the alpha fish would be the same size as the models, or if smaller, would find the model to be no larger than its own subordinate companions. Within two days, hierarchies were well-established and the alpha fish was determined by careful

observation. Tests were then conducted over a period of eight days, after which the tanks were emptied, cleaned, and refilled.

Experiment II: Twenty animals from Group A, all 8.5 cm. long, were assembled into five groups of four and placed in the experimental tanks. Again, within two days, hierarchies were established, and the alpha fish were determined by observation. Tests were conducted over a period of five days.

The alpha fish were then removed and the remaining fish rearranged to form new groups. Each new group consisted of fish which had not previously been together (except in the holding tank) and was placed in a tank not previously occupied by any of the fish in that group. Three new groups were thus established, and hierarchies again formed within two days. The alpha fish were determined by observation, and tests were conducted over a period of five days. The tanks were then emptied, cleaned, and refilled, and three more were added.

Experiment III: Thirty-two animals from Group B, ranging in size from 12.5 to 17.0 cm., were assembled into eight groups of four and placed in experimental tanks. Five days later, one hierarchy had begun to form, but all were not established until 16 days had elapsed. Testing was begun with four groups as soon as the alpha individuals could be determined. The remaining four groups took somewhat longer to become organized, and the beginning of testing was delayed accordingly. The tests covered a period of five days for each fish.

The test procedure was the same for all three experiments except where noted. Each fish was tested in its home tank, with the order of the tests randomized to minimize any effects of learning. A minimum of six hours elapsed between tests.

In preparation for a test, subordinates were removed and placed in a separate tank or container. A paper cover was taped to the front of the tank to prevent the fish from seeing the experimenter. To prevent them from seeing the model being placed into or removed from the water, an opaque plastic partition was set into the tank and the model was placed on the side opposite the fish.

When the paper cover, partition, and model had been placed, the fish was allowed a 10-minute acclimation period to overcome any excitement that may have occurred due to the preparation. Then the partition was carefully removed, and the position and coloration of the fish were noted (also the time). The actual testing period lasted two minutes, after which the partition was replaced, the model removed, and the water temperature read. Subordinates were then returned to the tank.

The tests were of three types:

1. Advancing model: The model was kept moving toward the fish for the entire two-minute period.

2. Stationary model: The model was held motionless in a natural position about one centimeter from the bottom of the tank, for the entire two-minute period. The distance from the fish varied according to the position of the fish when the partition was removed.

3. Retreating model: The model was kept moving away from the fish as much as possible during the two-minute period. When bringing the model back in the direction of the fish, care was taken to approach the fish indirectly. (Due to the difficulty involved in maintaining a consistent retreat period from one test to the next, this test was not used in Experiments II and III. Also, the results obtained with retreating models in Experiment I are not reported here, as the inconsistent test periods precluded statistical comparison.)

During the two-minute testing period, the behavior and any color changes of the fish were recorded on tape. All records were later transcribed into a notebook.

For Experiment I, the models used were unpainted control, alpha-I, submissive, and omega. Because the unpainted control appeared to elicit more aggression than did the other models, it was decided to use a modified version of it for the alpha model in Experiment II. The models used for that experiment were alpha-II, submissive, omega, black control, and white control. Experiment III was essentially a repetition of Experiment II, but the fish were larger than the models instead of the same size.

Irregularities: In two of the groups in Experiment I, the omega fish was killed by the alpha before the end of the series of tests. Each dead fish was removed as soon as discovered, and the remaining three were left as they were. Since the position of the alpha was not changed by the reduction of the number of subordinates, neither dead fish was replaced.

Two of the fish in Experiment II developed an unidentified growth on the fins. As far as it was possible to determine, this had no effect upon their behavior. Both continued to eat regularly, maintained their usual coloration, and continued their usual level of aggression toward subordinates. Therefore, the growth was not considered to interfere with the testing.

Both fish were treated for the fin growth once or twice daily by immersion for 10-15 seconds in a 1:15,000 solution of malachite green (three days) or methylene blue (four days). To allow maximum time for recovery, the treatment was given immediately after a test session. No effects were noted on either the fish or the fin growth.

Field Observations

Field observations were conducted during July-August, 1968 and 1969, and during May-August, 1970, at Lawrence Lake, Hickory Corners, Michigan (Barry County, TIN, R9W, S27; see Figure 3). Lawrence Lake is a marl, alkaline lake with an area of 4.9 hectares and a circumference of approximately 960 meters. Its maximum depth is 12.6 meters. The observation area was located at the East end of the lake, where a marl shelf extends approximately 15 meters out from the "shore." "Shore" is interpreted as the abrupt ending of the vegetation surrounding the lake. Vegetation at the East end of the lake includes cattails (*Typha latifolia*), bulrushes (*Scirpus acutus* and *S. americanus*), marsh cinquefoil (*Potentilla fruticosa*), and rushes (*Juncus spp.*). Most of the area is covered with spike rush (*Eleocharis sp.*), which grows in large, partially submerged clumps. While the edge of the sedge growth is considered to be the shore proper of the lake, the water extends back into the vegetation for some distance. The spaces between clumps of rushes provide chambers through which fish can swim in water only 15-20 cm. deep. In the observation area of the lake itself, there is a sparse growth of *Scirpus acutus*, bushy pondweed (*Najas guadalupensis*), stonewort (*Chara vulgaris*), and pondweeds (*Potamogeton alpinus* var. *tenuifolius*, and some *P. illinoiensis*). The marl shelf is gray in color, but is

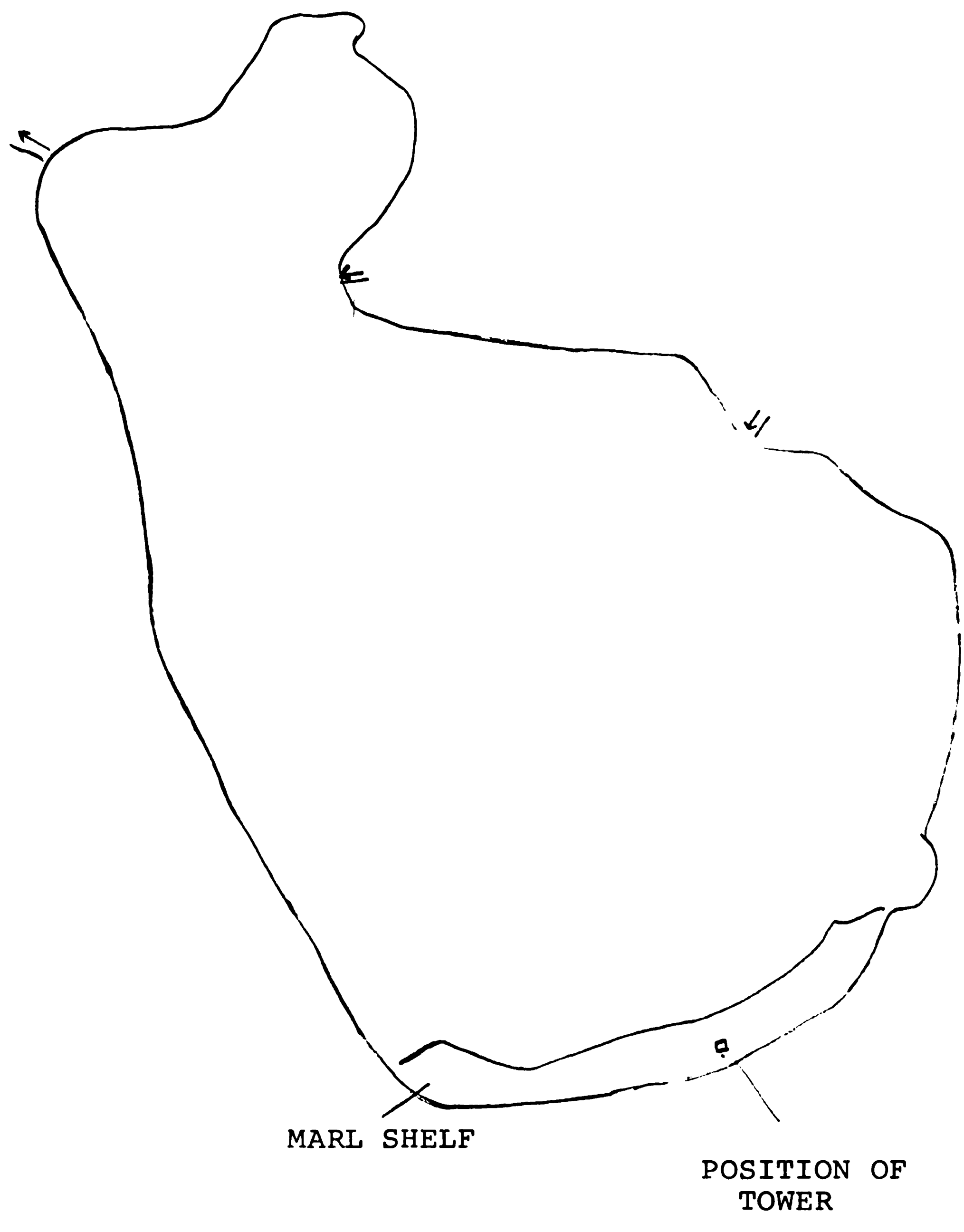

Figure 3. Lawrence Lake

covered with a sediment consisting largely of diatoms of many kinds, which give it a light brown color. The water over the shelf is very clear.

An observation tower (see Figure 5)[4] was placed two to three meters from the edge of the sedge growth as indicated in Figure 4, and left for nine days or longer without being used. This permitted the fish to become accustomed to the tower and to accept it as part of their natural environment. The tower was approached by entering the lake at a point about 50 meters to the North and walking along the shelf about three meters from the shore. Splashing and quick movements were carefully avoided. The observer wore the same type of clothing and carried the same equipment each time (except once, as noted below), and the fish apparently became accustomed very quickly to the approach of a human being. They remained in the area or soon returned if they were frightened away.

With the exception of females observed during the breeding season in 1970, only mature males were observed. These were readily identified as such by means of their nuptial coloration of white fin borders, which persisted throughout the observation period each year. A population study of the green sunfish in Lawrence Lake has apparently

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[4]Cross supports are shown on one side only, for simplification of the drawing, but were provided on all sides except that on which the ladder was located.

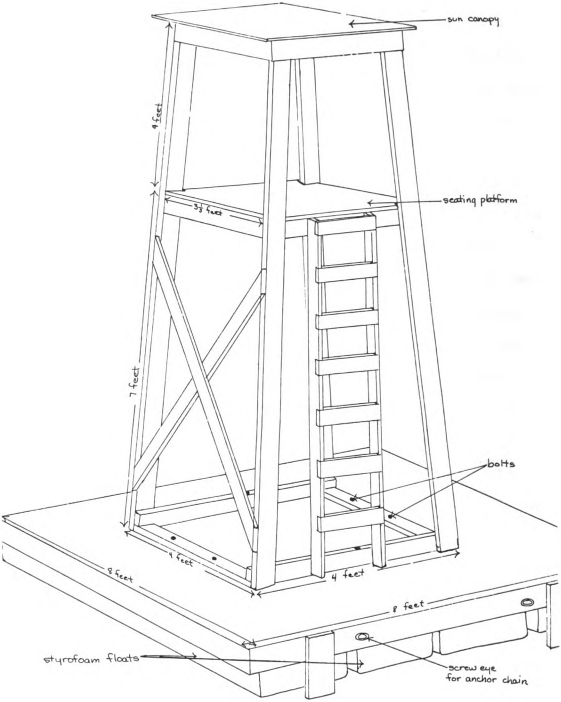

Figure 5. Observation tower.

never been undertaken. It seems probably, however, that green sunfish are not numerous in the lake. Except during the breeding season, those seen in the observation area were almost exclusively fully grown males, approximately 15-18 cm. long.

For identification, individuals were caught with a hook and line and tagged with brightly colored plastic ovals attached with thin, twisted-nylon cord.[5] With a curved needle, the cord was drawn through the dorsal muscle of the fish and back through the base of the dorsal fin membrane, then through an eyelet in the end of the plastic oval, and knotted securely. By varying the color and the placement of the tags, it was possible to observe several individuals at the same time. The fish were returned to the water immediately after tagging. An area of maximal pigment dispersion about three cm. in diameter could be seen around the needle punctures and also where the fish had been hooked when caught. These areas remained dark for a few days, until the wounds healed. Other darkened areas noted after a fish had been tagged proved to have even shorter duration. The tags apparently did not affect the fish, since no behavioral or coloration differences were noted between tagged and untagged individuals. One of the fish tagged in 1968 still

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[5]With thanks to Dr. Peter I. Tack, Department of Fisheries and Wildlife, Michigan State University, for supplying tags and information on their use.

bore its tag when seen the following summer. The tag was in good condition, although loosely attached and faded in color. The punctures had healed well and the fish seemed oblivious to the tag.

One of the fish observed during the breeding season could not be caught for tagging. It is suspected that it had been caught and tagged in a previous year. This fish was much larger than most that were seen, however, and its size, together with the individuality of its fin markings, enabled positive identification. Other breeding males were tagged, and after being replaced in the water, returned to their nests immediately. Breeding females were not tagged. Ten males were observed.

General observations were made each summer, and observations on breeding and pre-breeding activity were conducted during May-June, 1970. Data were recorded in a notebook while the observer sat on the platform of the tower. Binoculars and sunglasses with polarized lenses enabled close observation of coloration. At one time, the observer entered the water with mask and snorkel, in order to check underwater on the coloration as seen from above. There did not appear to be any discrepancy in what could be seen from above or below the water surface.

Two groups of four tagged fish were observed in a semi-natural situation in the lake, enclosed in a three-meter diameter fence made of half-inch hardware cloth.

Food obtained naturally by the enclosed fish was supplemented periodically with freshly caught insects.

Observations were usually made in the early afternoon, when the sun's angle permitted greatest visibility. Length of observation periods varied, depending on weather conditions, but a total of 44 hours was logged.

RESULTS

A. The sections on behavior of the green sunfish and coloration in the green sunfish summarized.

B. Hierarchical groups: the relationship between coloration and behavior. Tables 2-7.

The data for Group A were obtained from 40 fish, and those for Group B, from 28 fish. Where the observed values for ground color and barring were identical, they are presented in the same table. Expected values and deviations are not given where there were no responses or very few total responses, both to permit good fit in the tables and because the significance of such results is obvious in any case.

In Tables 4, 6, 10, and 14, low-intensity dominant behavior includes approaching, shoving, and raising the dorsal fin. Moderately high-intensity behavior includes driving, nipping, and spreading the opercula. Challenging, ramming, and fighting constitute high-intensity dominant behavior. In Tables 5, 7, 11, and 15, fleeing is considered high-intensity submissive behavior, while all other submissive actions are grouped together as low-intensity behavior.

Table 2. Number of actions at each coloration, Group A.

	Ground Color, Barring L-N	I-Lt	D-H	Σ	Iris Color R	W	B	Σ
Observed values					Observed Values			
dom.	888	690	296	1874	1580	74	220	1874
subm.	7	60	766	833	28	5	800	833
total	895	750	1062	2707	1608	79	1020	2707
Expected Values					Expected Values			
dom.	619.6	519.2	735.2		1113.2	54.6	706.0	
subm.	275.4	230.8	326.8		494.8	24.4	314.0	
Deviations					Deviations			
dom.	268.4	170.8	-439.2		466.8	19.4	-486.0	
subm.	-268.4	-170.8	439.2		-466.8	-19.4	486.0	

Null Hypothesis: Group A fish showed light, intermediate or dark ground color; and no barring, light barring or heavy barring with equal frequency.

Dominant: $P\{\chi^2 \geqslant 290.77\} < .001$, df = 2; highly significant; rejected.

Submissive: $P\{\chi^2 \geqslant 1293.34\} < .001$ df = f; highly significant; rejected.

Total: $P\{\chi^2 \geqslant 54.03\} < .001$, df = 2; highly significant; rejected.

Null Hypothesis: Group A fish showed red, white or black iris with equal frequency.

Dominant: $P\{\chi^2 \geqslant 2208.64\} < .001$, df = 2; highly significant; rejected.

Submissive: $P\{\chi^2 \geqslant 1474.87\} < .001$, df = 2; highly significant; rejected.

Total: $P\{\chi^2 \geqslant 1318.46\} < .001$, df = 2; highly significant; rejected.

	Ground Color L	I	D	Σ	Barring N	Lt	H	Σ	Iris Color R	W	B	Σ
	Observed values				Observed Values				Observed Values			
dom.	0	594	170	764	4	590	170	764	506	66	192	764
subm.	0	10	468	478	0	10	468	478	3	3	472	478
total	0	604	638	1242	4	600	638	1242	509	69	664	1242
	Expected Values				Expected Values				Expected Values			
dom.		371.5	392.5			368.3	391.7		313.1	42.5	408.4	
subm.		232.5	245.5			231.7	246.3		195.9	26.5	255.6	
	Deviations				Deviations				Deviations			
dom.		222.5	-222.5			221.7	-221.7		192.9	23.5	-216.4	
subm.		-222.5	222.5			-221.7	221.7		-192.9	-23.5	216.4	

Null Hypothesis: Group B fish showed light, intermediate, and dark ground color with equal frequency.

Dominant: $P\{\chi^2 \geq 734.98\} < .001$, df = 2; highly significant; rejected.
Submissive: $P\{\chi^2 \geq 897.28\} < .001$, df = 2; highly significant; rejected.

Total: $P\{\chi^2 \geq 622.39\} < .001$, df = 2; highly significant; rejected.

Null Hypothesis: Group B fish showed no barring, light barring and heavy barring with equal frequency.

Dominant: $P\{\chi^2 \geq 716.45\} < .001$, df = 2; highly significant; rejected.
Submissive: $P\{\chi^2 \geq 897.28\} < .001$, df = 2; highly significant; rejected.

Total: $P\{\chi^2 \geq 610.80\} < .001$, df = 2; highly significant; rejected.

Null Hypothesis: Group B fish showed red, white, and black iris with equal frequency.

Dominant: $P\{\chi^2 \geq 403.25\} < .001$, df = 2; highly significant; rejected.
Submissive: $P\{\chi^2 \geq 920.36\} < .001$, df = 2; highly significant; rejected.

Total: $P\{\chi^2 \geq 460.27\} < .001$, df = 2; highly significant; rejected.

Where color differences occurred, light ground color, no barring, and red iris were clearly associated with dominant behavior. Group B fish did not show light ground color at all, and showed absence of barring only a few times, but still showed lighter coloration, including red or white iris, for dominant behavior than for submissive behavior. Dark ground color, heavy barring, and black iris were clearly associated with submissive behavior.

Table 4. Number of actions at each of three intensity levels, Group A.

	Ground Color, Barring				Iris Color			
	L-N	I-Lt	D-H	Σ	R	W	B	Σ
	Observed Values				Observed Values			
low	358	253	129	740	587	46	107	740
mod. high	488	402	123	1013	914	27	72	1013
high	42	35	44	121	79	1	41	121
	Expected Values				Expected Values			
low	350.6	272.5	116.9		623.9	29.2	86.9	
mod. high	480.0	373.0	160.0		854.1	40.0	118.9	
high	57.4	44.5	19.1		102.0	4.8	14.2	
	Deviations				Deviations			
low	7.4	-19.5	12.1		-36.9	16.8	20.1	
mod. high	8.0	29.0	-37.0		59.9	-13.0	-46.9	
high	-15.4	-9.5	24.9		-23.0	-3.8	26.8	

Table 5. Number of submissive actions at each of two intensity levels, Group A.

	Ground Color, Barring				Iris Color			
	L-N	I-Lt	D-H	Σ	R	W	B	Σ
	Observed Values				Observed Values			
low	4	32	304	340	14	3	323	340
high	3	28	462	493	14	2	477	493
	Expected Values				Expected Values			
low		24.4	311.6		11.4		325.6	
high		35.6	454.4		16.6		474.4	
	Deviations				Deviations			
low		7.6	-7.6		2.6		-2.6	
high		-7.6	7.6		-2.6		2.6	

Table 6. Number of dominant actions at each of three intensity levels, Group B.

	Ground Color				Barring				Iris Color			
	L	I	N	Σ	N	Lt	H	Σ	R	W	B	Σ
	Observed Values				Observed Values				Observed Values			
low	0	169	73	242	1	168	73	242	121	27	94	242
mod. high	0	382	85	467	2	380	85	467	347	35	85	467
high	0	43	12	55	1	42	12	55	38	4	13	55
	Expected Values				Expected Values				Expected Values			
low		188.1	53.9			187.1	53.9		160.3	20.9	60.8	
mod. high		363.1	103.9			361.0	104.0		309.3	40.3	117.4	
high		42.8	12.2			41.9	12.1		36.4	4.8	13.8	
	Deviations				Deviations				Deviations			
low		-19.1	19.1			-19.1	19.1		-39.3	6.1	33.2	
mod. high		18.9	-18.9			19.0	-19.0		37.7	-5.3	-32.4	
high		.2	-.2			.1	-.1		1.6	-.8	-.8	

Table 7. Number of submissive actions at each of two intensity levels, Group B.

	Ground Color, Barring				Iris Color			
	L-N	I-Lt	D-H	Σ	R	W	B	Σ
	Observed Values				Observed Values			
low	0	3	278	281	0	0	281	281
high	0	7	170	197	3	3	191	197

Although Group B fish did not show the same degree of light coloration as did those of Group A, the data for Group B still indicate a tendency for coloration to be lighter as the intensity of dominant behavior increases. Coloration was darker for low-intensity actions. The data for Group A, however, do not show the same pattern. For low-intensity actions, the fish were darker in color more often than expected, but they were also darker more often than expected for high-intensity actions, and were light in color less often than expected. These seemingly confusing results are more easily understood when the social positions of the fish are considered (see Table 12, below). The high intensity activity performed by alpha and beta fish (62.8% of the total) was accompanied by lighter coloration (light or intermediate ground color, no barring or light barring, and red iris), while that performed by gamma and delta (omega) fish was accompanied by dark coloration.

C. Hierarchical groups: the relationship between coloration and social position. Tables 8-15.

Ten fish in each social position provided the data for Group A, while seven fish in each social position provided data for Group B. Again, where the observed values for ground color and barring were identical, they are presented in the same table. Expected values and deviations are not given in Tables 11, 13, 14 and 15, and in parts of other tables where too few data were available for rows and/or columns.

Table 8. Number of dominant actions shown by fish in each social position, Group A.

	Ground Color, Barring					Iris Color		
	L-N	I-Lt	D-H	Σ	R	W	B	Σ
	Observed Values					Observed Values		
α	656	530	35	1221	1122	49	50	1221
β	230	130	33	393	343	25	25	393
γ	2	24	175	201	109	0	92	201
δ	0	6	53	59	6	0	53	59
	Expected Values					Expected Values		
α	578.6	449.6	192.8		1028.8		143.2	
β	186.2	144.7	62.1		323.0		45.0	
γ	95.2	74.0	31.8		176.4		24.6	
δ	28.0	21.7	9.3		51.8		7.2	
	Deviations					Deviations		
α	77.4	80.4	-157.8		93.2		-93.2	
β	43.8	-14.7	-29.1		20.0		-20.0	
γ	-93.2	-50.0	143.2		-67.4		67.4	
δ	-28.0	-15.7	43.7		-45.8		45.8	

Table 9. Number of submissive actions shown by fish in each social position, Group A.

	Ground Color				Iris Color			
	L-N	I-Lt	D-H	Σ	R	W	B	Σ
	Observed Values				Observed Values			
α	2	0	0	2	2	0	0	2
β	3	4	40	47	3	0	44	47
γ	2	40	221	263	22	0	241	263
δ	0	16	505	521	1	5	515	521
	Expected Values							
β		3.2	40.8					
γ		19.0	242.0					
δ		37.8	483.2					
	Deviations							
β		.8	-.8					
γ		21.0	-21.0					
δ		-21.8	21.8					

Table 10. Number of dominant actions shown by fish in each social position, Group B.

	Ground Color				Barring				Iris Color			
	L	I	D	Σ	N	Lt	H	Σ	R	W	B	Σ
	Observed Values				Observed Values				Observed Values			
α	0	557	128	685	4	553	128	685	506	32	147	685
β	0	35	28	63	0	35	28	63	0	33	30	63
γ	0	0	4	4	0	0	4	4	0	0	4	4
δ	0	2	10	12	0	2	10	12	0	1	11	12
	Expected Values				Expected Values				Expected Values			
α		542.1	142.9			538.2	142.8		463.4	59.5	162.1	
β		49.9	13.1			49.8	13.2		42.6	5.5	14.9	
	Deviations				Deviations				Deviations			
α		14.9	-14.9			14.8	-14.8		42.6	-27.5	-15.1	
β		-14.9	14.9			-14.8	14.8		-42.6	27.5	15.1	

Table 11. Number of submissive actions shown by fish in each social position, Group B.

	Ground Color, Barring				Iris Color			
	L-N	I-Lt	D-H	Σ	R	W	B	Σ
	Observed Values				Observed Values			
α	0	0	0	0	0	0	0	0
β	0	0	38	38	0	0	38	38
γ	0	7	131	138	3	0	135	138
δ	0	3	299	302	0	3	299	302

According to the data in Tables 8 and 9, fish which held higher positions in the social hierarchy showed a clear tendency toward light or intermediate ground color, no barring or light barring, and red iris. Dark ground color, heavy barring, and black iris were shown by fish holding lower social positions. The same pattern appeared in Group B fish. Even though these did not show light ground color at all, and showed absence of barring only infrequently, the alpha and beta fish were still lighter in color than were the gamma and delta fish.

The pattern continued to hold true when different intensity levels of activity are considered (see Tables 12-15). Alpha and beta fish tended to remain light in color and retain red iris, while gamma and delta fish tended to remain dark in color with black iris, regardless of the type of intensity of activity.

Table 12. Number of dominant actions shown by fish in each social position at low, moderately high, and high intensities, Group A.

	Ground Color, Barring				Iris Color			
	L-N	I-Lt	D-H	Σ	R	W	B	Σ
				Low Intensity				
	Observed Values				Observed Values			
α	244	172	21	437	376	28	33	437
β	112	62	23	197	159	18	20	197
γ	2	14	61	77	47	0	30	77
δ	0	5	24	29	5	0	24	29
	Expected Values				Expected Values			
α	211.4	149.4	76.2		346.6	27.2	63.2	
β	95.3	67.4	34.6		156.3	12.2	28.5	
γ	37.3	26.3	13.4		61.1	4.8	11.1	
δ	14.0	9.9	5.1		23.0	1.8	4.2	
	Deviations				Deviations			
α	32.6	22.6	-55.2		29.4	.8	-30.2	
β	16.7	-5.4	-11.3		2.7	5.8	-8.5	
γ	-35.3	-12.3	47.6		-14.1	-4.8	18.9	
δ	-14.0	-4.9	18.9		-18.0	-1.8	19.8	
				Moderately High Intensity				
	Observed Values				Observed Values			
α	394	334	13	741	703	21	17	741
β	94	61	8	163	154	6	3	163
γ	0	7	88	95	57	0	38	95
δ	0	6	53	59	0	0	14	14
	Expected Values				Expected Values			
α	341.8	285.7	113.5		677.1		42.9	
β	75.2	62.9	24.9		147.6		9.4	
γ	43.8	36.6	14.6		89.3		5.7	
δ	27.2	22.8	9.0					
	Deviations				Deviations			
α	52.2	48.3	-100.5		25.9		-25.9	
β	18.8	-1.9	-16.9		6.4		-6.4	
γ	-43.8	-29.6	73.4		-32.3		32.3	
δ	-27.2	-16.8	44.0					

Table 12 (cont'd.)

	Ground Color, Barring L-N	I-Lt	D-H	Σ	Iris Color R	W	B	Σ
				High Intensity				
	Observed Values				Observed Values			
α	18	24	1	43	43	0	0	43
β	24	7	2	33	30	1	2	33
γ	0	3	26	29	5	0	24	29
δ	0	1	15	16	1	0	15	16
	Expected Values				Expected Values			
α	15.0	12.4	15.6		28.3		14.7	
β	11.4	9.6	12.0		21.1		10.9	
γ	10.0	8.4	10.6		19.1		9.9	
δ	5.6	4.6	5.8		10.5		5.5	
	Deviations				Deviations			
α	3.0	11.6	-14.6		14.7		-14.7	
β	12.6	-2.6	-10.0		8.9		-8.9	
γ	-10.0	-5.4	15.4		-14.1		14.1	
δ	-5.6	-3.6	9.2		-9.5		9.5	

Table 13. Number of submissive actions shown by fish in each social position at low and high intensities, Group A.

	Ground Color, Barring				Iris Color			
	L-N	I-Lt	D-H	Σ	R	W	B	Σ
	Low Intensity							
	Observed Values				Observed Values			
α	0	0	0	0	0	0	0	0
β	1	4	20	25	1	0	24	25
γ	2	19	100	121	12	0	109	121
δ	0	9	184	193	0	3	190	193
	High Intensity							
α	0	0	0	0	0	0	0	0
β	2	0	20	22	2	0	20	22
γ	0	21	121	142	10	0	132	142
δ	0	7	321	328	1	2	325	328

Table 14. Number of dominant actions shown by fish in each social position at law, moderately high and high intensities, Group B.

	Ground Color				Barring			
	L	I	D	Σ	N	Lt	D	Σ
	Low Intensity							
	Observed Values				Observed Values			
α	0	159	54	213	1	158	54	213
β	0	8	10	18	0	8	10	18
γ	0	0	3	3	0	0	3	3
δ	0	2	6	8	0	2	6	8

Iris Color

	R	W	B	Σ
	Observed Values			
α	121	19	73	213
β	0	7	11	18
γ	0	0	3	3
δ	0	1	7	8

Table 14. (cont'd.)

	Ground Color L	I	D	Σ	N	Barring Lt	D	Σ
	Moderately High Intensity							
	Observed Values					Observed Values		
α	0	359	66	425	2	357	66	425
β	0	23	18	41	0	23	18	41
γ	0	0	0	0	0	0	0	0
δ	0	0	1	1	0	0	1	1

Iris Color

	R	W	B	Σ
α	347	13	65	425
β	0	22	19	41
γ	0	0	0	0
δ	0	0	1	1

High Intensity

	L	I	D	Σ	N	Lt	D	Σ
	Observed Values					Observed Values		
α	0	39	8	47	1	38	8	47
β	0	4	0	4	0	4	0	4
γ	0	0	1	1	0	0	1	1
δ	0	0	3	3	0	0	3	3

Iris Color

	R	W	B	Σ
	Observed Values			
α	38	0	9	47
β	0	4	0	4
γ	0	0	1	1
δ	0	0	3	3

Table 15. Number of submissive actions shown by fish in each social position at low and high intensities, Group B.

	Ground Color, Barring					Iris Color		
	L-N	I-Lt	D-H	Σ	R	W	B	Σ
				Low Intensity				
	Observed Values					Observed Values		
α	0	0	0	0	0	0	0	0
β	0	0	28	28	0	0	28	28
γ	0	3	91	94	0	0	94	94
δ	0	0	159	159	0	0	159	159
				High Intensity				
α	0	0	0	0	0	0	0	0
β	0	0	10	10	0	0	10	10
γ	0	4	40	44	3	0	41	44
δ	0	3	140	143	0	3	140	143

D. Experiments with models

Very little dominant activity and virtually no submissive activity was shown toward stationary models. Because so few responses were made, the results are not presented here, except in Tables 18, 21, and 24, where responses toward stationary and advancing models are combined.

Table 16. Activity shown toward advancing models, Experiment I.

	α	S	ω	C	Σ
dom.	33	52	42	80	207
subm.	49	53	43	28	173
total	82	105	85	108	380

Table 16. (cont'd.)

	α	S	ω	C	Σ

Null Hypothesis: There was no difference in the amount of activity shown toward each model.

Dominant: $P\{\chi^2 \geq 24.06\} < .001$, df = 3; highly significant; rejected.

Submissive: $.02 < P\{\chi^2 \geq 8.34\} < .05$, df = 3; significant; rejected.

Total: $.10 < P\{\chi^2 \geq 5.66\} < .20$, df = 3; not significant; accepted.

The total amount of activity shown toward each model did not differ significantly among the models. For dominant and submissive behavior considered separately, however, significant differences did occur. Table 17 below lists the probabilities found when the models are compared more closely.

Significantly more activity of both kinds was shown toward the unpainted control model than toward the others combined. The submissive and omega models, considered together, elicited significantly more dominant behavior than the alpha-I model did.

In Table 18 below, the activities are grouped according to level of intensity. The data indicate that there were highly significant differences in the amount of activity elicited by the models at different intensity levels.

Table 17. Comparison of models, Experiment I.

	α-I + S + ω vs C
dom.	$P\{\chi^2 \geq 34.80\} < .001$, df = 1; highly significant
subm.	$P\{\chi^2 \geq 16.25\} < .001$, df = 1; highly significant
	α-I vs S + ω
dom.	$.02 < P\{\chi^2 \geq 4.91\} < .05$, df = 1; significant
subm.	$.80 < P\{\chi^2 \geq .03\} < .90$, df = 1; not significant
	S vs ω
dom.	$P\{\chi^2 \geq 1.07\} < .30$, df = 1; not significant
subm.	$.30 < P\{\chi^2 \geq 1.05\} < .50$, df = 1; not significant

Table 18. Kinds of responses shown toward stationary and advancing models, Experiment I

Observed Values	α-I	S	ω	C	Σ
backing up	15	25	14	37	91
turning toward, approach	4	11	5	5	25
tilting away, maintaining perpendicular or parallel position	20	17	23	42	102
challenge, opercle spread, nip	1	11	4	0	16
Σ	40	64	46	84	234
moving away or ahead of, avoiding	24	22	23	21	90
retiring to corner	4	13	20	6	43
fleeing	21	18	0	1	40
Σ	49	53	43	28	173

Expected Values	α-I	S	ω	C
backing up	16.3	22.1	17.5	35.1
turning toward, approach	4.5	6.1	4.8	9.6
tilting away, maintaining perpendicular or parallel position	18.2	24.8	19.7	39.3

Table 18. (cont'd.)

	Observed Values			
	α-I	S	ω	C
moving away or ahead of, avoiding	25.5	27.5	22.4	14.6
retiring to corner	12.2	13.2	10.7	6.9
fleeing	11.3	12.3	9.9	6.5
	Deviations			
	α-I	S	ω	C
backing up	-1.3	2.9	-3.5	1.9
turning toward, approach	-.5	4.9	.2	-4.6
tilting away, maintaining perpendicular or parallel position	1.8	-7.8	3.3	2.7
moving away or ahead of, avoiding	-1.5	-5.5	.6	6.4
retiring to corner	-8.2	-.2	9.3	-.9
fleeing	9.7	5.7	-9.9	-5.5

None of the deviations in Table 18 are particularly large, but a pattern is suggested. If the order in which the rows are listed is considered the order of increasing intensity, the submissive model elicited more behavior of lower intensity than expected. The omega model elicited more behavior of higher intensity than expected. The control model proved to elicit more dominant behavior at all intensity levels than did the others, and more than expected at two levels. A significantly greater amount of low-intensity submissive behavior was also shown toward the control model than toward the others. Less activity of both kinds than expected was shown toward the alpha-I model, except at high intensity levels.

Table 19 presents data from Experiment II. For both dominant and submissive activity, significant differences occurred in the number of responses shown toward each model. Total responses were also significantly different, although at a lower level. Table 20 lists the probabilities found when the models are compared more closely.

Table 19. Activity shown toward advancing models, Experiment II.

	α-II	S	ω	Bk	W	Σ
dom.	201	242	201	103	119	866
subm.	32	48	56	135	112	383
total	233	290	257	238	231	1249

Null Hypothesis: There was no difference in the amount of activity shown toward each model.

Dominant: $P\{\chi^2 \geqslant 81.66\} < .001$, df = 4; highly significant; rejected

Submissive: $P\{\chi^2 \geqslant 103.07\} < .001$, df = 4, highly significant; rejected

Total: $.02 < P\{\chi^2 \geqslant 9.78\} < .05$, df = 4; significant; rejected

Table 20. Comparison of models, Experiment II.

	α-II + S + ω vs Bk + W
dom.	$P\{\chi^2 \geqslant 99.0\} < .001$, df = 1; highly significant
subm.	$P\{\chi^2 \geqslant 108.57\} < .001$, df = 1; highly significant
	α-II vs S + ω
dom.	$.10 < P\{\chi^2 \geqslant 2.09\} < .20$, df = 1; not significant
subm.	$.001 < P\{\chi^2 \geqslant 9.53\} < .01$, df = 1; significant
	S vs ω
dom.	$.02 < P\{\chi^2 \geqslant 9.53\} < .05$, df = 1; significant
subm.	$.30 < P\{\chi^2 \geqslant .63\} < .50$, df = 1; not significant
	Bk vs W
dom.	$.20 < P\{\chi^2 \geqslant 1.16\} < .30$, df = 1; not significant
subm.	$.10 < P\{\chi^2 \geqslant 2.12\} < .20$, df = 1; not significant

Table 21. Kinds of responses shown toward stationary and advancing models, Experiment II.

	Observed Values					
	α-II	S	ω	Bk	W	Σ
backing up	87	70	101	60	71	389
turning toward, approach	7	8	16	4	10	45
tilting away, maintaining perpendicular or parallel position	75	117	92	37	48	369
challenge, opercle spread nip	41	55	13	6	2	117
Σ	210	250	222	107	131	920
tilting toward, being passively pushed	0	4	8	50	41	103
moving away or ahead of, avoiding	11	23	29	50	47	160
retiring to corner	22	21	20	31	12	106
fleeing	0	0	0	5	12	17
Σ	33	48	57	136	112	386

Table 21. (cont'd.)

	α-II	S	ω	Bk	W
	Expected Values				
backing up	88.8	105.7	93.9	43.5	55.4
turning toward, approach	10.3	12.2	10.9	5.2	6.4
tilting away, maintaining perpendicular or parallel position	84.2	100.3	89.0	42.9	52.5
challenge, opercle spread, nip	26.7	31.8	28.2	13.6	16.7
tilting toward, being passively pushed	9.2	13.4	15.9	36.6	27.9
moving away or ahead of, avoiding	14.3	20.8	24.7	56.8	43.4
retiring to corner	9.5	13.8	16.4	37.6	28.7
	Deviations				
backing up	-1.8	-35.7	7.1	14.7	15.6
turning toward, approach	-3.3	-4.2	5.1	-1.2	3.6
tilting away, maintaining perpendicular or parallel position	-9.2	16.7	3.0	-5.9	-4.5
challenge, opercle spread, nip	14.3	23.2	-15.2	-7.6	-14.7
tilting toward, being passively pushed	-9.2	-9.4	-7.9	13.4	13.1
moving away or ahead of, avoiding	-3.3	2.2	4.3	-6.8	3.6
retiring to corner	12.5	7.2	3.6	-6.6	-16.7

The deviations in Table 21 indicate that the alpha-II and submissive models elicited more high-intensity dominant behavior than expected as well as more submissive behavior of moderately high intensity. Fewer low-intensity responses were shown toward these models than were expected. The omega model received more low-intensity dominant responses followed the same pattern as for the alpha-II and submissive models.

Although the black control model received fewer dominant and more submissive responses than the white model, the pattern of deviations is generally the same for both. More responses of lower intensity and fewer of high intensity were elicited when compared with the expected values.

Table 22. Activity shown toward advancing models, Experiment III.

	α-II	S	ω	Bk	W	Σ
dom.	157	159	172	142	135	765
subm.	251	256	172	330	358	1367
total	408	415	344	472	493	2132

Null Hypothesis; There was no difference in the amount of activity shown toward each model.

Dominant: $.20 < P\{\chi^2 \geqslant 5.61\} < .30$, df = 4, not significant; accepted

Submissive: $P\{\chi^2 \geqslant 78.45\} < .001$, df = 4; highly significant; rejected

Total: $P\{\chi^2 \geqslant 32.30\} < .001$, df = 4; highly significant; rejected

There was no significant difference in the amount of dominant behavior shown toward each of the five models. They did differ significantly, however, in the amount of submissive behavior elicited.

Table 23 lists the probabilities found when the models are compared more closely with regard to submissive responses.

Table 23. Comparison of models, Experiment III.

α-II + S + ω vs Bk + W

P $\{\chi^2 \geqslant 72.84\} < .001$, df = 1; highly significant

α-II vs S + ω

P $\{\chi^2 \geqslant 588.92\} < .001$, df = 1; highly significant

S vs ω

P $\{\chi^2 \geqslant 1648.83\} < .001$, df = 1; highly significant

Bk vs W

P $\{\chi^2 \geqslant 114.09\} < .001$, df = 1; highly significant

Table 24. Kinds of responses shown toward stationary and advancing models, Experiment III.

	α-II	S	ω	Bk	W	Σ
backing up	87	95	80	82	93	437
turning toward, facing, approach	4	2	3	3	3	15
tilting away, maintaining perpendicular or parallel position	68	62	89	59	42	320
challenge, opercle spread, nip	1	1	2	0	0	4
Σ	160	160	174	144	138	776
tilting toward, being passively pushed, other movement	39	44	40	72	81	276
moving away or ahead of, avoiding	104	103	85	145	172	609
retiring to corner	33	56	8	76	69	242
fleeing, bumping into wall	78	54	41	40	39	252
Σ	254	257	174	333	361	1379

Null Hypothesis: There was no difference in the amount of activity shown at each of four intensity levels for dominant activity.

Table 24. (cont'd.)

	α=II	S	ω	Bk	W

P $\{\chi^2 \geq 737.39\} < .001$, df = 3; highly significant; rejected

Null Hypothesis: There was no difference in the amount of activity shown at each of four intensity levels for submissive activity.

P $\{\chi^2 \geq 656.15\} < .001$ df = 3; highly significant; rejected

Expected Values

	α-II	S	ω	Bk	W
backing up	89.5	90.6	97.6	81.4	77.9
tilting away, maintaining perpendicular or parallel position	65.5	66.4	71.4	59.6	57.1
tilting toward, being passively pushed, other movement	50.8	51.5	34.8	66.7	72.2
moving away or ahead of, avoiding	112.2	113.5	76.9	147.0	159.4
retiring to corner	44.6	45.1	30.5	58.4	63.4
fleeing, bumping into wall	46.4	46.9	31.8	60.9	66.0

Deviations

	α-II	S	ω	Bk	W
backing up	2.5	-4.4	17.6	-.6	-15.1
tilting away, maintaining perpendicular or parallel position	-2.5	4.4	-17.6	.6	15.1
tilting toward, being passively pushed, other movement	-11.8	-7.5	5.2	5.3	8.8
moving away or ahead of, avoiding	-8.2	-10.5	8.1	-2.0	12.6
retiring to corner	-11.6	10.9	-22.5	17.6	5.6
fleeing, bumping into wall	31.6	7.1	9.2	-20.9	-27.0

The probabilities listed in Table 23 show that the black and white control models elicited more submissive behavior than did the models which were colored more naturally. The white model received more submissive actions than the black model did. Among the more natural models, more submissive responses were shown toward the alpha-II model than toward the submissive and omega models. The omega model elicited significantly fewer responses than did the submissive model.

Although the differences in the total number of dominant responses shown toward each model were not significant, when responses of different intensities are compared, significance is found. Comparing the pattern of deviations in Table 24 with those in Table 21 (Experiment II), the alpha-II model shows the same pattern for submissive responses but a reverse one for dominant responses. The submissive model shows the same pattern as before: fewer responses of low intensity and more of high intensity than expected. The pattern is reversed for dominant responses shown toward the omega model. The latter also received more submissive responses than expected in all categories except "retiring to corner," where there were fewer than expected.

For the control models, the distribution of submissive responses was the same in both experiments if the low deviation of -2.0 (moving away, etc.) is disregarded. More responses of low intensity and fewer of high intensity were received than were expected. A reverse pattern was found for dominant responses.

E. The Relationship Between Coloration and Territoriality.

Table 25 presents the data obtained from the six territorial pairs that were observed for 60 minutes each.

Table 25. Number of actions at each coloration, territorial fish.

	Ground Color, Barring				Iris Color			
	L-N	I-Lt	D-H	Σ	R	W	B	Σ
approach	53	83	0	136	131	1	4	136
nip	1	0	0	1	1	0	0	1
opercle spread	5	39	0	44	44	0	0	44
challenge	0	2	0	2	2	0	0	2
fin raise	4	11	0	15	12	0	3	15
total	63	135	0	198	190	1	7	198
moving away	10	8	0	18	17	1	0	18
other movement	0	2	0	2	1	1	0	2
total	10	10	0	20	18	2	0	20

From these data, it is clear that the fish assumed light coloration and red iris, which are associated with dominance, during nearly all of their activity. Their coloration was like that of the alpha fish in a hierarchy, and like alpha fish, they showed little submissive behavior.

The territorial pair observed for 30 minutes at Evergreen Park, Illinois, showed similar coloration: intermediate ground color, light barring, and red iris for all activity. Their activity consisted almost entirely of mutual approaches and spreading of the opercula.

One clear case of territoriality that was not connected with nesting activity was observed in Lawrence Lake. Fish No. 3 was tagged on July 12, 1968, and when released, assumed a position behind a post in front of the observation tower (Point A; see Figure 6). From time to time he was seen in the area driving green sunfish away. The territory apparently claimed by No. 3 is delineated in Figure 3. It extended under the raft also, but it was not possible to determine how far. No. 3 was absent from the territory on July 23, when another green sunfish was tagged and released in the area. The new fish went immediately to Point A, which was No.3's usual resting place. Five minutes later, No. 3 returned and drove away the intruder. Thereafter, he drove away all fish that entered the territory during the remainder of the observation period. The next day, however, No. 3 was not seen in the area, nor was he seen at all after July 23.

At all times, No. 3 maintained light or intermediate ground color, no barring or light barring, and red iris. His dorsal fin spot was usually vivid, and his bars intensified during drives. In short, his coloration was much like that of the territorial fish in the laboratory.

F. The Relationship Between Coloration and Breeding

Table 26 combines the actions of six tagged male green sunfish that were observed for varying lengths of time. The total observation time was 14 hours.

Almost no activity was accompanied by light ground color and absence of barring, but most of the dominant activity did involve intermediate ground color rather than dark, and red iris rather than black. Most of the submissive activity was accompanied by dark ground color, heavy barring, and black iris, as was true of laboratory fish.

While females approaching the nests were almost always driven away, occasionally a male would guide a female to the nest when she came close enough. During this activity, the male was usually dark in color, but had a prominently red iris. During spawning, the male often became as dark as the female, but again, the red iris of the male was very bright, in sharp contrast to the black iris of the female. (Females generally assumed extremely dark coloration, from dark ground and heavy barring to black-and-silver.

After spawning, most of the activity of the nesting males consisted of leaving the nest temporarily as though to go out "looking for intruders" (which usually did not materialize), returning to the nest, and fanning the eggs. During this activity, the fish generally showed intermediate ground color, light barring, and red iris.

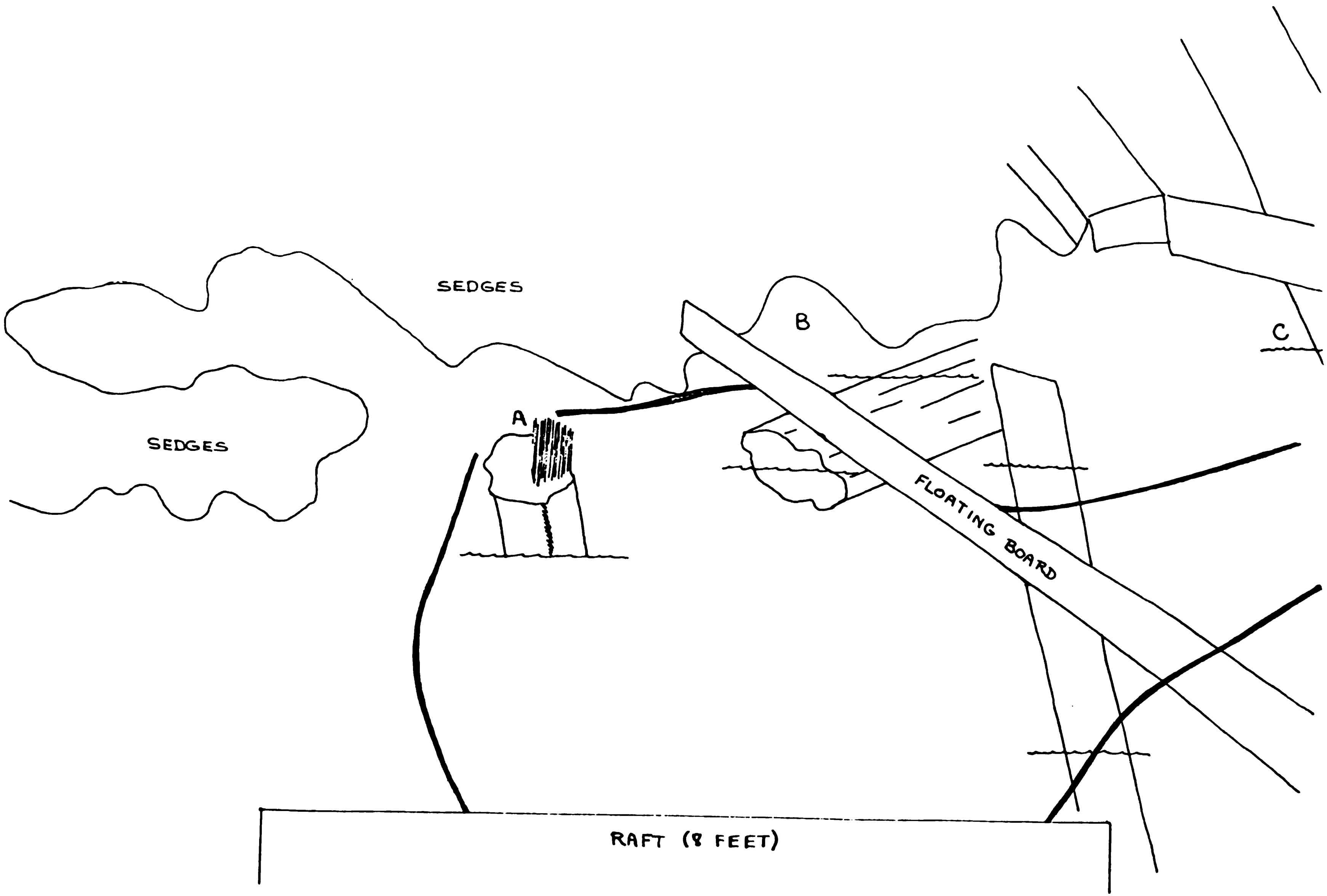

Figure 6. Territory claimed by fish no. 3.

Table 26. Number of actions at each coloration, breeding fish.

	Ground Color, Barring				Iris Color			
	L-N	I-Lt	D-H	Σ	R	W	B	Σ
approach	0	42	2	44	5	0	39	44
drive	0	87	60	147	143	0	4	147
nip	0	1	3	4	4	0	0	4
opercle spread	0	90	41	131	130	0	1	131
enter territory of another	0	6	3	9	5	0	4	9
enter nest of another	0	1	0	1	1	0	0	1
circle	0	6	2	8	6	0	2	8
shove	0	1	0	1	1	0	0	1
challenge	0	2	0	2	2	0	0	2
total	0	236	111	347	297	0	50	347
guide female to nest	0	4	13	17	17	0	0	17
spawn	0	19	35	54	51	0	3	54
total	0	23	48	71	68	0	3	71
leave nest	2	337	37	376	350	0	16	376
return to nest	3	357	54	414	393	0	21	414
fan eggs	0	581	25	606	530	0	76	606
circle in nest	0	3	2	5	5	0	0	5
total	5	1278	118	1401	1288	0	113	1401
fleeing	1	20	102	123	20	0	103	123
moving away	0	0	2	2	0	0	2	2
other movement	0	1	1	2	1	0	1	2
avoiding	1	2	0	3	3	0	0	3
tilt	0	0	1	1	0	0	1	1
total	2	23	106	131	24	0	107	131

DISCUSSION

The three features of coloration that were chosen for this study were selected because preliminary observation seemed to indicate that they were particularly important relative to the social behavior of the species. Data on the presence or absence of fin spots were not taken, since preliminary observations did not reveal any consistent pattern in their case. Greenberg (1947) reported that the dorsal fin spot faded quickly if a fish lost a fight. This was observed, but on many occasions, an omega fish on the verge of being killed by an alpha had a vivid dorsal fin spot. Greenberg's (1947) decision that the dorsal fin spot is a sign of alertness is probably correct. Work is called for to determine the actual significance of this feature of coloration in green sunfish. A continuation of the experiments with models that were begun in this study may provide an answer.

On the basis of the work of McDonald and Kessle (1968) and McDonald et al. (1968), Greenberg's notations on coloration, and the results of this study, evidence now strongly supports the hypothesis that light coloration is associated with dominance and dark coloration with submissiveness in the green sunfish. The data obtained in this study also indicate a tendency for coloration to become lighter as the intensity of dominant behavior increases, at least in non-breeding fish. It would appear to follow that green sunfish should become darker as the intensity of submissive behavior increases. The data from this study did not bear this out, simply because gamma and delta (omega) fish were almost always extremely dark to begin with, and their coloration could not change as their behavior changed.

Of greater significance is the apparent fact that the social position held by the fish has more influence on its coloration than does the actual behavior. A gamma or delta fish, for example, will occasionally perform some dominant actions, but during these actions will almost always retain its dark coloration. This proved to be true even for highly intensive dominant activity such as challenging or fighting.

Similarly, an alpha fish would be expected to retain its light coloration during submissive activity. This would be difficult to test in a hierarchical group, since alpha fish seldom show submissive behavior. In the experiments with models, however, the fish tested were all of alpha rank, and responded submissively to the advancing models. When they did, they nearly always retained their light coloration if they were light to begin with. This was more evident in the fish from Group A, which were generally lighter in color than those of Group B. It is significant that Group B alpha fish were also lighter in color than their subordinates, and showed red iris for approximately 74% of their activity.

Poor adaptation to the laboratory and maintenance of Group B fish in tanks that were too small for fish of their size are considered the most probable reasons for the difference in coloration between these fish and those of Group A. Group B fish were maintained for several weeks after the conclusion of the experiments, and two alpha fish eventually did become very light. Several others assumed red iris, but retained their dark ground color and barring. Had larger tanks and more time been available, it is predicted that all of the Group B alpha fish eventually would have become light.

A striking difference in coloration was observed between laboratory fish and those in Lawrence Lake. Lake fish all had the coloration of laboratory alpha fish, except when resting over a dark substrate. Even then, the fish were dark brown or gray-brown in color, with red iris. This coloration was not noted in the laboratory fish. It is probably a form of protective coloration, serving to conceal the fish over their dark background. When such fish emerged from their resting places among the rushes and entered the open water above the marl shelf, they paled within 15 seconds to light of intermediate ground color with light barring. Upon returning to the rushes, they darkened again within 15 seconds.

Lake fish being driven by others did not darken, nor did they lose their red iris color. At no time was submissive behavior in lake males accompanied by the dark coloration that is so characteristic of submissive fish in the laboratory. Breeding females, however, did resemble submissive laboratory fish in terms of coloration.

An effort to explain the differences observed between fish in the lake and those in the laboratory brings up interesting possibilities for further study. One obvious difference between the two environments is the greater density of animals in the laboratory. The opportunity for contact between animals is greatly increased, and a submissive fish has nowhere to go to escape the aggression of another. McDonald et al. (1968) suggested that the dark coloration of a submissive fish may be a stimulus that elicits attack. Stringer and Hoar (1955) found this to be true for underyearling kamloops trout.

Several times during this study, however, incidental observations seemed to contradict this. Cases were observed in which a light-colored but submissive fish was continually attacked very severely. When it finally darkened, the aggression subsided to some degree. This suggests that dark coloration may serve as a sign of subordination. Perhaps a socially inferior fish shows the proper degree of "humility" by darkening, and does so because no other alternative is available. In a natural environment, a submissive fish can easily flee from an aggressor. Darkening as a sign of subordination would not be necessary. The dark coloration of females during breeding may be related to this. In order to spawn, a female green sunfish must approach an extremely aggressive male. Perhaps the male's attacks upon the female are subdued somewhat because of her color. Some means should be devised to test this.

The coloration of territorial fish is easily enough explained. Two fish are most likely to become territorial in the laboratory when they are matched in sex, size, and aggression. Both behave as dominant individuals, showing dominant behavior of high intensity and very little submissive behavior, if any. From the results reported above, it is predictable that these fish would show light coloration and red iris.

Non-breeding fish in Lawrence Lake typically showed light or intermediate ground color, light barring, and red iris. No evidence was found of dominance-subordination relationships. Fully grown males were often seen traveling together in groups of two or three, with all of the group members showing typical coloration. If one of these same groups were to be placed in a laboratory, however, it is almost certain that a hierarchy would soon develop and some of the fish would become dark in color. Why does this not happen in the lake? Further work may explain these phenomena.

Spawning males were often indistinguishable from females, except for their brilliant red iris color. The black vertical bars intensified and the interstitial bars became distinctly yellow in both sexes. When spawning ceased, the fish returned to their previous coloration. Barring also often intensified in fish that were vigorously driving others, and became more subdued when the activity ceased. This suggests that the intensification of barring may be related to the degree of excitement experienced by the fish.

Iris color appears to be a more certain indicator of dominance than either ground color or barring. Aggressive fish are almost always light or intermediate in ground color, with little or no barring. They may, however, become very dark. When this occurs, the iris usually remains bright red. Exceptions can usually be attributed to some outside factor such as an unsuitable environment.

Several significant results occurred in the experiments with models. In Experiment I, it became evident even before all of the tests were completed that the fish were reacting aggressively toward the unpainted control model. Perhaps because of its light color it resembled a dominant fish and was taken for a rival by the fish being tested. For this reason, it was decided that the alpha-II model should be a modified version of the unpainted control. A black dorsal fin-spot and eyes with red iris and black pupil transformed the unpainted model into one which the fish might recognize even more readily as a rival. The results seemed to confirm this. Two of the eight fish tested attacked the new model violently.

In Experiment II, the submissive model elicited significantly more dominant behavior than did the alpha-II model, and more submissive behavior was shown toward the submissive and omega models than toward the alpha-II. The fact that the models were advancing toward the fish being tested may explain this. Since submission is not the only cause of dark coloration in green sunfish, a fish which is dark, but which behaves aggressively, may still be recognized as a possible rival.

The one outstanding feature of the black and white models was the amount of submissive behavior they elicited. The fish behaved as though afraid of these models. Perhaps the models presented contradictory stimuli. They were shaped like fish, but were unnaturally colored. As a result, they may have been so alien to the fish being tested that they were regarded as objects to be feared. This hypothesis could be tested by comparing the responses to several naturally colored models with those to several models painted with bright but totally unnatural colors.

Much more work should be done with models. The results of the above experiments indicate some possible lines of investigation, but the data so far are not definite enough to serve as the basis for any conclusions. Tendencies were found, but more data are needed to determine whether these are real or apparent. Specific experiments are needed to discover the aspects of coloration to which the fish actually respond, and their relative significance.

SUMMARY AND CONCLUSIONS

1. Green sunfish were observed at two laboratory locations (Michigan State University) and in the natural environment of Lawrence Lake, Hickory Corners, Michigan, for the purpose of determining the relationship between coloration and social behavior.

2. General observations were made on coloration as it relates to dominance, subordination, territoriality, and breeding.

3. The coloration of fish holding different social positions within a hierarchy was compared, as well as that of fish engaged in different intensity levels of behavior.

4. Dominance in the green sunfish was associated with light or intermediate ground color, no barring or light barring, and red iris. White iris also occurred. Submissiveness was associated with dark ground color, heavy barring, and black iris.

5. Territorial fish in the laboratory and in Lawrence Lake showed dominant coloration.

6. Male green sunfish show nuptial coloration consisting of white borders on the dorsal, caudal, anal, and pelvic fins. In a laboratory environment in this locality,

these appear in mid-January and persist until mid-October, gradually fading. There are no other differences in coloration between males and females except those related to sociality. (Males usually outrank females in hierarchies, and thus the latter are usually submissively colored.)

7. During breeding, males are generally dominantly colored while females show submissive coloration. During actual spawning, both sexes may show intensified barring, and may be indistinguishable (in terms of coloration), except for iris color. The iris of the female is black, while that of the male is bright red. Intensified barring shown by spawning fish (or by individuals that are vigorously driving others) is considered to be an indicator of excitement.

8. Iris color was considered to be a more certain indicator of dominance than either ground color or barring. Dominant fish may show dark ground color and heavy barring, but usually show red iris.

9. The social position held by a green sunfish is apparently more closely related to its coloration than is its actual behavior. A high-ranking fish tends to remain dominantly colored even when acting submissively. Gamma and delta (omega) fish tend to remain submissively colored during dominant activity.

10. There was a tendency for fish to become lighter in color as the intensity level of dominant behavior increases.

A corresponding darkening with increasing intensity of submissive behavior was not noted, since submissive fish are generally extremely dark for all behavior.

11. Experiments with models were conducted to determine whether particular colorations elicited specific behavior patterns. Models colored to resemble alpha, submissive, and omega (extremely submissive) individuals were used. Control models were uniformly black or white or unpainted. Alpha fish were tested in their home tanks.

12. More aggression was shown toward the unpainted control model than toward the naturally colored models. A modified version of the unpainted model was used to represent an alpha fish in subsequent experiments. The new model elicited violent aggression.

13. Stationary models elicited little or no submissive behavior.

14. When advanced toward the fish being tested, the submissive model elicited significantly more dominant behavior, and the submissive and omega models elicited more submissive behavior than did the second alpha model. This suggests that a dark-colored fish that behaves aggressively is recognized as a rival by an alpha fish.

15. The black and white models elicited significantly more submissive behavior than did the naturally colored models. It is suggested that the apparent fear

shown by the fish was due to the unnatural coloration of the control models.

16. Several avenues for possible future investigation are suggested.

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