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Piscivorous Feeding Behavior of Largemouth Bass: An Experimental Analysis

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Abstract

Largemouth bass *Micropterus salmoides* are the dominant top carnivores of many North American lakes and reservoirs and are very popular sport fish, but the actual behavioral mechanisms of their feeding are still poorly known. In laboratory experiments we broke predation into its component parts: location, pursuit, attack, and handling of prey. The distance at which largemouth bass can locate forage fish increases with prey size, with prey motion (when prey are small), and with light intensity. In the pursuit phase of the predation cycle, largemouth bass are more likely to choose prey with large apparent size, closer proximity, or greater motion. When bluegills *Lepomis macrochirus* were the experimental prey, the number of attempted attacks by largemouth bass before the prey was ingested increased with bluegill size, within broad limits. At high light intensities bluegills can locate modest-size largemouth bass (29 cm total length) long before the predators locate them, but at low light intensities, the advantage is reversed.

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The study of predator–prey relationships as they affect energy flow and community structure has been in the forefront of modern research in ecology (Lindeman 1942; Hall 1964; Paine 1969), particularly in the study of zooplankton (Brooks and Dodson 1965; Hall et al. 1970; O'Brien 1979). However, only recently has similar attention beed paid to the feeding behavior of piscivorous fish (Hall and Werner 1977; Savino and Stein 1982). In many North American lakes, the largemouth bass *Micropterus salmoides* is a top predator. Even though the types of organisms that largemouth bass will eat are well documented. little is known about its feeding behavior (Heidinger 1975). In the work reported here, we experimentally studied the influence of prey size, prey species, and ambient light intensity on largemouth bass as they locate fish prey, and also the ability of bluegill prey (*Lepomis macrochirus*) to locate an approaching largemouth bass.

There have been many studies of gut composition of wild largemouth bass (McLane 1947; Dubets 1954; Schneidermeyer and Lewis 1956; Snow 1971; Lewis et al. 1974; Olmstead 1974; Zweiacker and Summerfelt 1974; see Emig 1966 for a summary of earlier studies). Generally, about 50% of the largemouth bass captured have empty stomachs; of those with discernible gut contents, many had eaten shad *Dorosoma* spp. Beyond this, a variety of prey species and sizes has been observed in largemouth bass diets, and few obvious generalities have emerged. Thus, although gut studies may indicate what, and to some extent when, certain prey are eaten, they do not reveal the reasons for diet selection, which may include predator preference, ease of prey capture, or high prey visibility.

Some researchers have used feeding experiments in aquaria or small ponds to overcome some of the problems inherent in gut studies of wild fish. Lewis et al. (1961) found that largemouth bass in small tanks fed more heavily upon golden shiners than on tadpoles or crayfish; in small ponds, however, they preferred tadpoles and crayfish over fish (Lewis and Helms 1964). Espinosa and Deacon (1973) found that largemouth bass in aquaria ate Virgin spinedace *Lepidomeda mollispinis* and salamanders more frequently than golden shiners *Notemigonus crysoleucas* or goldfish *Carassius auratus*. Despite these and similar studies, no one has clearly demonstrated the behavioral mechanisms of largemouth bass predation.

Considerable work has been done relating the size of largemouth bass to the size of the prey it eats. Lawrence (1958) found that the maximum size of prey a largemouth bass would eat is limited only by the spacing between the esophageal cleithrum bones. Tarrant (1960) found that largemouth bass size was positively correlated with preference for the larger of two sizes of green sunfish *Lepomis cyanellus* offered; however, Wright (1970) found no consistent relationship between the sizes of largemouth bass and the forage fish they ate.

Thus there is need for more detailed study in order to understand the mechanisms leading to observed stomach contents and forage preferences of largemouth bass. One approach is to break the act of predation into its component parts according to the model first set forth by Holling (1959) for predation by a mantid, and subsequently used by Elliott et al. (1976) for lions, by Gerritsen and Strickler (1977) for invertebrate planktivores, and by Wright 1981 and Wright and O'Brien (in press) for zooplanktivorous fish. As each predator seeks food, it must locate prey, pursue it, attack it, and capture it. Each of these components has a probability of success. The product of these probabilities predicts the likelihood of any given prey being eaten. Prey can avoid being eaten if they can reduce the probability of just one step in the sequence to near zero; conversly, feeding success of the predator is increased if the product of all the probabilities is maximized. We applied these concepts to our study of largemouth bass.

Methods

Location of Prey

To determine the ability of largemouth bass to locate prey, we measured the predator's reaction distance to different sizes of bluegill, redfin shiner *Notropis umbratilis*, and minnows *Pimephales* spp. A reaction of largemouth bass to a located prey was judged to have occurred when the bass oriented directly at the prey, rotated its eyes so both looked at the prey, and markedly increased its swimming speed. The reaction was judged by an observer positioned along the tank near where the reaction was anticipated, and the precise point of reaction was marked on a centimeter scale along the side of the tank. The distance from this mark to the stationary prey was taken as the reaction distance.

Reaction-distance experiments were conducted in a long narrow aquarium (500 × 58 × 30 cm). One end of the tank was of clear plastic; the other end was expanded and divided into four compartments, each with a sliding door opening to the rest of the tank. Depth of the water varied from 15 to 20 cm. Light was provided by 12, 50-watt fluorescent lights suspended 35 cm above the water surface; lights were wrapped with combinations of grey and black cloth to regulate light intensity. Illuminance was measured at the depth of the prey, generally 5 cm, with an International Light Model IL700 photometer. The water was continuously filtered through diatomaceous earth to keep turbidity low.

Prey fish were spinally pithed and their lengths were measured to the nearest mm. "Motionless" prey were suspended in the tank on a thin piece of wire. "Moving" prey were suspended from an HO scale model train, which ran back and forth across the width of the tank at approximately 25 cm/second. Prey were placed anywhere from 1.5 to 3.5 m from the compartments holding the largemouth bass.

Three largemouth bass, 13, 29, and 35 cm total length (TL), were used to determine the effect of predator size on reaction distance to bluegills of varying size (3.3 to 9.9 cm TL). The 29-cm largemouth bass also was used to determine reaction distance to bluegills at light intensities of 3,340, 103, 5.59, 1.49, and 0.195 lux, and reaction distance to moving and stationary redfin shiners of varying size (3.1 to 7.5 cm TL). To insure a reasonably constant hunger level, we always used largemouth bass that had not eaten within 48 hours of the experiment. The number of trials on any given day depended on the size of prey and predator, but, in general, experimentation was stopped when there was a noticeable bulge in the largemouth bass.

Choice of Prey

A 29-cm largemouth bass was presented with pairs of pithed, motionless bluegills within the reaction distance of predator to prey. "Apparent prey size," a measure of the prey image projected on retina of the predator was calculated as the arc tangent of the ratio of prey length and the distance between the prey and the compartment door.

The effect of motion on prey choice between various sizes of minnows was examined with 13-, 20-, and 30-cm largemouth bass. Pairs of prey were presented, one fish suspended from the train device and the other stationary. The closer prey was moved at some times and the further prey at others.

The data were grouped into 16 classes of 0.25° difference in apparent size. The number of observations per apparent size class ranged from 4 to 23. The lowest numbers of observations were made where differences in apparent size were great and prey choice was one-sided. We made 150 observations when both prey were stationary, and 323 when one prey was moving.

Attack Success

Attack success of largemouth bass was measured in a 244- × 244-cm aquarium in which opaque acrylic plastic sheets formed a circular arena 243 cm in diameter. Water depth was 20–25 cm; light intensity at the surface was 1,200 lux. Largemouth bass were housed in the corners of the tank and had access to the arena through sliding doors. A 20-liter aquarium in one corner of the larger aquarium was used to acclimate bluegill prey to water conditions for at least 24 hours before an experiment.

For each trial, a prey of known length was placed in the arena and left for 5 minutes. A largemouth bass then was allowed access to the arena and its unsuccessful attacks were counted. We considered an attack successful if the predator grasped the prey in any way. A released bluegill always was recaptured immediately. Ten observations per 1-cm prey-size class were made for a 13- and a 22-cm largemouth bass.

Location of Predator by Prey

The distance at which bluegills detected an oncoming largemouth bass was measured in the long tank. For each trial, a bluegill between 3.7 and 10.0 cm was placed in a 20-liter aquarium at one end of the tank and allowed 24 hours to acclimate to given a light intensity. Zooplankton then were added to the aquarium and, when a bluegill was feeding in what appeared to be a normal way, a largemouth bass was released from the far end of the tank. When a bluegill became aware of the largemouth bass, it suddenly stopped feeding and completely extended its dorsal and anal fins. When this response occurred, the distance between predator and prey was measured along the top of the tank. Orientation of prey was not strictly controlled, but the predator was not released unless a bluegill faced across or toward the line of attack. The approach speed of the largemouth bass varied from a slow cruise to a rapid dash. A 29-cm largemouth bass was used at light intensities of 3,340, 103, 5.59, and 1.49 lux (N = 23, 20, 14, 18, respectively); a 13- and a 20-cm predator were used at 3,340 lux (N = 20 and 21, respectively).

Reaction distances of predators and prey were analyzed by a computer program that could compare many regression lines (Howick 1981). This program computed least-squares regression coefficients, calculated the statistics to test for equality of slopes and intercepts to zero, computed an F statistic to test for equality of slopes, and computed Q statistics for Student–Newman–Keuls (SNK) least-significant-range (LSR) pairwise comparisons of slopes and intercepts. Algorithms were derived from Zar (1974).

Results

Location of Prey

The reaction distances of largemouth bass preying on bluegills or redfin shiners in bright light increased linearly with prey size; regression slopes differed significantly between these two prey species (Fig. 1). Predator size did not affect reaction distance of largemouth bass noticeably. Slopes of the reaction-distance versus prey-length regressions for 35-, 29-, and 13-cm largemouth bass all were significantly different from zero (Table 1) but not from each other ($F = 0.95$; df = 2,71; $P > 0.05$); none of the intercepts differed from zero.

Prey motion influenced reaction distances of a 29-cm largemouth bass (Fig. 2). Regression slopes for reaction distance versus prey length differed significantly between moving and stationary redfin shiners. When redfin shiners were small, the largemouth bass reacted from a greater distance to moving than to stationary prey, but the regressions converged as prey size increased. A similar trend was found with moving and stationary bluegills.

Reaction distance of the 29-cm largemouth bass varied with light intensity but only when the two lowest light intensities were used (Table 2). There appeared to be no obvious decline in reaction distance until the light was less than 5 lux (Fig. 3). However, there was considerable variability, particularly with the data collected at 103 lux, such that the slopes of the 5.6-lux

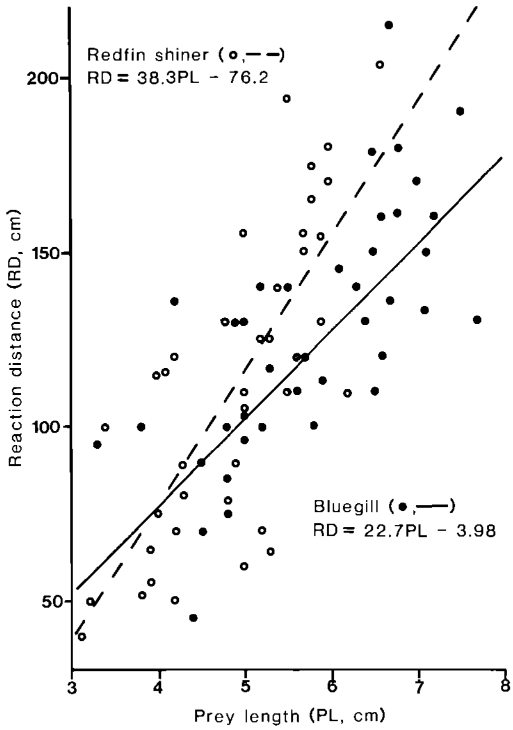

FIGURE 1.—*Reaction distance of a 29-cm largemouth bass preying on different sizes of bluegills and redfin shiners at high light intensity (3,340 lux). Slopes of the two regression lines are significantly different* (F = 6.06; *df* = 1,76; P < 0.025).

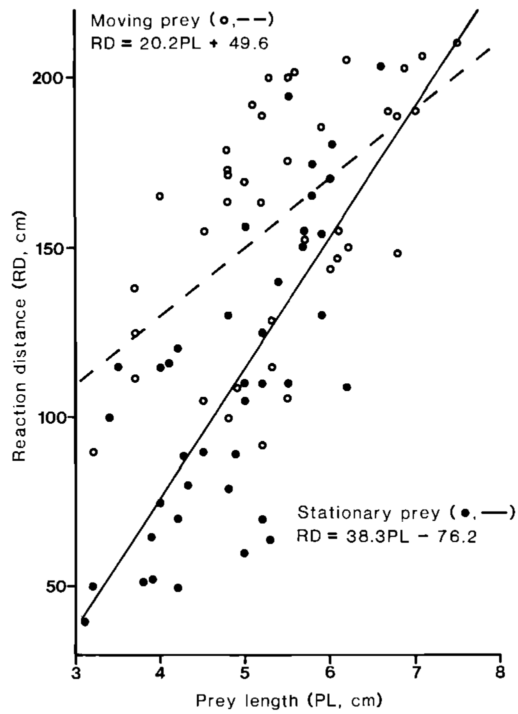

FIGURE 2.—*Reaction distance of a 29-cm largemouth bass preying on different sizes of moving and stationary redfin shiners at high light intensity (3,340 lux). Slopes of the regression lines are significantly different* (F = 6.83; *df* = 1,76; P < 0.025).

regression are significantly different from the 1.5- and 0.2-lux regression but also from the 103-lux regression (Table 2).

Choice of Prey

When the 29-cm largemouth bass was given a choice between two stationary bluegills, it always chose the closer prey, unless the further one appeared greater than 0.25° of arc larger (Fig. 4). Choice between closer and further prey was equal when the closer prey appeared about 0.50° smaller than the further prey; at greater differences in apparent size, the further but apparently larger prey was chosen more often.

When minnow prey were caused to move, the proximity, apparent size, and motion of the prey

TABLE 1.—*Statistical summaries for regression of reaction distance (cm, ordinate) of largemouth bass preying on motionless bluegills of various lengths (cm, abscissa). Asterisk (*) denotes* P < 0.01 *for* t-*test* (*df* = N − 2) *of equality with zero. Light intensity was 3,340 lux just below the water surface.*

Fish total length, cm				
Largemouth bass	Bluegill	*N*	Slope ± SD (*t*)	Ordinate intercept, cm (*t*)
35	4.8–9.6	17	24.1 ± 3.62 (6.65*)	−17.6 (0.65)
29	3.3–7.7	40	22.7 ± 3.71 (6.11*)	−3.8 (0.19)
13[a]	3.1–7.8	20	16.1 ± 4.29 (3.75*)	26.3 (1.29)

[a] This largemouth bass reacted to, but could not swallow, bluegills larger than 5.2 cm.

TABLE 2.—*Statistical summaries for regression of reaction distance (cm, ordinate) of a 29-cm largemouth bass preying on motionless bluegills of various lengths (cm, abscissa) at five light intensities. Asterisk (*) denotes* P < *0.05 for* t*-tests (*N = *40; df = 38) of equality with zero. Values in the same column with a letter in common are not significantly different (Student–Newman–Keuls test;* P < *0.05.*

Light intensity, lux	Bluegill total length, cm	Slope ± SD (*t*)	Ordinate intercept, cm (*t*)
3,340	3.3–7.7	22.7 ± 3.71 (6.11*) a,b	−3.98 (0.19)
103	3.2–9.9	13.0 ± 2.58 (5.05*) c	44.0 (2.65*)
5.59	2.9–9.8	23.3 ± 2.24 (10.4*) a	−14.7 (0.91)
1.49	4.2–8.0	13.7 ± 3.31 (4.15*) b,c	−1.85 (0.10)
0.195	4.5–9.5	3.32 ± 2.65 (2.65*) d	12.9 (1.48)

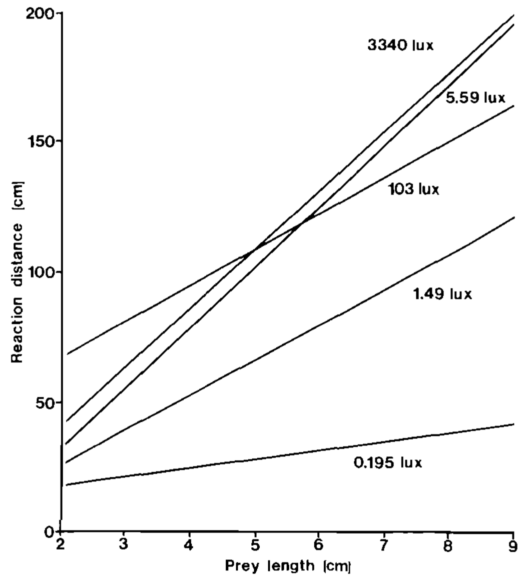

FIGURE 3.—*Reaction distance of 29-cm largemouth bass to different-sized bluegills at different light intensities. Forty observations were made at each light intensity. Points are omitted for clarity; regression statistics are in Table 2.*

all affected choice behavior. If the closer prey was moving, it almost always was chosen, even when it appeared smaller. Bias towards the moving prey decreased if it was the further prey (Fig. 4).

Attack Success

Largemouth bass had more difficulty capturing bluegills as prey size increased, and the smaller the predator the smaller the prey it could capture. However, a Kruskal–Wallis test revealed no significant differences between increasing prey size and number of attacks for either the 13- or 22-cm predator (χ^2 = 1.37, df = 2 and χ^2 = 9.247, df = 5, respectively). The overall mean number of attacks before success was

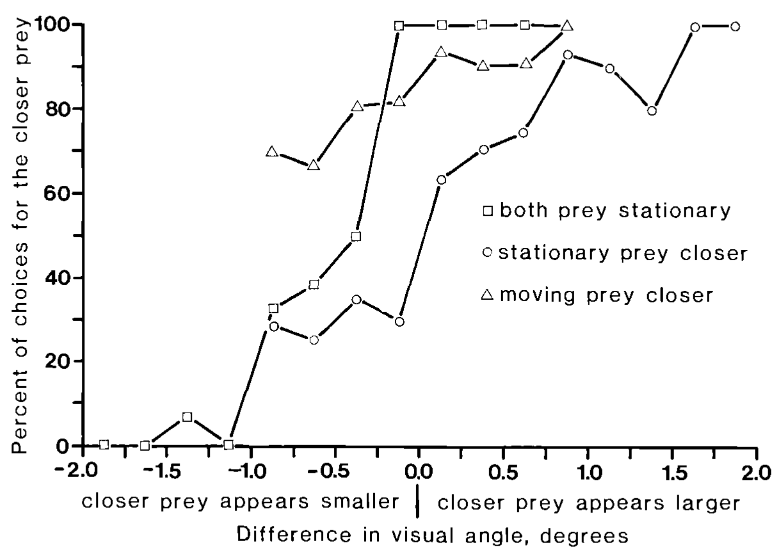

FIGURE 4.—*Proportion of choices by a 29-cm bass for the closer of two prey as a function of difference in apparent prey size. Bluegills were used when both prey were stationary.* Notropis *spp. and* Pimephales *spp. were used in comparisons of moving and stationary prey.*

TABLE 3.—*Statistical summaries for regression of reaction distance (cm, ordinate) of bluegills of various lengths (cm, abscissa) to an approaching 29-cm largemouth bass at five light intensities. None of the slopes were significantly different from zero (t-tests; df = N − 2; P > 0.05).*

Light intensity, lux	Bluegill total length, cm	*N*	Slope ± SD (*t*)	Ordinate intercept, cm	Mean reaction distance, cm
3,340	3.7–9.6	23	3.29 ± 3.62 (0.91)	169	200
103	3.8–10.0	20	−0.72 ± 3.36 (0.22)	122	121
5.59	3.7–9.9	14	−2.80 ± 6.55 (0.43)	96.3	77.6
1.49	3.9–9.6	18	−4.32 ± 2.07 (2.08)	59.6	33.2

3.0. The largest bluegill observed eaten by the 13-cm bass was 5.5 cm; that by the 22-cm predator was 9.5 cm. These yield ratios of prey length to predator length of 0.42 and 0.43, respectively.

Location of Predator by Prey

Reaction distances of bluegills, when approached by a largemouth bass, were independent of their own size; no regression slopes were significantly different from zero regardless of bluegill size or illuminance (Table 3). However, mean reaction distance to an approaching predator did decline with decreasing light intensity (Fig. 5). Unlike the decline of reaction distance of predator to prey, the bluegill reaction distance showed no obvious threshold in decline with lowered light intensity.

The reaction distance of bluegills to approaching largemouth bass of varying size increased as predator size increased (Table 4) and, as before, bluegill size did not affect this. A one-way analysis of variance showed that differences in prey reaction distance with varying predator size were significant ($F = 30.4$; df = 2,61; $P < 0.001$).

Discussion

Location of Prey

Reaction distance of largemouth bass was linearly related to prey length, and the regression lines passed through the origin. It seems that largemouth bass respond to a constant visual angle subtended by the prey on their retinas, and that some threshold of retinal stimulation is necessary to elicit a response. With bluegill as prey, largemouth bass require a visual angle of 2.7° before they react. Bluegills themselves react to *Daphnia magna* at a visual angle of approximately 0.48° when light intensity is high (Werner and Hall 1974; Confer and Blades 1975;

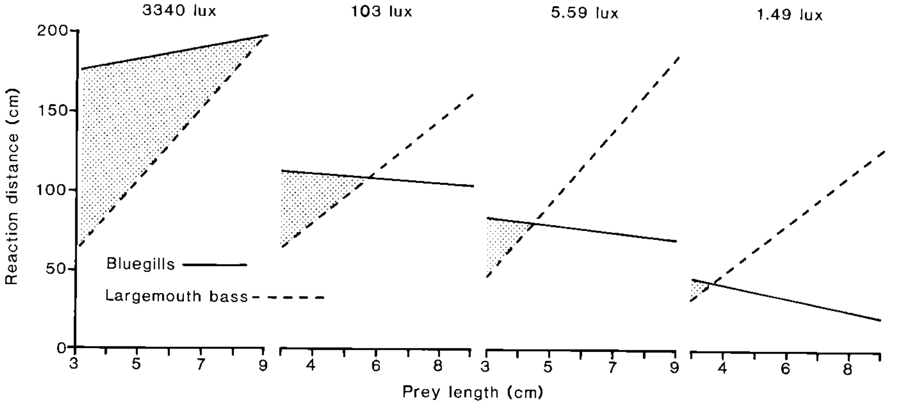

FIGURE 5.—*Reciprocal reaction distances of a 29-cm largemouth bass and bluegills of various sizes at four light intensities. Shading denotes the "safe area" where bluegills react to the largemouth bass at a greater distance than the predator reacts to bluegills.*

TABLE 4.—*Statistical summaries for regression of reaction distance (cm, ordinate) of bluegills of various lengths (cm, abscissa) to three sizes of approaching largemouth bass at 3,340 lux. None of the slopes were significantly different from zero (t-tests; $df = N - 2$; $P > 0.05$).*

Total fish length, cm					
Largemouth bass	Bluegill	*N*	Slope ± SD (*t*)	Ordinate intercept, cm	Mean reaction distance, cm
29	3.7–9.6	23	3.29 ± 3.62 (0.91)	169	200
20	4.5–9.3	21	−2.16 ± 8.02 (0.27)	133	118
13	4.5–9.3	20	0.51 ± 7.98 (0.06)	74.1	77.5

Vinyard and O'Brien 1976). This suggests that largemouth bass have poorer visual acuity than bluegills, or at least that bluegills recognize a located object as prey at greater distances than do largemouth bass.

Prey motion also affected the distance at which largemouth bass located prey, but only when prey were small. Because we held prey movement constant at 25 cm per second, the larger prey, which could be seen by largemouth bass at greater distances, had lower angular velocity. The angular velocities of moving 7-cm and 3-cm prey at the points of location by the largemouth bass were 7.4° and 12.8° per second, respectively. This difference appears to represent a threshold angular movement of about 7.5° per second needed to sufficiently increase retinal stimulation so that prey could be seen at a greater distance.

These findings suggest that small prey fish should reduce their cruise speeds and thereby reduce their angular velocity. Indeed, small fish are known to swim more slowly than large ones (Beamish 1970; Alexander 1974). Furthermore, fish tend to swim more slowly at low light intensities, when perceived angular velocities would be higher due to shorter reaction distances of predators.

Choice of Prey

Largemouth bass, unlike bluegills (O'Brien et al. 1976), chose the closer of two prey of equal apparent size. It may be that largemouth bass can judge distances and determine the absolute size of their prey.

Prey movement, which increased reaction distance to some prey, also increased the probability of attack. Wright and O'Brien (in press) found that moving copepods were more likely to be pursued by white crappies *Pomoxis annularis* than stationary ones. Often, a bluegill's first reaction to an oncoming largemouth bass is to "freeze," a response that may improve its chance of survival because motionless prey are less easily located and less frequently chosen.

Factors Affecting Attack Success

The number of attacks until capture seemed to increase with increasing bluegill size, although this was not statistically demonstrable. Werner (1977) found that the number of strikes per capture for largemouth bass feeding on green sunfish also increased as the prey : predator size ratio increased, but reported a somewhat less abrupt increase, perhaps because of differences in the shape of the prey. Green sunfish are more fusiform than bluegills, which allows them to be somewhat faster in swimming but less maneuverable than bluegills.

Handling of Prey

Based on measurements of largemouth bass mouth width and fish prey height, Lawrence (1958) estimated that the largest bluegill a 13-cm and 22-cm largemouth bass could ingest would be 4.9 and 7.4 cm, respectively. However, we found that these two sizes of largemouth bass could ingest prey of 5.5 and 9.5 cm. These differences may be of little practical consequence. Wright (1970) found that largemouth bass of two different sizes both preferred small prey over larger ones. He suggested that ease of capture, rather than ease of handling, best explained these results. Because evasion success of bluegills increases rapidly the larger they are, the maximum prey size largemouth bass can handle may not be as important in determining prey vulnerability as has been suggested (Swingle 1950).

Location of Predator by Prey

When bluegills first sight an oncoming largemouth bass, they try to retreat. In a shallow pond, 10-cm bluegills maintained a distance of at least 2 m from a 44-cm largemouth bass whenever possible. Furthermore, in our experiments with location of largemouth bass by bluegills, the initial dorsal-fin response of bluegills sometimes was followed by backwards swimming away from the predator. This kind of retreat allowed the bluegills to minimize surface area visible to the largemouth bass and also to keep the predator in view. We note that bluegill pectoral fins are very clear, and speculate that this "back-peddling" response may be the ultimate cause for transparent fins.

When bluegills could retreat no further, they oriented themselves perpendicularly to the oncoming largemouth bass, and remained in this position until attacked. They then attempted to flee. This perpendicular orientation maximizes the distance between bluegill and largemouth bass and also forces the predator to attack from the side, giving the bluegill its best chance of escape. Furthermore, once an attack is begun, a largemouth bass connot change direction (Nyberg 1971).

Dill (1974a, 1974b) studied the escape reaction of the zebra danio *Danio rerio* to an approaching predator and reported a much shorter "startle distance." Like other cyprinids, zebra danios are primarily schooling fish. Often the first reaction of a fish school to the approach of a predator is to close ranks; actual flight from attack usually does not occur until attack is imminent, when the chaotic movement of many small prey may "confuse" the predator (Shaw 1978). Thus, the startle distance of schooling fish would be expected to be different from that of nonschooling fish like bluegills, regardless of visual acuity.

Light intensity has an important influence on the startle response of bluegills. At high light intensities bluegills can locate largemouth bass before they themselves can be located. However, at low light intensities (1.49 lux), largemouth bass can see most bluegills further than the predators can be seen. Thus, the crepuscular feeding habits of large largemouth bass, well known to anglers, probably are required if these predators are to capture bluegill. Only the smallest bluegills, those less than 4 cm, would be able to locate largemouth bass first under low light conditions. This safety factor inherent in small size has been largely unappreciated in considerations of fish predator–prey relationships. Once a bluegill is larger than about 4 cm, it becomes increasingly vulnerable to predators until it grows too large to be handled and swallowed.

These relationships may place important constraints on largemouth bass feedings. Big largemouth bass ambush by day and cruise by twilight, but it would be profitable for small ones to cruise at high light intensity because many encountered bluegills might be too large. Intermediate-size largemouth bass might ambush during bright light and then begin cruising at lower light intensities.

We believe this component analysis is an important first step in the development of a mathematical model of largemouth bass feeding. Such a model will enhance both our understanding of the species' feeding ecology and the management of this widely distributed and important fish.

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