Experimental Analysis of Prey Selection by Largemouth Bass: Role of Predator Mouth Width and Prey Body Depth

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Abstract.—Piscivorous fish are size-selective predators. Although sizes of prey selectively ingested by piscivores traditionally have been measured in terms of prey length relative to predator length, the relationship between prey body depth (measured dorsoventrally) and piscivore mouth gape may be a more appropriate measure of prey size selection. In 2-d feeding trials with three sizes of largemouth bass *Micropterus salmoides*, I offered various sizes of shallow-bodied fathead minnows *Pimephales promelas* and deep-bodied pumpkinseeds *Lepomis gibbosus* in assemblages of one or both species. All sizes of predators preferred pumpkinseeds with body depths well below the maximum size ingestible. Small predators also preferred fathead minnows with body depths below the maximum size ingestible, whereas intermediate and large predators selectively ingested the largest fathead minnows offered. Largemouth bass never ingested prey of body depth greater than their own external mouth width. Although lengths of selectively ingested fathead minnows and pumpkinseeds differed, largemouth bass showed highest preferences for prey of similar body depths regardless of taxonomic identity. These results suggest that, in addition to setting constraints on maximum sizes of prey that can be ingested by piscivores, the relationship between prey body depth and piscivore mouth gape may also be important in selection of prey within the range of ingestible sizes. Therefore, body depth may be more useful than the traditional measure of prey length as a common measure for examining prey selection by gape-limited piscivores over a wide array of prey species.

Piscivorous fish are gape-limited predators, consuming only prey they can swallow whole. Because prey are generally swallowed head- or tail-first, their body depth (measured dorsoventrally) relative to the size of a piscivore's mouth determines whether they can be ingested (Swingle 1950; Lawrence 1958; Werner 1977; Tonn and Paszkowski 1986). Thus, in any particular habitat prey with body depths greater than the largest piscivore gape are invulnerable to ingestion. The vulnerability of prey within the range of ingestible sizes is determined by other factors such as size distributions of piscivores and prey, prey encounter rates with piscivores, and predator-avoidance behaviors of prey (Wahl and Stein 1988; Hambright et al., in press).

Prey-selection behavior of piscivores also influences the vulnerability of prey. Optimal foraging theory postulates that predators maximize the ratio between the benefits gained and the costs incurred in obtaining prey. Obviously, the benefits gained increase as a function of prey size, but cost, in particular that due to handling time, also increases rapidly with prey size (Werner 1974). Hoyle and Keast (1987, 1988) demonstrated that, for two piscivores (largemouth bass *Micropterus salmoides* and grass pickerel *Esox americanus*), the weight-adjusted handling time for prey of equiv-

alent lengths varied with body shape: it was lowest for shallow-bodied bluntnose minnows *Pimephales notatus* and tadpoles *Rana catesbeiana* and higher for deeper-bodied yellow perch *Perca flavescens* and bluegills *Lepomis macrochirus*. In addition prey body depth has been shown to influence other cost-related aspects of ingestion by piscivores, such as pursuit time and capture success (Moody et al. 1983; Webb 1986). I here present further evidence that prey body depth in relation to piscivore mouth size is important in determining the sizes of prey selectively consumed by gape-limited piscivores.

Methods

To examine the importance of body depth in prey selection by largemouth bass, I used two species that represent extremes in fish body shapes. Fathead minnows *P. promelas* are fusiform with shallow bodies, whereas pumpkinseeds *L. gibbosus* are gibbous with much deeper bodies.

I conducted feeding trials in which three size-classes of largemouth bass fed on three to five size-classes of fathead minnows and pumpkinseeds offered in assemblages of single or mixed species. The trials were run from 8 June to 15 September 1989 in two large tanks measuring 3.90 × 1.25 × 0.56 m deep (volume, 2.73 m³) and 2.25 m in

diameter × 0.57 m deep (volume, 2.27 m³). Four small tubs (40 × 25 × 12 cm deep) containing sediments in which the macrophytes *Myriophyllum spicatum* and *Ceratophyllum demersum* were growing were placed in each tank to a density of 32–40 stems/m². Macrophytes provide shelter for prey and largemouth bass without reducing the predator's feeding success (Savino and Stein 1982). I added zooplankton (primarily *Daphnia pulex* and *Ceriodaphnia reticulata*) to each tank before an experiment began as food for the prey. Light was provided by overhead fluorescent lights (14 h light : 10 h dark cycle) and by sunlight panels in the ceiling. Water temperature ranged from 17 to 25°C during the course of the experiments.

Largemouth bass were angled with barbless hooks from lakes and ponds near Ithaca, New York, during summer 1988 and transferred to a holding pond. In May 1989, all largemouth bass used in feeding trials were angled from the holding pond, measured for standard length (SL) and external mouth width, and placed into large (2.73-m³) laboratory holding tanks in groups of two large fish or three small and intermediate fish (Table 1). External mouth width (measured with mouth closed as the distance between the outer edges of the maxillary bones just beneath the eyes) was used because Lawrence (1958) found that it was a good estimate of the distance between the cleithrum bones, which limit maximum sizes of prey consumed by largemouth bass. Fish with any noticeable damage to the jaws were not used in feeding trials. Although all largemouth bass grew during the summer, growth of individuals in each of the three groups was not enough to change their maximum ingestible prey size-class based on predator mouth width (Table 1). Before they were used in feeding trials, all largemouth bass were acclimated for at least 2 weeks to a semidaily routine of being netted and transferred to another tank.

Fathead minnows and pumpkinseeds were trapped and seined from other holding ponds and divided into seven classes by standard lengths: 20–29, 30–39, 40–49, 50–59, 60–69, 70–79, and 80–89 mm. Although the experiments were designed to test the importance of prey body depth, standard length was used because it is relatively simpler, faster, and less harmful to measure on live fish than is body depth, particularly on very small, fragile individuals and on individuals with full guts. Later, I converted standard length (SL) measurements to body depth (BD, measured as the linear distance from the base of the pelvic girdle

TABLE 1.—Sizes (mean ± SE) of largemouth bass used in feeding trials. Measurements were made before (June) and after (September) the period in which the predators were used in feeding trials.

Size	Month	Standard length (mm)	External mouth width (mm)
Small	Jun	113.0±1.4	12.9±0.9
(N = 3)	Sep	140.3±2.0	17.4±0.9
Intermediate	Jun	213.0±1.4	25.7±1.0
(N = 3)	Sep	218.7±3.9	25.5±0.6
Large	Jun	273.0±1.4	33.8±2.0
(N = 2)	Sep	279.0±0.0	34.5±2.1

to the dorsal ridge) using the following regressions, which were determined for live fish. For fathead minnows,

$$BD = -2.08 + 0.279(SL);$$
$$N = 54, r^2 = 0.91. \tag{1}$$

For pumpkinseeds,

$$BD = -3.25 + 0.463(SL);$$
$$N = 72, r^2 = 0.99. \tag{2}$$

In trials with single prey species, prey sizes depended on availability. However, because I wanted to compare the relative importance of length and body depth, I attempted to select a similar range of SL size-classes for each prey species, with the body depth of at least one SL size-class larger than the average mouth width of the largemouth bass. This was not possible for fathead minnows used in trials with intermediate and large largemouth bass, because fathead minnows rarely attain lengths greater than 65 mm SL (Carlander 1969). In the mixed-prey species trials, I used only the three SL size-classes that could be represented by individuals of both prey species (35, 45, and 55 mm SL).

I began a feeding trial by measuring 10 prey (sometimes fewer, depending on availability—see Figure 1) in each of three to five size-classes and introducing them into a tank. Prey were allowed to acclimate for 15–30 min before a group of largemouth bass was added. After 2 d, largemouth bass were netted and transferred to another tank, and all remaining prey were collected, counted, and measured. Observations of prey in adjacent holding tanks without largemouth bass showed occasional deaths due, presumably, to handling stress. Therefore, dead prey (12 of 1,380 prey used) collected after each feeding trial were counted as not ingested, because the cause of death, either handling stress or predator attack, was unknown. Three

trials were conducted for each group of large-mouth bass with fathead minnows only, pump-kinseeds only, and both prey species. Because large largemouth bass ingested relatively few pumpkin-seeds in the mixed-species trials, one additional trial was conducted, giving a total of four mixed-species trials for the large fish. To reduce the ef-fects of hunger, largemouth bass were fed daily (between experiments) ad libitum with both fat-head minnows and pumpkinseeds.

The Manly–Chesson preference index α_i (Manly 1974; Chesson 1983) was calculated for each prey size-class in each feeding trial as

$$\alpha_i = \log_e[(n_{i0} - r_i)/n_{i0}] \Big/ \sum_{j=1}^{m} \log_e[(n_{j0} - r_j)/n_{j0}]; \tag{3}$$

$i = 1, 2, \ldots, m$; m is the number of prey size-classes, r_i is the number of individuals of prey size-class i ingested, and n_{i0} is the number of individuals of prey size-class i present at the beginning of a feeding trial. Because the numerical value of α_i is in part a function of the number of size-classes offered, and because the number of size-classes offered differed among sets of feeding trials (e.g., between intermediate largemouth bass feeding on fathead minnows and pumpkinseeds in the single-species trials), α_i was normalized to ϵ_i, an electiv-ity index ranging from -1 for total avoidance to $+1$ for total preference with 0 representing no preference:

$$\epsilon_i = (m\alpha_i - 1)/[(m - 2)\alpha_i + 1]. \tag{4}$$

Effects of prey size (SL) and species on predator preference were examined by analysis of variance with α_i values (ϵ_i is used here solely for display purposes—see Chesson 1983).

Because prey body depth probably has an im-portant influence on prey-handling time for gape-limited piscivores (Gillen et al. 1981; Hoyle and Keast 1987), I estimated handling time for the three sizes of largemouth bass feeding on various sizes of fathead minnows and pumpkinseeds. I then compared observed prey-size preferences with those predicted to maximize weight ingested per handling time. Handling time (H_t) for largemouth bass feeding on generic minnows and sunfish was calculated as a function of relative prey and pred-ator lengths by use of the following regressions from Hoyle and Keast (1987) for bluntnose min-nows,

$$H_t = 1 + 0.267$$
$$\cdot \exp[13.347(\text{prey TL/predator FL})], \tag{5}$$

and bluegills,

$$H_t = 1 + 2.147$$
$$\cdot \exp[10.875(\text{prey TL/predator FL})]; \tag{6}$$

TL and FL are total and fork lengths. I then used the generic estimates of H_t to predict body depths of fathead minnows and pumpkinseeds that would maximize prey weight per handling time; I did this by plotting prey weight per handling time as a function of body depth. Prey wet weight (W) was calculated from the following regressions deter-mined for live fathead minnows,

$$\log_e W = -14.14 + 3.79(\log_e SL),$$
$$N = 51, r^2 = 0.94, \tag{7}$$

and live pumpkinseeds

$$\log_e W = -11.22 + 3.20(\log_e SL),$$
$$N = 72, r^2 = 0.99. \tag{8}$$

Prey body depth was calculated with regressions (1) and (2). Prey total length and largemouth bass fork length used by Hoyle and Keast (1987) were converted to standard length: SL = TL/1.26 for fathead minnows; SL = TL/1.25 for pumpkin-seeds; and SL = FL/1.13 for largemouth bass (Car-lander 1969, 1977).

Results

In trials with one prey species, small predators ingested small fathead minnows and pumpkin-seeds selectively, whereas intermediate and large predators ingested large fathead minnows but small pumpkinseeds selectively (Figure 1; Table 2). This trend was repeated in trials with both prey species except that large predators virtually ignored pumpkinseeds. Although sizes of ingested fathead minnows and pumpkinseeds differed on the basis of length, largemouth bass showed highest pref-erences for prey of similar body depths regardless of taxonomic identity—again with the exception of large predators in trials with mixed prey species (Figure 2). Pumpkinseed body depths preferred by all groups of predators were well below the pred-ators' mouth widths. This pattern was similar for all predators feeding on fathead minnows, al-though intermediate and large predators always selectively consumed the largest size-class of body depth available (i.e., the upper end of the size range for fathead minnows). As suggested by Lawrence (1958), the external mouth width of largemouth bass was a good indicator of maximum prey size ingested (Table 3). In all cases prey with body depths greater than the mean mouth width of the predators were never ingested (as indicated by $\epsilon_i = -1$ in Figure 2).
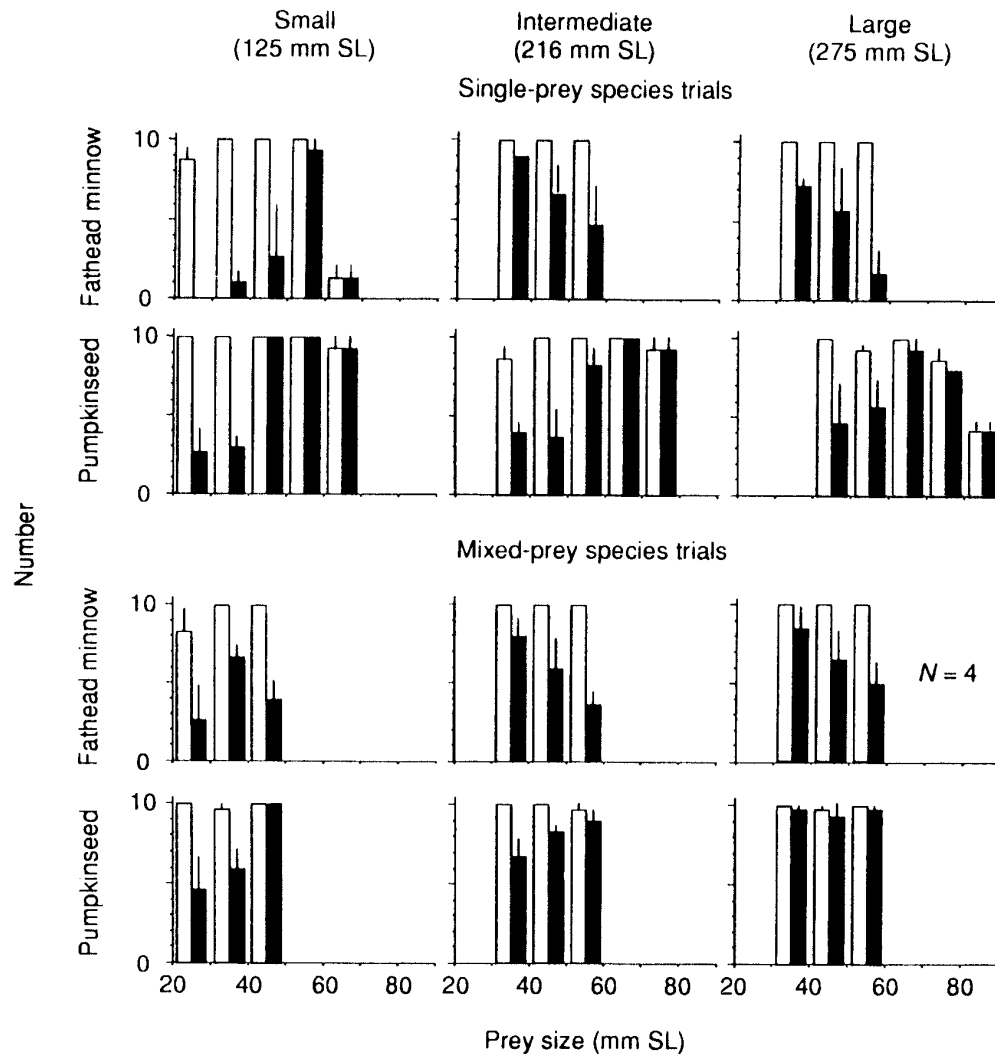
FIGURE 1.—Mean (+SE) of initial (open bar) and final (solid bar) numbers of fathead minnows and pumpkinseeds in feeding trials with small, intermediate, and large largemouth bass (SL is standard length); $N = 3$ except where otherwise noted. See Table 1 for size-classes of predators.

TABLE 2.—Results of analysis of variance performed on α_i values for small, intermediate, and large largemouth bass feeding on three to five standard length size-classes of fathead minnows and pumpkinseeds in trials with single and mixed species of prey. Refer to Table 1 for predator size-classes and to Figure 1 for prey size-classes; MS = mean sum of squares.

| Prey	Source	Small			Intermediate			Large		
		df	MS	P	df	MS	P	df	MS	P
				Single-species trials						
Fathead	Size	4	0.091	0.001	2	0.195	0.007	2	0.279	0.002
minnows	Error	9	0.011		6	0.016		6	0.014	
Pumpkinseeds	Size	4	0.226	<0.001	4	0.183	<0.001	4	0.209	0.004
	Error	10	0.003		10	0.008		10	0.027	
				Mixed-species trials						
Both	Size	2	0.044	0.047	2	0.011	0.347	2	0.094	0.038
	Species	1	0.048	0.059	1	0.083	0.011	1	0.473	<0.001
	Size × species	2	0.024	0.155	2	0.089	0.003	2	0.119	0.019
	Error	12	0.011		12	0.009		12	0.024	
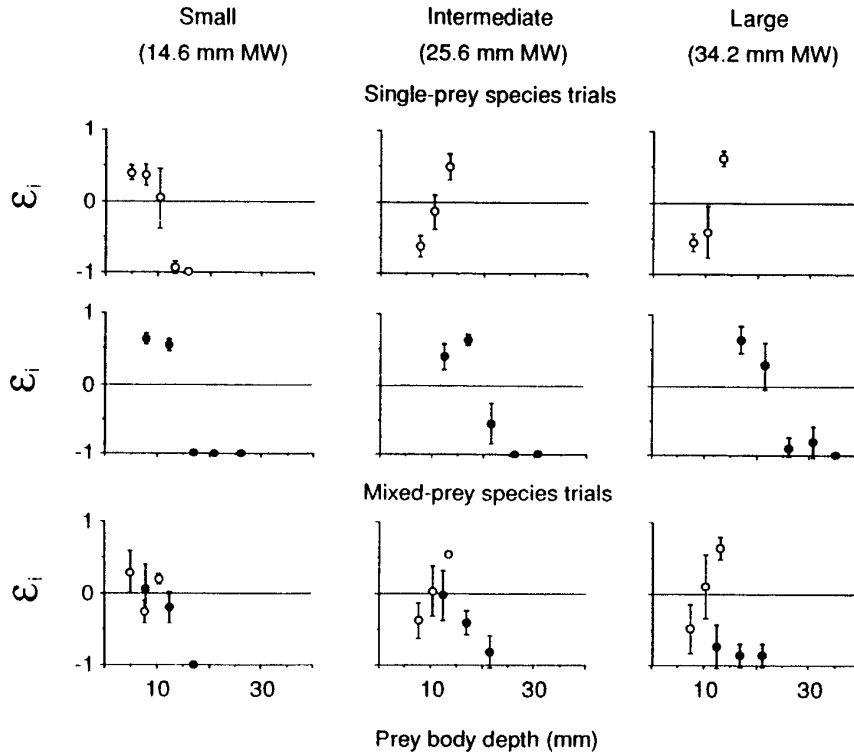
FIGURE 2.—Mean ($\pm$SE) electivity index, ϵ_i (Chesson 1983), for three size-classes of largemouth bass feeding on fathead minnows (open circles) and pumpkinseeds (solid circles) of various body depths. Values of ϵ_i range from -1 for total avoidance to $+1$ for total preference, with 0 representing no preference. Mean mouth width (MW) for each group of largemouth bass (calculated from measurements made before and after feeding trials) is given in parentheses.

According to the prey weight/handling time curves calculated from Hoyle and Keast (1987) and plotted as functions of prey body depth for the three predator groups, the body depths of fathead minnows and pumpkinseeds that provide the highest weight per handling time increase with predator size and are consistently larger for pumpkinseeds than for fathead minnows (Figure 3). Comparisons of observed and predicted prey-size preferences suggest that the ratio of prey weight and handling time may be adequate for predicting sizes of fathead minnows selectively ingested by largemouth bass, but the ratio tends to overestimate the sizes of selectively ingested pumpkinseeds.

Discussion

Lakes containing piscivores tend to be dominated by deep-bodied prey species such as sunfish, yellow perch, and gizzard shad *Dorosoma cepe-*

TABLE 3.—Predicted and actual maximum body depths (standard lengths in parentheses) of fathead minnows and pumpkinseeds ingested by small, intermediate, and large largemouth bass. Predicted values are based on the mean external mouth widths of the predators. Prey standard lengths were calculated with equations (1) and (2) in the text by substituting the mean predator mouth width for prey body depth. Asterisks indicate prey sizes exceeded the naturally occurring size ranges listed in Carlander (1969, 1977).

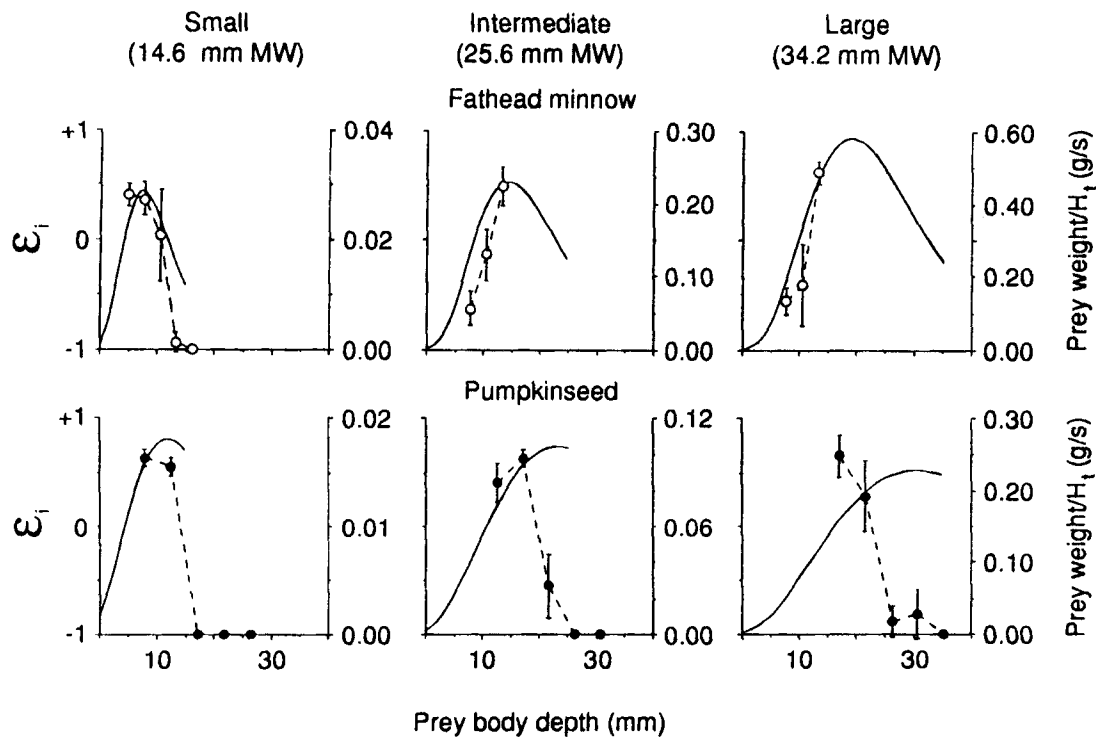| Largemouth bass group	Mean external mouth width (mm)	Maximum size of fathead minnow (mm)		Maximum size of pumpkinseed (mm)	
		Predicted	Ingested	Predicted	Ingested
Small	14.6	14.6	13.3	14.6	13.0
		(59.8)	(55)	(39.6)	(35)
Intermediate	25.6	25.6	13.3	25.6	22.2
		(99.2*)	(55)	(62.3)	(55)
Large	34.2	34.2	13.3	34.2	31.5
		(130.0*)	(55)	(80.9)	(75)

FIGURE 3.—Estimated prey weight/handling time (H_t) ratios for fathead minnows and pumpkinseeds (solid curve), and mean ($\pm$SE) electivity index (ϵ_i) values from single-prey species trials in Figure 2 (dashed line), plotted as functions of prey body depth for small, intermediate, and large largemouth bass. Mean mouth width (MW) for each group of largemouth bass (calculated from measurements made before and after feeding trials) is given in parentheses.

dianum. Smaller, shallow-bodied species such as minnows tend to dominate piscivore-free lakes (Jenkins 1967; Cooper et al. 1971; Tonn and Magnuson 1982; Rahel 1984). Although prey-species preference is highly variable across piscivore species, populations, and even individuals, laboratory and field studies have demonstrated that selective feeding by piscivores is a driving force behind this distributional pattern of prey shapes in lakes (Swingle 1950; Lewis and Helms 1964; Stroud and Clepper 1979; Prejs 1987).

Perhaps the most important variable in the selective feeding of piscivores is prey size. Gut analyses show that piscivores are size-selective and that prey size typically increases with piscivore size (Parsons 1971; Knight et al. 1984). Although the upper limit in prey size is constrained by the relationship between piscivore mouth size and prey body depth, piscivores tend to consume prey sizes that are much smaller than the maximum possible (Lawrence 1958; Gillen et al. 1981). The high occurrence of small prey sizes in piscivore guts is usually assumed to reflect the high relative abundance of these sizes in the prey assemblage (Hoyle and Keast 1987). However, prey size distributions in piscivore guts can be skewed toward sizes

smaller than those most abundant in the assemblage, especially when the assemblage is dominated by deep-bodied species such as sunfish, alewives *Alosa pseudoharengus,* and gizzard shad (Gillen et al. 1981; Knight et al. 1984). Using a simple graphical model and census data from a small lake, Hambright et al. (in press) illustrate that this pattern can be explained simply as an interaction between prey body depths available and mouth widths in the piscivore population. If encounters are random, the probability of a particular prey fish encountering a piscivore of mouth width large enough to ingest it decreases as prey body depth increases. As a result, most or all sizes (juveniles to adults) of shallow-bodied species will be highly vulnerable to piscivory. Ingestion of deep-bodied species will be concentrated on the smaller (younger) individuals in the populations, whereas larger adults occupy a size refuge with very low vulnerability to piscivory.

In the present study, preference of intermediate and large predators for fathead minnows and pumpkinseeds with similar body depths was equivalent to preference for adult fathead minnows but juvenile pumpkinseeds. Small largemouth bass tended to prefer juveniles of both spe-

cies. This pattern of selection appeared independent of relative prey abundance. Prey were distributed evenly across size-classes (with a few exceptions) at the beginning of each feeding trial, although the distribution of prey sizes changed during the 2-d experiment, resulting in occasional depletion of one or two size-classes. Thus, the preferences observed provide a conservative measure of selection by the largemouth bass. Any tendency for the predators to track the more abundant size-classes would have directed them toward the remaining prey (i.e., the larger pumpkinseeds and smaller fathead minnows), thereby potentially reducing the observed preferences.

Presumably, the factors behind selection for prey with similar body depths are related to handling of prey. However, according to the prey weight/handling time curves calculated from Hoyle and Keast (1987), the body depth that provides the maximum prey weight ingested per handling time is different for the two prey species. In addition, results of Hoyle and Keast's (1987) field test indicate that largemouth bass tended to eat smaller pumpkinseeds and yellow perch than predicted based on handling time alone. A similar pattern was noted by Gillen et al. (1981) in which tiger muskellunge (F_1 hybrid of female muskellunge *Esox masquinongy* × male northern pike *E. lucius*) consistently ingested bluegills smaller than those predicted. In my experiments, largemouth bass also showed little preference for the sizes of pumpkinseeds that were predicted to maximize the prey weight ingested per handling time. For the limited sizes of fathead minnows offered to intermediate and large largemouth bass, observed preferences did match predictions from the prey weight/handling time curves, but it was not possible to determine how larger body depths of fathead minnows would have influenced the outcome of the trials. Gillen et al. (1981) documented that tiger muskellunge ranging from 90 to 310 mm TL (exclusive of the 250-mm class) selectively ingested minnows (*Notropis* spp. and fathead minnows) smaller than the largest size offered, even though all minnows offered were similar in body depth to those used in my study. This pattern, plus the tendency for the small predators in my experiments to selectively ingest fathead minnows smaller in body depth than their own mouth width, suggests that the inclusion of larger fathead minnows in the trials with intermediate and large predators would not have substantially altered the outcomes.

Lack of agreement between the prey weight/

handling time predictions and the results of the feeding trials with pumpkinseeds does not mean necessarily that largemouth bass were not maximizing energy gains relative to costs. Rather, the curves for pumpkinseeds could be incorrect or, more likely, other costs become important as prey body depth approaches piscivore mouth width. Unlike fathead minnows, pumpkinseeds have hard fin spines which, in addition to increasing handling time, also increase the probability of injury to the piscivore during ingestion (Hoogland et al. 1956; Gillen et al. 1981). Other probable costs include energy or time used to search for and pursue prey, plus energy spent in unsuccessful capture attempts. Werner (1977) concluded that pursuit time is negligible for swift-striking piscivores, but Moody et al. (1983) found that tiger muskellunge required longer pursuit times to capture bluegills than to catch fathead minnows. Search time, although very important in natural conditions, was probably not very important in my tanks, which were well-lighted and had a macrophyte density below that shown to influence search time for largemouth bass (Savino and Stein 1982).

Webb (1986) demonstrated that differences in body shape between fathead minnows and bluegills favored ingestion of fathead minnows by largemouth bass. Capture success for bluegills was reduced because the depth of their body tended to shift the target of attack toward the head or tail, thereby increasing the number of successful escapes. Other antipredator adaptations (schooling, cover seeking, response threshold) can also reduce the capture success of piscivores (Howick and O'Brien 1983; Moody et al. 1983; Anderson 1984; Webb 1986; Wahl and Stein 1988). Because my experiments were conducted in large tanks, these factors could have played a much more important role than in the 500- to 700-L tanks of previous experiments (Howick and O'Brien 1983; Hoyle and Keast 1987, 1988; Wahl and Stein 1988).

The relationship between prey body depth and piscivore mouth width clearly sets constraints on maximum prey sizes that can be ingested by gape-limited piscivores. These two factors also may play an important role in the selection of prey by piscivores within the range of ingestible prey sizes. Because many factors that influence prey selection by piscivores may also be associated with prey body depth, it is impossible to assign a singular role to body depth. Nonetheless, my results suggest that body depth is more useful than the traditional measure of prey length as a common measure for prey size selection by gape-limited

piscivores feeding on an array of deep-bodied and shallow-bodied species.

Management of piscivorous fishes is becoming a centerpiece in lake management schemes aimed at water quality enhancement through reduction of planktivorous fish biomass. Thus, simple size relationships between piscivores and their prey, as presented here, may help to predict results of piscivore–planktivore interactions and community-level effects after piscivore manipulations (Jenkins and Morais 1978; Hambright et al., in press).

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