Predation by Pellet-Reared Tiger Muskellunge on Minnows and Bluegills in Experimental Systems

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Predation by Pellet-Reared Tiger Muskellunge on Minnows and Bluegills in Experimental Systems

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Abstract

Studies in Wisconsin lakes have shown that stocked tiger muskellunge (F hybrid of female muskellunge, Esox masquinongy x male northern pike, E. lucius) reared on live food survive better than those reared entirely on dry pellet food. We evaluated the ability of pellet-reared hybrids to convert to a minnow (Notropis spp. and Pimephales promelas) or bluegill (Lepomis macrochirus) diet in laboratory aquaria and hatchery ponds. In aquaria, 86-310-mm (total length) tiger muskellunge selected cyprinids that were about 40% of their own length and bluegills that were about 30% of their length, sizes closely predicted by an optimal foraging construct (time from prey capture to complete prey ingestion + prey dry weight). Using these prey sizes, we tested hybrids (130, 150, and 170 mm long) in conversion experiments in aquaria and ponds. During experiments, prey were maintained at a constant density and predators were sampled periodically to determine the proportion eating fish. Tiger muskellunge converted more slowly to bluegills than to minnows in both aquaria and ponds. In aquaria, 85% of the hybrids converted from pellets to minnows by day 3, whereas only 68% converted to bluegills. By day 5, conversions to minnows and bluegills were 95% and 82%, respectively. In ponds, 73% of the hybrids converted to minnows by day 5 and 89% by day 14. No hybrids had eaten bluegills by day 3 and only 53% converted by day 14. The apparently limited ability of pellet-reared tiger muskellunge to switch to a bluegill diet may influence survival and growth of these predators in reservoirs dominated by a centrachid forage base.

The tiger muskellunge (F hybrid of female muskellunge, Esox masquinongy x male northern pike, E. lucius) is stocked in lakes for sportfishing and control of undesirable fishes (Graff 1978). It can be economically cultured on artificial diets and may reach large sizes after stocking. However, field studies in Wisconsin lakes have shown that survival of hybrids reared on fish in hatcheries was much higher than that of hybrids reared on pellets (Johnson 1978). Poor survival could result if hybrids do not develop their ability to stalk and catch live prey by the time they reach stocking size, or if the time for
this behavioral change is so long that starvation reduces their viability. We conducted experiments in the laboratory and small ponds to determine how quickly hybrids reared on pellets converted to a diet of minnows (Notropis spp. and Pimephales promelas) or bluegills (Lepomis macrochirus).

Methods

Hybrids, reared entirely on dry pellet food, were obtained from Wolf Lake Hatchery, Michigan and Kineaid Fish Farm, Ohio. We held these fish in 500-liter tanks at 15-17 C and fed them pellets. For laboratory trials, individuals were acclimated over 24 hours to experimental temperatures. During the acclimation period, fish were fed pellets or minnows or bluegills. Hereafter, we refer to fish that were always fed pellets as naive, whereas those that were fed live prey for at least 1 day were termed experienced. Once a hybrid captured its first prey, its predatory efficiency did not increase during subsequent captures (see Results).

Prey-Size Selection

In preliminary trials, we determined the appropriate size of minnows and bluegills to use in subsequent experiments based on optimal foraging theory (Schoener 1971; Werner 1974, 1977; Werner and Hall 1974). Optimal prey size is operationally defined as the size with a minimal ratio of handling time (time from prey capture to complete prey ingestion, \( H_t \), in seconds) per unit of dry weight of prey (\( W_t \), in milligrams); that is, with a minimal cost/benefit ratio, \( C/B = H_t/W_t \) (Werner 1974). This approach has been used successfully to predict prey sizes chosen by predators in the laboratory and field (Werner 1974; Kisalalioglu and Gibson 1976; Stein 1977).

Size-selection and optimal foraging experiments were conducted in 100-liter aquaria at water temperatures of 19-23 C. Hybrids were separated into six total length classes (millimeters): 86-90, 126-130, 146-150, 166-170, 246-250, and 306-310. Prey types also were divided into six length classes (millimeters): 26-30, 36-40, 46-50, 56-60, 66-70, and 76-80. Throughout the paper, we identify these length classes of predator and prey by the highest value in each range. Experienced hybrids were acclimated individually in aquaria and starved for at least 24 hours. We placed one prey from each length class in aquaria, and recorded the size class of the first prey that was eaten (usually within 5 minutes after prey introduction). Twenty such trials for each hybrid length class were conducted. During size-selection experiments, we measured handling times (\( N = 12 \)) for each predator and each prey length class. We dried 10 each of bluegills and minnows from each length class (\( N = 60 \) per prey type) for 48 hours at 80 C, and weighed them (nearest 1.0 mg). We compared handling time per prey dry weight (\( C/B \)) with the prey sizes most frequently chosen in size-selection experiments. We measured total length (to the nearest 1.0 mm) and greatest body depth (nearest 0.1 mm) of 60 minnows and 60 bluegills (10 per length class) and established equations relating these variables. We used these relationships to establish if hybrids based their prey selection on length or body depth.

Hybrid Behavior

We compared predatory efficiencies of naive and experienced hybrids. Naive individuals were starved for 24 hours in 100-liter aquaria before minnows were introduced. Minnows that were not eaten within 30 minutes were removed. This procedure was repeated daily until the hybrid ate its first minnow. On the day the first minnow was consumed, we recorded the time from prey introduction to capture. Times to capture for these naive fish were compared to times to capture for experienced hybrids (1-14 days on a fish diet). We also compared the number of strikes per capture for 25 naive and 25 experienced hybrids (170 mm) that were given 60-mm minnows.

Diet Conversion in Aquaria

During 5-day experiments in a 700-liter aquarium (19-21 C), 40 minnows or bluegills that spanned the optimal size were introduced to 40 naive hybrids (150 or 170 mm) that had been starved 24 hours. The smaller hybrids were given 51-60-mm minnows or 31-40-mm bluegills; the larger hybrids were given 61-70-mm minnows or 41-50-mm bluegills. Every 12 hours, enough prey were added to maintain a density of 40 prey per tank (57/ma). Twenty hybrids were removed daily and the proportion that had eaten fish was determined by pumping (days 2 and 4) or dissecting (days 1, 3, 5) the stomachs. Fish whose stomachs were pumped...
were returned to the aquarium; dissected fish were replaced from stock tanks in the same proportion (naive:experienced) revealed by stomach analyses. This insured no change in group learning conditions. For 150-mm hybrids, there were three experiments with minnows and two with bluegills; for 170-mm predators, there were two experiments with minnows and three with bluegills. In the first bluegill experiment conversion by hybrids was low; therefore, sampling was extended to 9 days in subsequent experiments.

Diet Conversion in Pon&Two diet conversion experiments were conducted in 0.05-hectare ponds at London Fish Farm, Ohio. Ponds were 1.5 m deep and contained a moderate (about 18%) bottom cover of macrophytes (average density, about 40 stems/m²). Reed canary grass (Phalaris arundacea) and terrestrial grasses grew out of the water within 1 m of pond margins; Chara spp. was widely distributed throughout the ponds. Secchi disc readings always exceeded 1.5 m (N = 10) and oxygen was always above 12 mg/liter. A maximum-minimum thermometer, submerged to a depth of 1 m, was read every other day. Mean water temperatures were 23°C during the first experiment (termed the August experiment) and 17°C for the second experiment (termed the October experiment).

We stocked each of five ponds with 125 tiger muskellunge between 120 and 130 mm at the beginning of the August experiment and with 124 between 160 and 175 mm at the beginning of the October experiment. Two ponds contained bluegills; three ponds contained fathead minnows (P. promelas). For each prey type, two ponds were stocked with 250 prey per pond every other day; density increased from 0.25 to 1.9 prey/m³ during the course of the experiment. These densities were somewhat higher than inshore prey densities in Ohio reservoirs (R. F. Carline and R. A. Stein, unpublished data). Length ranges of minnows and bluegills spanned the optimal sizes for hybrids. For the August and October experiments, respectively, mean lengths of minnows were 53 mm (range 36-60 mm) and 59 mm (31-90 mm), and mean lengths of bluegills were 32 mm (21-45 mm) and 37 mm (21-55 mm). The fifth pond contained at least 10,000 minnows (range 16-80 mm), or about 10 prey/m³, for the duration of both experiments. This pond was used to determine the ability of tiger muskellunge to convert from pellets to minnows in the presence of particularly abundant prey. At least 100 prey from each pond were measured at the beginning and end of each 14-day experiment. Naive hybrids, obtained from Kincaid Fish Farm, were stocked in the ponds; prey were added the next day. The percentage of hybrids converting to fish was determined from a sample of 15 per pond, obtained by seining on days 1, 3, 5, 7, 11, and 14. Sample fish were weighed, measured, and dissected. Gut contents were identified; minnows and bluegills were measured.

Results

Prey-Size Selection

Size of prey selected by experienced hybrids increased with predator size (Fig. 1). Lengths of prey offered were not large enough to ade-
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The median length and body depths of minnows and bluegills were calculated using equations:

For minnows: \(\text{BD} = 1.13 + 0.14\times\text{BL}\), with \(N = 60\) and \(r = 0.91\).

For bluegills: \(\text{BD} = 3.38 + 0.36\times\text{BL}\), with \(N = 60\) and \(r = 0.98\).

Confidence intervals for the median lengths were calculated using Walsh averages (Hollander and Wolfe 1973).

Predators, ranging from 90 to 170 mm, frequently selected minnows 37-43% of their mean length and bluegills 25-30% of their length. However, when prey size was selected in terms of body depth rather than length, hybrids selected larger bluegills than minnows (Fig. 2). While prey length provides a convenient variable for measuring prey size selection, body depth may be equally important in influencing predator choice.

Cost/benefit analysis (\(Ht/Wt\)) was useful in explaining size-selection results. The cost of handling prey increased with prey length; prey of a given size were handled in less time by large predators than by small ones (Fig. 3). Handling times were longer for bluegills than for minnows of the same length. When these handling times are incorporated into cost/benefit calculations (\(Ht/Wt\)), it is apparent that the range of "profitable" prey sizes (low handling costs per food return) broadens as these predators grow (Fig. 4). The lowest point on each curve, which represents the theoretical optimal prey size in...
PREY SELECTION BY TIGER MUSKELLUNGE

Handling time as a function of the total length of bluegills and minnows for six length classes of experienced tiger muskellunge (indicated in the upper right-hand corner of each panel).

In terms of energetics, was about 40% of total length of tiger muskellunge for minnows and about 30% of predator total length for bluegills. The shape of a C/B curve provides a relative measure of diet breadth (Werner 1974). Tightly folded curves suggest a narrow range of profitable prey sizes or narrow diet breadth, whereas broad C/B curves indicate a wide diet breadth. Clearly, for small (90, 130 mm) predators, the curve was tightly folded, and a relatively small increase in prey length beyond the minimum Ht/Wt resulted in a large increase in handling costs per food return. In hybrids longer than 170 mm, C/B ratios remained low over a wide range of prey lengths. Thus, diet breadth increased gradually as predator size increased.

Hybrid Behavior

Diet history influenced predatory behavior of tiger muskellunge in aquaria. Experienced hybrids captured minnows more quickly than did their naive counterparts (Mann-Whitney U-test, P < 0.025, N = 90). Median time to capture by experienced hybrids was 75 seconds (range 5-600 seconds, N = 77) compared with 540 seconds (range 10-740 seconds, N = 13) for naive predators. Thus, some learning may have occurred as these predators converted to live food. Experienced hybrids had fewer strikes per capture than naive ones, although this difference was not quite significant (mean, 1.3 and 2.0 strikes/capture, respectively, t-test, P = 0.15). Once hybrids had eaten their first fish, strikes per capture in subsequent predation acts did not change (Mann-Whitney U-test, P > 0.05). Overall, experienced predators captured prey more efficiently than naive ones.

Diet Conversion

In laboratory experiments a large portion of naive hybrids converted to minnows or bluegills.
After 5 to 9 days, but conversion to minnows was more rapid than to bluegills (arcsin transformation, t-test, P < 0.05; Fig. 5). By day 5, 90-95% of both hybrid sizes had converted to minnows, whereas only 70-85% had converted to bluegills (Fig. 5). By day 7, 80% of the 150-mm hybrids had converted to bluegills and by day 9, nearly 100% of 170-mm predators had converted. The conversion by 170-mm hybrids was generally faster than that of 150-mm fish.

In both the August and October pond experiments, naive hybrids converted rapidly to minnows. Because conversion rates did not differ among the three minnow ponds (Friedman's test, P > 0.05; Fig. 6), data were combined for each experiment. More than 70% of the hybrids had converted to minnows by day 5 and more than 90% by day 14. In two of the ponds, minnow densities ranged from 0.25 to 1.9 prey/m²; in the third pond, densities were 10 prey/m². Thus, prey densities within this range did not influence conversion rate of naive hybrids to minnows. In both experiments, naive tiger muskellunge converted slowly to bluegills and no differences existed between ponds within either experiment (Friedman's test, P > 0.05; Fig. 6). No predator ate a bluegill before day 3. Less than 10% had converted by day 5 and only 28-53% by day 14.

In both experiments, conversion to bluegills was highest on day 14, after ponds had been partly drained overnight. This reduction in pond volume prevented access by bluegills to inshore cover, possibly increasing their vulnerability to predation. Percentages of hybrids converting to bluegills were much lower than...