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Predation by Tiger Muskellunge on Bluegill: Effects of Predator Experience, Vegetation, and Prey Density

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Abstract

Many pellet-reared tiger muskellunge (F_1 hybrid of female muskellunge *Esox masquinongy* and male northern pike *E. lucius*) do not survive stocking in reservoirs dominated by bluegill *Lepomis macrochirus* prey. Poor survival may occur because few hybrids capture bluegills. In a previous study done in hatchery ponds, only 10% of naive hybrids (those never before exposed to live prey) captured bluegills during 15 days. In similar ponds, we tested the effects of predator experience (using hybrids previously exposed to bluegill prey), vegetative cover, and bluegill density on the number of hybrids capturing prey. Few experienced or naive hybrids captured bluegills at low prey density, regardless of the presence or absence of vegetation. When bluegill density was increased from 1 to 5 prey/m^2 in ponds or to 40/m^2 in aquaria, many hybrids captured bluegills. Our pond study suggests that most hybrids will not fare well when stocked in lakes where only bluegill forage is present.

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Esocids have been stocked in lakes and reservoirs throughout the midwestern United States because they are highly regarded as sport fish and are reputed to be voracious predators (Goddard and Redmond 1978; Haas 1978; Hesser 1978). One esocid, the tiger muskellunge, an F_1 hybrid of female muskellunge *Esox masquinongy* and male northern pike *E. lucius*, has been favored in many management programs; it is as sought after as muskellunge by anglers and is more easily reared on artificial diets (Graff 1978). Unfortunately, survival of tiger muskellunge after stocking has been low or inconsistent (Johnson 1978). Poor survival of hybrids may be caused in part by the invulnerability of certain prey species. When offered prey of optimum size (as determined from laboratory preference experiments), many tiger muskellunge captured fathead minnows *Pimephales promelas* whereas few captured bluegills *Lepomis macrochirus* (Gillen et al. 1981). If stocked in centrarchid-dominated reservoirs, hybrids may grow slowly, remain in a size range vulnerable to predators for prolonged periods (Stein et al. 1981), and be susceptible to other sources of mortality such as disease and starvation. If more hybrids captured centrarchid prey, poststocking survival might increase.

Pellet-reared tiger muskellunge may capture bluegills rarely because of their lack of experience with live bluegills. We hypothesized that exposure of naive hybrids to bluegills before stocking would increase their consumption of bluegills compared to hybrids with no previous exposure. Experienced esocid predators require less time to capture fathead minnows and fewer strikes per capture (Gillen et al. 1981). Other predators feeding on novel prey show

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TABLE 1.—*Summary of experimental conditions for studies of tiger muskellunge (hybrid) predation. All prey were bluegills unless otherwise noted. Each aquarium or pond experiment was duplicated.*

Experiment type and number	Experimental facility	Facility dimensions: length × width × depth (m)	Hybrid		Prey			Vegetation density (stems/m^2)	Water temperature	
			Number	Length range (mm)	Density (number/m^2)	Length (mm)			Mean	Range
						Mean	Range			
Experience										
EI	Hatchery raceway	7 × 2 × 1	300	155–170	179	42	21–61	0	19	18–20
EII	Ponds	34 × 11 × 1.5	128[a]	165–180	1	42	20–59	75[b]	22	18–26
			128[c]	165–180	1	62	50–83[d]			
Vegetation										
VI	Quadrats	33 × 16 × 1	125	170–180	1	39	23–52	0	24	21–27
			125	170–180	1	39	23–52	2,000		
VII	Aquaria	2 × 0.5 × 0.5	40	175–195	40	39	35–45	1,000	20	17–23
Density										
DI	Ponds	34 × 11 × 1.5	138	185–220	1	44	27–61	75[c]	14	10–18
					5					
DII	Quadrats	33 × 16 × 1	50	175–195	5	29	18–46	0	22	20–24
								1,000		
DIII	Tanks	2.4 (diameter) × 1	3	185–195	1	38	35–40	1,000	19	
					5					

[a] Experienced hybrids (exposed to bluegills in hatcheries).

[b] Vegetation within 1 m of shoreline.

[c] Naive hybrids (never exposed to live prey previously).

[d] Prey were fathead minnows.

increased reactive distances, increased tendency to attack, and increased success (Beukema 1968; Ware 1971; Godin 1978; Milinski 1979) as their experience with prey increases. The experiments of Gillen et al. (1981) also suggest that bluegill density and vegetative cover may affect hybrid predation on bluegills; that is, predation increases if bluegills lose access to the refuge of vegetation and become more concentrated. Therefore, we conducted experiments to determine the effect of bluegill density and vegetative cover on tiger muskellunge predation.

Methods

All hybrids were reared on dry pellet food at the Ohio Department of Natural Resources' Kincaid Fish Farm, Latham, Ohio. Fish that were fed pellets exclusively were considered naive, whereas those that had eaten live prey at least once before being tested were considered experienced. For pond experiments, hybrids were stocked immediately after transport from the hatchery. Water temperatures during pond experiments were measured with a maximum-minimum thermometer submerged to a depth of 1 m. Secchi-disc transparency ranged from 0.6 to 1.5 m. In the laboratory, hybrids were maintained before experiments in a 500-liter tank at 15–19 C and fed pellets. All experiments were replicated once. We analyzed variation between replicates with Wilcoxon signed-rank tests and pooled data if replicates did not differ ($P > 0.05$), unless otherwise stated.

Predator Experience

We hypothesized that a greater number of experienced predators compared to naive predators would capture bluegills. In these "experience experiments," we first allowed hybrids to gain experience with live prey (EI, Table 1) by feeding them bluegills at high densities in a hatchery trough. After 2 weeks we dissected a sample of 20 hybrids to estimate the proportion that were eating bluegills; 19 had bluegills in their stomachs. We then stocked 128 of these experienced hybrids in each of two ponds at the Ohio Department of Natural Resources' London Fish Farm (EII, Table 1). Ponds were 1.5 m deep and contained a moderate (range 2–35%) bottom cover of *Ceratophyllum* spp. and filamentous algae. Reed canary grass *Phalaria arundacea* and terrestrial grasses grew in the littoral zone within 1 m of the pond margin.

One day after fish were stocked, we added 500 optimum-sized bluegills (25% of hybrid total length) to each pond, thus approximating that prey density ($1/m^2$) found in Ohio reservoirs (Stein et al. 1982). The results of this experiment were compared to previous studies (Gillen et al. 1981) in which naive tiger muskellunge were fed bluegills in these same ponds. To assess if hybrids were behaving as in previous experiments, we also stocked two other randomly assigned ponds with 128 naive hybrids and 500 optimum-sized fathead minnows per pond (40% of hybrid total length). To maintain nearly constant prey density, we added prey every 4 days, making conservative estimates of losses due to hybrid predation and assuming no prey losses to avian predators. By day 22, bluegills were growing out of the size range preferred by hybrids (mean length of bluegills had increased from 42 to 58 mm), whereas hybrids had grown little. To remedy this problem, we doubled the ration added after day 22, which increased bluegill density from 1.0 to $1.2/m^2$ and thus reduced the mean length of bluegills to 52 mm (determined when all prey were retrieved from drained ponds).

After prey were stocked, 15 hybrids were sampled every 4 days for 29 days. Hybrids were weighed (to 0.1 g), measured (total length, to 1 mm), and dissected. Stomach contents were identified to fish species or invertebrate phylum. The proportion of tiger muskellunge containing fish prey was then calculated.

Our estimate of predation, the proportion of hybrids containing fish, was conservative and included only those predators that had eaten and still contained food in their stomachs when captured. Bevelhimer (1983) indicated that stomach contents of hybrids were not completely evacuated in 24 hours. If daily ration was one bluegill per hybrid per day, then on the day of sampling, we estimated the number of hybrids in the whole population that captured a daily ration. Rarely were hybrids found with more than one bluegill in their stomachs. Error in the estimate might have arisen from sampling every 4 days but should affect all treatments equally and should not obscure differences among them.

Vegetation

To determine whether or not vegetation decreases the number of naive hybrids capturing bluegills, we manipulated the amount of vegetative cover and noted changes in hybrid predation in both pond and laboratory experiments. Pond experiments (VI, Table 1) were conducted at Hebron (Ohio) National Hatchery in a single pond that was divided into four quadrats by 9.2-mm-mesh nets. Two vegetated quadrats contained dense rye grass *Lolium perenne* (2,000 stems/m^2; mean height = 70 cm) and two cleared quadrats contained rye grass mowed to a height of 5 cm. We examined presence and absence of vegetation rather than a range of densities because we were interested only in extreme changes in the number of predators capturing bluegills. We stocked each quadrat with 125 naive hybrids followed by 500 optimum-sized bluegills per quadrat. Hybrids were sampled and prey replaced every 4 days for 16 days and the proportion of hybrids containing bluegills determined.

Laboratory experiments by Gillen et al. (1981) demonstrated that many tiger muskellunge capture bluegills ($40/m^2$) in a 700-liter aquarium without structure. To determine if structure would reduce number of hybrids capturing bluegills, we repeated these experiments in the same aquarium with added structure (VII, Table 1). Vegetation was simulated with 0.5-m lengths of yellow polypropylene rope (4 mm diameter), attached to the aquarium bottom at a density of 1,000 stems/m^2. Free ends of the rope floated to the surface, simulating a dense stand of vegetation flexible enough to allow free movement of both predators and prey.

We introduced into the tank 40 naive hybrids, starved for 24 hours, along with optimum-sized bluegills and added bluegills three times a day to maintain their density at 40 per tank or $40/m^2$. Then, each day for 5 days, we randomly removed 20 hybrids and determined the proportion eating fish, either by dissection or by inspection of body contours. Dissection always confirmed results (either presence or absence of prey in stomach) of inspection. We returned inspected fish to the aquarium; dissected fish were replaced in the same proportion (naive : experienced) as that revealed by stomach analysis. This procedure insured no change in group learning conditions and maintained constant predator density.

Prey Density

To determine the influence of prey density, we conducted an experiment in 0.05-hectare

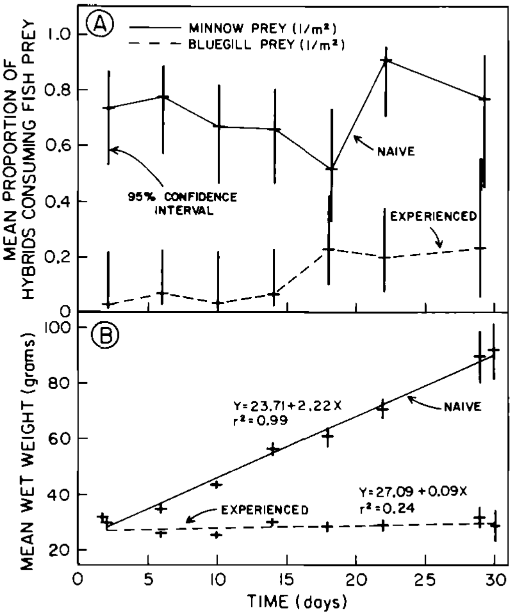

FIGURE 1.—*(A) Proportions of naive and experienced tiger muskellunge that consumed fish prey in 0.5-hectare ponds. Naive fish had been fed on commercial pellets before they were stocked in ponds with fathead minnows; experienced fish had eaten bluegills in the hatchery before they were stocked in ponds with bluegills. (B) Growth of naive and experienced tiger muskellunge. Each point in each panel represents 30 predators (15 per pond), except on the last sample day when 13 predators per pond were collected.*

ponds at London Fish Farm (DI, Table 1). In each of four ponds, we stocked 138 hybrids, then randomly chose two ponds to stock with 500 bluegills and two to stock with 2,500 bluegills. All bluegills were of optimal size. Secchi-disc depth was about 1 m. Every 4 days for 22 days, we removed, measured, and weighed 15 hybrids and analyzed their stomach contents to determine the proportion consuming bluegills.

A second and similar experiment was conducted in the divided pond (VI) at the Hebron National Fish Hatchery where we had already established and maintained bluegill density at $1/m^2$ and where 50 experienced hybrids remained in each quadrat. We added 2,000 bluegills to all quadrats to bring prey density to $5/m^2$ (DII, Table 1). Every 2 days for 7 days, we sampled and handled 15 hybrids as described previously.

On a smaller scale, we filled outdoor tanks with 1,000 artificial stems/m^2 (DIII, Table 1), then introduced three naive hybrids and either 4 or 22 prey. The densities established (1 or $5/m^2$) closely approximated prey densities used in pond experiments. We inspected body contours of predators daily for 3 days in the low-prey-density experiment and daily for 4 days in the high-density experiment.

Results

Predator Experience

When stocked in ponds, as few experienced hybrids as naive hybrids (Gillen et al. 1981) captured bluegills (Wilcoxon signed-rank sum test; $P \geq 0.44$). Also, the percentage of experienced hybrids preying on bluegills was significantly less than that of naive hybrids preying on fathead minnows (Wilcoxon signed-rank sum test; $P \leq 0.01$; Fig. 1). Mean percentage of hybrids that ate fathead minnows was 72%. Mean percentage of hybrids that ate bluegills never exceeded 25% except at the end of 4 weeks when ponds were drained and the percentage increased to 92%.

Hybrids that were fed fathead minnows grew significantly faster than those that were fed bluegills (test for the equality of linear regression slopes; $P \leq 0.05$; Fig. 1). Hybrids feeding on fathead minnows grew from a mean length of 172 to 261 mm whereas those in bluegill ponds reached 193 mm in the same time.

Vegetation

Presence or abundance of vegetation did not affect proportion of tiger muskellunge preying on bluegills. In ponds, proportions of hybrids capturing bluegills (1 prey/m^2) did not differ between vegetated and cleared quadrats (Wilcoxon signed-rank sum test; $P \geq 0.25$; Fig. 2, A panels), and was never more than 17% (means: vegetated quadrats = 4%, cleared quadrats = 7%). Hybrids increased in length only 10 mm in both quadrats.

A small tear (0.13 × 0.3 m) was found at the base of the netting separating one set of cleared and vegetated quadrats, which explained why on day 13, 24 more hybrids had been sampled in the cleared quadrat than had been stocked. Because results in these quadrats were statistically similar to those in the separated quadrats (Wilcoxon signed-rank sum test; $P \geq 0.31$), they were included in the analysis.

As in pond experiments, laboratory experiments (VII) showed no effect of vegetation on

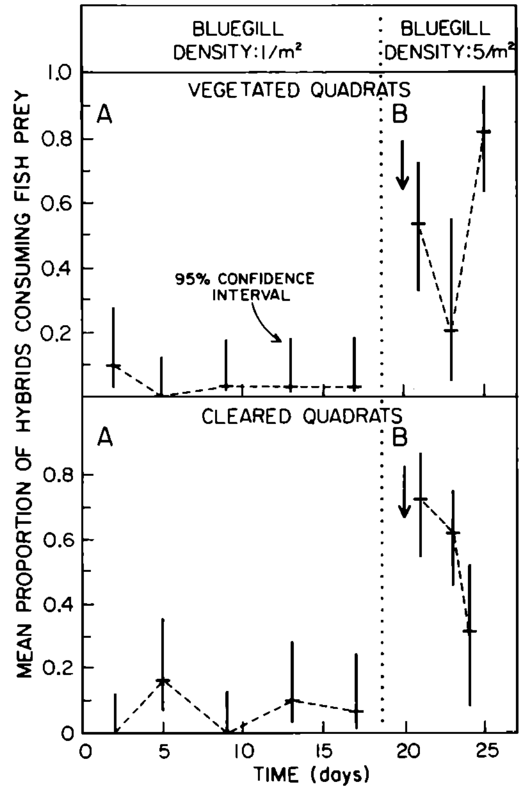

FIGURE 2.—*Proportions of naive tiger muskellunge that ate bluegills in vegetated (1,800 stems/m²) and cleared (vegetation mowed to a height of 5 cm) 0.05-hectare quadrats. Each point (A panels) represents 30 predators (15 per replicated quadrat). Prey density was increased from 1/m² (A panels) to 5/m² (B panels) on day 20 indicated by the arrow. Each point (B panels) represents 11 to 47 hybrids.*

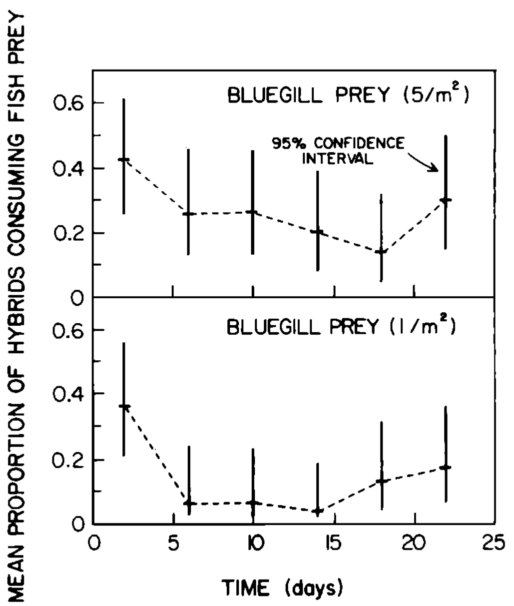

FIGURE 3.—*Proportions of naive tiger muskellunge that ate bluegills stocked at two densities (1 and 5/m²) in 0.05-hectare ponds. Each point represents 30 predators (15 per replicate pond), except on the last sample day when the number sampled varied from 11 to 39 per pond.*

predation. At high bluegill densities (40/m²), over 90% of hybrids consumed bluegills on day 1 and the proportion remained high through the end of the experiment, though structure in the aquarium was dense. In the absence of cover, 78% of hybrids consumed bluegills (40/m²) in an aquarium (Gillen et al. 1981).

Prey Density

Increased prey density significantly increased the proportion of hybrids preying on bluegills. In pond experiments (DI), more hybrids captured bluegills at prey densities of 5/m² than at densities of 1/m² (Wilcoxon signed-rank sum test; $P \leq 0.05$; Fig. 3). Percentage of hybrids consuming bluegills was 14% and 26% for low and high densities of bluegills, respectively. These results were significantly different, but were not large enough to cause differential growth (test for equality of regression slopes; $P \geq 0.05$). Hybrids feeding at low prey density grew from a mean length of 202 to 209 mm whereas those at high density grew from 206 to 210 mm.

When we increased bluegill density at the end of the vegetation experiments in the divided pond (DII), percentage of hybrids feeding increased significantly from a daily mean of 6% to 55% (Wilcoxon rank-sum test; $P \leq 0.05$; Fig. 2). Growth of hybrids averaged only 1–2 mm in any quadrat during this short experiment.

In outdoor tanks (DIII), proportion of feeding hybrids varied directly with prey density. The mean percentage of hybrids that ate bluegills was 11% at low prey density (1/m²), never exceeding 33%. In contrast, the mean percentage eating bluegills was 75% at high prey density (5/m²).

Frequency of prey sizes eaten by hybrids in pond experiments corresponded closely to the frequency of prey sizes offered (Tomcko 1982).

This close correspondence suggests that the sizes computed by Gillen et al. (1981) as "optimal" were readily eaten by the hybrids.

Discussion

Predaceous fishes capture more prey when they become experienced with that prey (Hoogland et al. 1956; Ware 1971; Godin 1978; Milinski 1979; Werner et al. 1981), when they forage in open water compared to dense structure (Glass 1971; Coen et al. 1981; Savino and Stein 1982), and when prey are dense (Holling 1966; Ware 1972). Therefore, we hypothesized that predator experience, low vegetation density, and high prey density should increase tiger muskellunge predation on bluegills. Regardless of whether hybrids were experienced or naive, or in dense vegetation or open water, most did not capture bluegills. Only at high prey densities ($>5/m^2$) did many tiger muskellunge capture bluegills. Tiger muskellunge response to prey density suggested a typical vertebrate functional response to prey density (Holling 1966), though a range of prey densities is necessary to fully define functional response.

Experienced tiger muskellunge responded, as do other experienced predators, to novel prey offered at high density; they learned to capture or avoid prey. Ware (1971) found that juvenile rainbow trout *Salmo gairdneri* exposed for 11 days to novel, inanimate prey (liver chunks at $15/m^2$) required less time to complete feeding sequences and attacked prey from longer distances than did naive fish. Similarly, as bluegills became more experienced with species of *Chironomus* ($>50/m^2$) and *Daphnia* ($100/m^3$), their capture rate increased (Werner et al. 1981). Both northern pike and European perch *Perca fluviatilis* learned to avoid threespine and tenspine sticklebacks *Gasterosteus aculeatus* and *Pygosteus pungilius* (Hoogland et al. 1956; prey densities $\geq 5/m^3$). In our experiments, many tiger muskellunge apparently learned to capture bluegills after exposure to high-density bluegill prey ($179/m^2$, EI). But this learning did not increase captures at the low prey density ($1/m^2$, EII) commonly found in reservoirs.

Our experiments were not designed to explain why tiger muskellunge differed from other predators in their response to vegetation. Tiger muskellunge have a different morphology and use different strike tactics than other predators when feeding on fathead minnows in the absence of structure (Webb 1983). How predator hunting techniques change in the presence of structure is unknown.

Both our field and laboratory experiments indicate that many hybrids captured fathead minnows compared to the few hybrids that captured bluegills. This difference may arise because of prey-species characteristics. Bluegills are more maneuverable than fathead minnows (Tomcko 1982; Moody et al. 1983), and their spines and deep body contribute to relatively long handling times by hybrids (Gillen et al. 1981). In general, other esocids readily consume soft-rayed and fusiform prey (Mauck and Coble 1971; Weithman and Anderson 1977; Goddard and Redmond 1978; Stein et al. 1982; Tomcko 1982). The presence of soft-rayed prey in reservoirs may increase hybrid growth and probably their survival.

Bluegill density, rather than vegetation density or experience of the predator, may be an important consideration when hybrids are stocked in a reservoir. Because centrarchid-dominated forage bases are common in Ohio reservoirs, because centrarchids commonly occur at densities below $1/m^2$, and because few hybrids capture bluegills at this density, growth of hybrids stocked in these waters could be poor and survival low. In waters where other soft-rayed or fusiform prey such as gizzard shad *Dorosoma cepedianum* are available, hybrids may be stocked with an expectation of reasonable growth and success.

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