

Habitat Use and Susceptibility to Predation of Four Prairie Stream Fishes: Implications for Conservation of the Endangered Topeka Shiner

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Local extirpations of the federally endangered Topeka Shiner (*Notropis topeka*) have been linked to the introduction of Largemouth Bass (*Micropterus salmoides*). However, because other native minnow species have persisted at these locations, our objective was to test whether Topeka Shiners were more susceptible to predation by Largemouth Bass than other native minnows. We conducted behavioral observations of Topeka Shiners, Red Shiners (*Cyprinella lutrensis*), Bluntnose Minnows (*Pimephales notatus*), and Common Shiners (*Luxilus cornutus*) in an indoor experimental stream, in which we examined the interactive effects of cover and the presence of a predator on longitudinal and lateral position, height in water column, cover use, and activity of these minnows. Significant differences in habitat use and response to bass were observed among species, but there was no evidence to suggest that Topeka Shiners would be more susceptible to predation than other native species. Subsequent experiments in outdoor experimental streams that allowed Largemouth Bass to forage on an assemblage of these four minnows indicated that consumption rates across species were similar, further suggesting that Topeka Shiners were not more susceptible to predation than the other minnows. Although our experiments suggest that Largemouth Bass randomly prey on this guild of minnows, the added mortality and potential indirect effects of this introduced predator likely have negative effects by further reducing the abundance of already rare Topeka Shiners.

INTRODUCED predators can have a wide range of detrimental effects on native aquatic communities (e.g., Garman and Nielsen, 1982; Rincon et al., 1990; Flecker and Townsend, 1994) and are recognized as a threat to global biodiversity (Moyle and Light, 1996; Mack et al., 2000). One species that has been implicated in the decline and disappearance of native fishes is the Largemouth Bass, *Micropterus salmoides* (e.g., Graham, 1993; Gratwicke and Marshall, 2001; Cho et al., 2003). The popularity of Largemouth Bass as a sport fish is evident from the worldwide introduction of this species (Robbins and MacCrimmon, 1974; Welcomme, 1992). In Kansas and other midwestern states, Largemouth Bass are widely stocked into farm ponds and reservoirs for recreational purposes (Cross and Collins, 1995). In the Flint Hills region of Kansas, such stockings have been implicated in the decline of the native Topeka Shiner (*Notropis topeka*), a federally endangered species (W. Layher, Univ. Arkansas Pine Bluff, 1993, unpubl.; Schrank et al., 2001; Mammoliti, 2002).

Topeka Shiners were once widespread and abundant in small to mid-sized streams of the Great Plains including portions of Iowa, Kansas, Minnesota, Missouri, Nebraska, and South Dakota (Tabor 2002). However, major declines in distribution and abundance throughout the species' range led to the listing of the Topeka Shiner as a federally endangered species in

1999 (Tabor, 1998), and they are currently estimated to occupy less than 10% of their historic geographic range (Tabor, 2002).

Topeka Shiners are found in cool, clear pools of small streams draining upland prairies (Minckley and Cross, 1959). Streams such as these were numerous in western Kansas prior to "plowing of the prairie sod," and Topeka Shiners once exhibited a continuous distribution across the state (Cross, 1967). Some records suggested that Topeka Shiners were historically more abundant outside of the eastern Flint Hills region of Kansas (Minckley and Cross, 1959). However, most populations west of the Flint Hills were extirpated prior to 1935 (Cross and Moss, 1987), presumably as a result of extreme sedimentation, eutrophication, and ground water depletion from agricultural practices (Minckley and Cross, 1959; Cross and Moss, 1987). In Kansas, Topeka Shiners now occur almost exclusively (but see Eberle et al., 1989; Stark et al., 2002) in low-order, upland streams of the Flint Hills where favorable conditions persist, primarily because of shallow, rocky soils that have prevented cultivation (Minckley and Cross, 1959; Tabor, 1998).

Although most of the historic extirpations of Topeka Shiner populations were a result of habitat loss and alteration, several recent studies suggested that introduced predators might now pose the greatest threat to the persistence of

Topeka Shiners in Flint Hills streams. Tributary impoundments stocked with Largemouth Bass are common throughout the Flint Hills (Cross and Collins, 1995; Tabor, 1998). Schrank et al. (2001) predicted extirpation of Flint Hills populations of Topeka Shiners with increased abundance of Largemouth Bass and higher numbers of small impoundments in the watershed. In Missouri, Winston (2002) found that the decline of Topeka Shiners over time was associated with an increase in the abundance of Largemouth Bass. Most documented declines or extirpations of Topeka Shiner populations following construction of small impoundments have been partially attributed to predation by introduced Largemouth Bass (W. Layher, Univ. Arkansas Pine Bluff, 1993, unpubl.; Hatch, 2001; Mammoliti, 2002). However, these correlative studies provided no direct evidence to illustrate that predation by Largemouth Bass was responsible for the extirpation of those populations. The presence of Largemouth Bass is likely coincident with physical changes in the stream or watershed and declines in Topeka Shiner populations could be related to those alterations. For example, Mammoliti (2002) suggested that the construction of an impoundment would increase downstream sedimentation and turbidity, which in turn could negatively affect reproductive and feeding behaviors of Topeka Shiners.

Although there is an abundance of correlative evidence suggesting that native stream fishes are eliminated through predation by Largemouth Bass (e.g., Findlay et al., 2000; Schrank et al., 2001; Scoppettone et al., 2004), to our knowledge no studies have explicitly shown that direct predation by bass is the actual mechanism responsible for the disappearance of a species. Food habits studies of Largemouth Bass populations in lotic systems reported that native fishes made up the majority of the diet of adult Largemouth Bass (McLane, 1947; Scalet, 1977), but another study reported that Largemouth Bass fed most heavily on the most abundant prey (Moyle and Holzhauser, 1978). This type of prey switching, based on abundance, makes direct predation seem an unlikely mechanism for the extirpation of a single species (Begon et al., 1996), because Largemouth Bass would have to selectively forage on individuals of a particular species, even as they become rare.

Alternatively, there are several hypotheses why Topeka Shiners would be more susceptible to predation by Largemouth Bass than other native minnows. First, Topeka Shiners may be naïve prey because they lack evolutionary history with Largemouth Bass. Several studies report a limited response by native prey species to an in-

troduced predator, presumably resulting from a lack of evolutionary interaction (Magurran, 1990; Blinn et al., 1993; Johnson et al., 1993). Although native predators (e.g., Creek Chub *Semotilus atromaculatus*, Green Sunfish *Lepomis cyanellus*) coexist with Topeka Shiners in Kansas, these predators may feed less efficiently or may behave such that Topeka Shiners are able to escape predation. Predation of Topeka Shiners by Largemouth Bass also may be facilitated because both species are known to use similar in-stream physical habitat, particularly deep pools and woody debris (A. Kuitunen, Minnesota Dept. of Natural Resources, 2001, unpubl.; Wheeler and Allen, 2003). Thus, an increased encounter frequency may lead to an increase in predation of Topeka Shiners by Largemouth Bass.

To build on the observed distributional pattern described above, we aimed to quantify the innate responses (i.e., habitat shifts, behavioral changes) of a guild of four native minnows, including Topeka Shiners, to the presence of Largemouth Bass. Those data then were used to predict susceptibility to predation of the prey species and a subsequent experiment quantified predation rates of Largemouth Bass on the different species. We initially hypothesized that Topeka Shiners and other native minnows would be equally susceptible to predation by Largemouth Bass. Our hypothesis was based on the observations that Topeka Shiners have an evolutionary history with piscivores other than Largemouth Bass and that they have habitat and foraging requirements similar to other native minnows.

MATERIALS AND METHODS

Habitat use.—The goals of this experiment were to quantify habitat use of Topeka Shiner (both captive reared and wild), Red Shiner (*Cyprinella lutrensis*), Common Shiner (*Luxilus cornutus*), and Bluntnose Minnow (*Pimephales notatus*) in response to Largemouth Bass and cover and to relate those behaviors to the relative susceptibilities to predation. The last three species were chosen because they often are found in association with Topeka Shiners (Minckley and Cross, 1959; Winston, 2002). Twenty Topeka Shiners reared in captivity were supplied by the Kansas Biological Survey in Lawrence, Kansas, and were first-generation fish from a stock of wild individuals collected from Deep Creek, Riley County, Kansas. Another 20 individuals were collected directly from Deep Creek. The three other species were collected from mid-sized streams in the Kansas River basin near Manhat-

tan, Kansas. Individuals of each species were held in separate raceways at 20 C, exposed to a 12:12 photoperiod, and fed ad libitum. Ten individuals of each species were selected for each experimental trial. Test fishes were mature adults ranging from 40–70 mm SL for Red Shiners, Bluntnose Minnows, and Topeka Shiners. Common Shiners were slightly larger and ranged in size from 40–100 mm SL. All individuals were used only once, except in Topeka Shiner trials because of the low number of available test fish. The 20 individual Topeka Shiners were not used in consecutive predator treatments, and test assemblages were never comprised of the same 10 individuals. The predator treatment was a free-swimming Largemouth Bass (230–300 mm TL) with its mouth secured shut with a cable tie to prohibit consumption of the minnows. Largemouth Bass were collected from surrounding streams and reservoirs, maintained in large (approximately 2.5 m³) holding tanks, and periodically fed a mixed diet of Red Shiners, Common Shiners, and Bluntnose Minnows. A rock complex (approximately 0.1 m³) comprised of large cobble and located near the edge of the pool was included in cover treatments. Treatment combinations were single species assemblages of each of the five prey types in the presence and absence of bass, with and without cover. Trials were replicated three times for a total of 60 trials.

To quantify habitat use, behavioral observations were conducted in a circulating indoor experimental stream that consisted of two pools connected by J-shaped channels. Riffles were screened at the upstream and downstream ends and only a single riffle-pool-riffle sequence was used so that the entire trial area could be viewed with a stationary underwater video camera. Pool dimensions were 130 cm in diameter with a depth of 56 cm, and riffles were 40 cm wide and 16 cm deep. Surface area of the trial arena was 2.4 m² (i.e., a fish density of approximately 4.2 fish m⁻²). Riffles had a 5 cm deep layer of coarse gravel, whereas the pool received no substrate; substrate was left out of pools to simulate bedrock- or silt-bottomed pools. Flow was created by placing a submersible pump (3000 liters/h⁻¹) behind the upstream screen. Water temperature was held constant at 20 C using a water chilling unit, and a mean light intensity of 1000 lux (range of 590–1310 lux) was provided by overhead fluorescent fixtures.

Each trial began by placing the 10 minnows in the stream at 1600 h on the day prior to observation. Fish were allowed to acclimate overnight, and observations began the next morning at 0800 h. If it was a predator treatment, a

Largemouth Bass was placed in the stream five minutes prior to the beginning of the trial. The entire trial was videotaped for six hours.

Habitat use was quantified at 30-min intervals throughout the 6-h trial (i.e., 12 observations per trial). Each observation consisted of recording the location and activity of all individuals. Longitudinal location was recorded as upstream riffle, downstream riffle, and pool. The pool was divided vertically into equally spaced bottom, middle, and top sections and laterally as center and edge, and the number of individuals occurring within each category was recorded. Categories were used because the camera position did not allow for the fine scale resolution required for continuous measurement. In cover treatments, the number of individuals within the rock complex was recorded. Activity was estimated at each interval by tracing the movement of one randomly selected fish on a stream diagram and counting the number of transects crossed in 30 sec.

For all statistical analyses, wild and captive Topeka Shiners were treated as separate groups to examine differences between the behavior of fish from natural systems and those raised in captivity. Because both height in the water column (bottom, middle, top) and lateral position (center, edge) were recorded as categorical data, these responses were translated into continuous variables by assigning the median height of the three vertical sections (bottom = 9.3 cm, middle = 27.9 cm, top = 46.5 cm) to each individual occurring in a particular section. Fish occurring in center and edge areas received scores of 21.2 cm and 51.2 cm, respectively, which represented the median distance from the pool center for each of the two sections. Because observations taken throughout the length of a trial were not independent, observations taken on individual fish were averaged to obtain a single mean value (i.e., average of 120 possible observations) for each of the response variables. Separate factorial ANOVAs were conducted to examine the individual and interactive effects of prey species, Largemouth Bass, and cover on each of the response variables for the treatment combinations. To account for the inflation of the Type I error rate that occurs with multiple comparisons, a Bonferroni correction was used to adjust the critical alpha level for these tests (i.e., $\alpha = 0.05/5 = 0.01$). When a treatment effect was nonsignificant ($P > 0.01$), trials were pooled across the treatment and reanalyzed. Post hoc comparisons with sequential Bonferroni (Rice, 1989) adjustments on the previously adjusted alpha level (i.e., $\alpha = 0.01/5 = 0.002$) were used to

examine differences in the response of single species as they responded to cover and bass. Although this was likely an overly conservative approach (i.e., inflated Type II error rate), analyses starting with $\alpha = 0.10$ only would have yielded three additional significant treatment effects.

Prey susceptibility.—The goal of this experiment was to test consumption rates of Largemouth Bass on an assemblage of Topeka Shiners, Red Shiners, Bluntnose Minnows, and Common Shiners in an outdoor experimental stream. Largemouth Bass were allowed to forage freely on the minnow assemblage and by counting the remaining fishes it was possible to quantify each species' susceptibility to predation. Red Shiners, Common Shiners, and Bluntnose Minnows were collected from the same locations as those used in the indoor experiment. Topeka Shiners (500 individuals) were obtained from an excess population spawned at the Lost Valley State Fish Hatchery, Warsaw, Missouri. The parent population of these fish came from Deep Creek, Kansas. Largemouth Bass were collected as described above. All fishes were held in separate holding tanks at the Konza Prairie Biological Station (KPBS); minnows were fed flake food, and Largemouth Bass received a diet of live minnows. To avoid the possibility of Largemouth Bass developing a "searching image" (sensu Hughes and Croy, 1993) for prey species used in the experiments, bass were fed different species of minnows than those used in the trials.

The experimental stream facility, located at the KPBS (Riley County, Kansas), is similar to stream mesocosms that have been used to assess fish behavior and habitat use (Gelwick and Matthews, 1993) including some studies that evaluated interactions among adult piscivores and their cyprinid prey (e.g., Fraser and Cerri, 1982; Schlosser, 1988). Experimental streams allowed exploration of interactions between a nonnative predator and a native endangered species without releasing these organisms into natural systems.

Each stream unit included two pools connected by a riffle, with an additional upstream riffle (total surface area 6 m²). An assemblage of 10 randomly selected individuals of each of the four test species (i.e., 40 fishes) resulted in a prey density of 7.6 fish m⁻², which is typical of streams in this region (KG, unpubl. data). An attempt was made to use minnows of approximately the same size within a replicate. Overall, the largest species was Common Shiner (mean = 48 mm; 34–66 mm SL) followed by Topeka Shiner (mean = 46 mm; 38–57 mm SL), Bluntnose Minnow (mean = 42 mm; 33–52 mm SL),

and Red Shiner (mean = 40 mm; 31–45 mm SL). Stream units were filled with natural gravel substrate and were sculptured to form concave pool bottoms and riffles that were deepest near one edge with gravel sloping up to the water surface at the other edge. Depth in the riffle (0.2 m) was sufficient to allow movement of the Largemouth Bass between pools. Flow was created using an electric trolling motor that drew water from the downstream pool through a tube (15 cm diameter) buried under the gravel into a collection box in the upstream riffle. Wire mesh (0.5 cm) prohibited minnows from entering the collection box area containing the motor and propeller. Water temperature was recorded using a temperature logger, and ranged from 6.2–17.9 C (mean = 11.6 C \pm 2.3 C) throughout the length of the seven-day trial; daily fluctuations in temperature averaged 3.3 C. A cloth canopy provided shade and daytime light intensity averaged 5750 lux (range of 300–11,000 lux). Cover was provided in the forms of large gravel substrate and a large cavity beneath the return tube in all treatments. Largemouth Bass and minnows often were observed within the cavity area using the tube as an overhead cover structure.

Minnows were placed randomly into stream units and allowed to acclimate for at least 24 h. At this point a single Largemouth Bass (160–240 mm) was introduced into four randomly selected pools. Because of the coarse substrate, four additional trials without a predator served as a control treatment and were used to estimate the efficiency of capture of all minnows after the experiment. The experiment was terminated after seven days, at which time fishes were removed from the streams using a backpack electrofishing unit and minnow traps. Because we were unable to account for all fishes in a single sampling event, treatment and control streams were sampled on multiple days with equal sampling effort. Sampling concluded when no new fishes were captured in any of the experimental stream units. The response variable was the number of individuals of each prey species consumed over the length of the trial. Because of the isolation of these systems and the short duration of our experiment, we assumed that missing fishes were the result of predation by the Largemouth Bass. Controls offered an additional means of calibration for variable recapture efficiency of the various prey species.

Because there were differences in recapture rates among species in control streams, we corrected Largemouth Bass consumption rates for each species. Adjustments were made by sub-

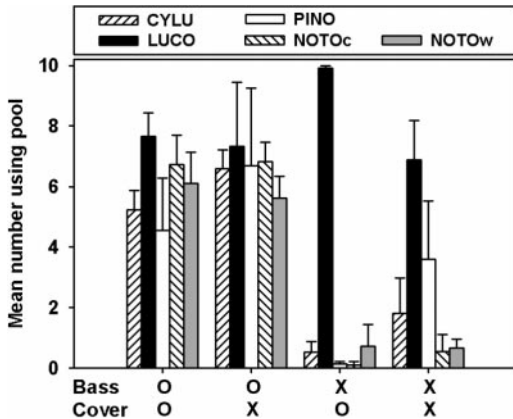


Fig. 1. Mean number (+ 1 SE) of *Cyprinella lutrensis* (CYLU), *Luxilus cornutus* (LUCO), *Pimephales notatus* (PINO), captive-raised *Notropis topeka* (NOTOc), and wild-caught *Notropis topeka* (NOTOw) that occurred in the pool of an experimental stream across various combinations of the absence (O) or presence (X) of a Largemouth Bass and/or rock complex in the pool (cover).

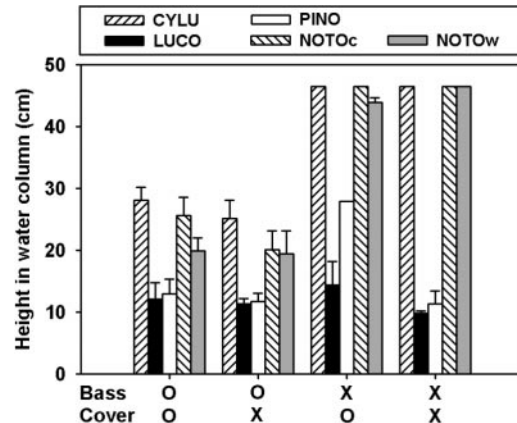


Fig. 2. Mean height in water column (+ 1 SE) of *Cyprinella lutrensis* (CYLU), *Luxilus cornutus* (LUCO), *Pimephales notatus* (PINO), captive-raised *Notropis topeka* (NOTOc), and wild-caught *Notropis topeka* (NOTOw) individuals that occurred in the pool of an experimental stream. Prey species were subjected to combinations of the absence (O) or presence (X) of a Largemouth Bass and/or rock complex in the pool (cover).

tracting the average number of individuals of a species missing across control treatments from the number of individuals of that species missing in a given predator treatment. Error variance was not equal across groups (Levene's test, $F_{3,16} = 3.972$, $P = 0.027$); thus, a Kruskal-Wallis one-way ANOVA was used to test for differences among species in the number of individuals consumed.

RESULTS

Habitat use.—The presence of Largemouth Bass changed pool use by three of the five prey (Fig. 1). ANOVA results indicated a significant species \times bass interaction ($F_{4,50} = 4.791$, $P = 0.002$) and post hoc comparisons for each species indicated that Red Shiners, wild Topeka Shiners, and captive Topeka Shiners decreased pool use in the presence of bass (P -values < 0.001). Cover had no significant effect on pool use with or without Largemouth Bass present.

Height in the water column was dependent on species, presence of cover, and presence of bass (i.e., three-way interaction $F_{4,40} = 4.222$, $P = 0.006$; Fig. 2). In the absence of bass, Common Shiners and Bluntnose Minnows generally occupied the lowest third of the water column, whereas Red Shiners, captive Topeka Shiners, and wild Topeka Shiners tended to occur in the middle third of the water column. In the presence of bass, both captive and wild Topeka Shiners, and Red Shiners were closer to the water surface regardless of the presence or absence of

cover (P -values < 0.001). Position in the water column varied with the presence of bass and cover (i.e., bass \times cover interaction $P = 0.002$) for Bluntnose Minnows. With bass present and cover absent, Bluntnose Minnows significantly increased their height in the pool, whereas when bass and cover were present there was no difference in height compared to when bass were absent.

There were significant species \times cover ($F_{4,40} = 4.126$, $P = 0.007$) and species \times bass ($F_{4,40} = 8.794$, $P < 0.001$) interactions among species with regard to lateral position in the pool (Fig. 3). However, changes in lateral position were subtle as most fishes primarily used the outer section of the pool and rarely were observed near the center. Post hoc comparisons only indicated a significant bass effect on captive Topeka Shiners ($P < 0.001$).

In the absence of a predator, more than half of the individuals of all species except Red Shiners used cover; on average, 20% of the Red Shiners occurred in cover (Fig. 4). There were significant overall effects of species ($F_{4,20} = 14.966$, $P < 0.001$) and bass ($F_{1,20} = 13.415$, $P = 0.002$) on cover use. However, there was no significant effect of bass in post hoc comparisons perhaps because this was a weak response of prey as decreased cover use was largely caused by emigration from the pool. Wild and captive Topeka Shiners reduced their use of cover noticeably, although this change was not

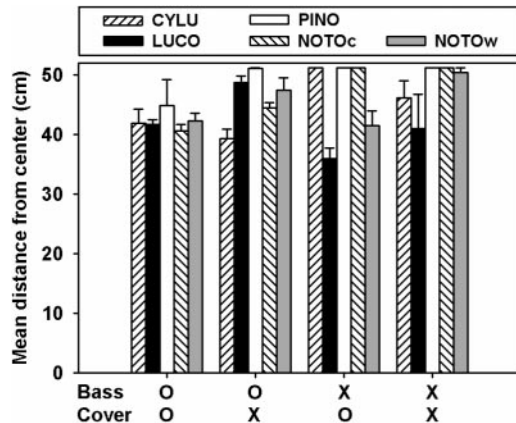


Fig. 3. Mean distance from the pool center (+ 1 SE) of *Cyprinella lutrensis* (CYLU), *Luxilus cornutus* (LUCO), *Pimephales notatus* (PINO), captive-raised *Notropis topeka* (NOTOc), and wild-caught *Notropis topeka* (NOTOw) that occurred in the pool of an experimental stream. Prey species were subjected to combinations of the absence (O) or presence (X) of a Largemouth Bass and/or rock complex in the pool (cover).

significant ($P = 0.003$ and $P = 0.008$, respectively). There was no change in cover use by Bluntnose Minnows ($P = 0.709$) or Common Shiners ($P = 0.931$) in the presence of bass, as they continued to use cover, on average, 85% and 55% of the time, respectively. Red Shiners tended to decrease use of cover in the presence of bass, but this effect was not significant ($P = 0.201$).

The presence of Largemouth Bass reduced activity levels of all species except Common Shiners (Fig. 5). ANOVA results indicated overall significant species ($F_{4,50} = 4.595$, $P = 0.003$) and bass ($F_{1,50} = 27.643$, $P < 0.001$) effects. Post hoc comparisons found that the only significant reductions in activity levels were for captive and wild Topeka Shiners (corrected P -values < 0.001). Although activity of Red Shiners and Bluntnose Minnows declined with bass, these responses were not significant ($P = 0.007$ and $P = 0.128$, respectively). There was no significant effect of cover on activity level with or without bass for any species.

Prey susceptibility.—All Topeka Shiner and Common Shiner individuals were recaptured from control trials resulting in a 100% recapture efficiency for these two species. However, we were only able to recover an average of nine (range 8–10) of the 10 individuals of Bluntnose Minnows and Red Shiners in control treatments. Thus, we used these data to adjust the calculated consumption rates from predator trials.

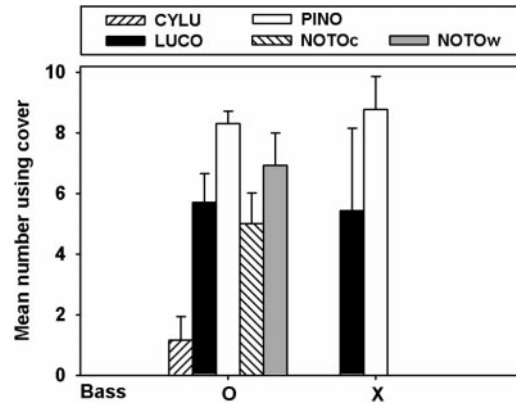


Fig. 4. Mean number (+ 1 SE) of *Cyprinella lutrensis* (CYLU), *Luxilus cornutus* (LUCO), *Pimephales notatus* (PINO), captive-raised *Notropis topeka* (NOTOc), and wild-caught *Notropis topeka* (NOTOw) that used cover in the pool of an experimental stream in the absence (O) or presence (X) of a Largemouth Bass.

After correcting for capture efficiency, Largemouth Bass consumed on average 4.12 (range 2–6) Red Shiners, 2.88 (range 0–6) Bluntnose Minnows, 1.72 (range 0–3) Common Shiners, and 1.48 (range 0–4) Topeka Shiners. Although Largemouth Bass consumption of Red Shiners was twice as high as that of Topeka Shiners or Common Shiners, these differences were not significant ($H = 1.881$, $df = 3$, $P = 0.597$) because of a high degree of variability among individual Largemouth Bass in their prey selec-

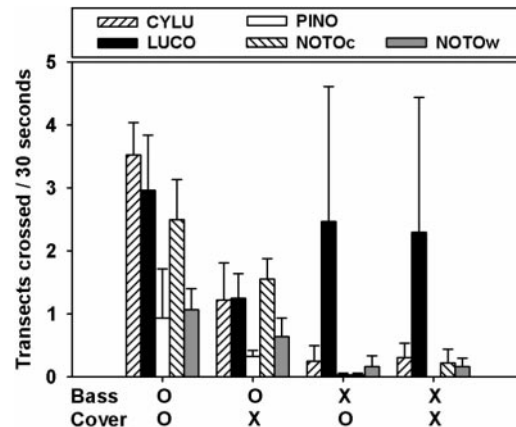


Fig. 5. Activity levels (+ 1 SE) of *Cyprinella lutrensis* (CYLU), *Luxilus cornutus* (LUCO), *Pimephales notatus* (PINO), captive-raised *Notropis topeka* (NOTOc), and wild-caught *Notropis topeka* (NOTOw) in an experimental stream. Prey species were subjected to combinations of the absence (O) or presence (X) of a Largemouth Bass and/or rock complex in the pool (cover).

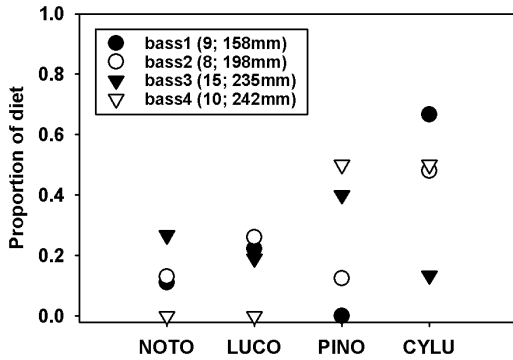


Fig. 6. Proportion of *Cyprinella lutrensis* (CYLU), *Luxilus cornutus* (LUCO), *Pimephales notatus* (PINO), and *Notropis topeka* (NOTO) in the diet of individual Largemouth Bass foraging in experimental streams. Initial prey availability was 10 individuals of each of the four species. Numbers in parentheses give the total number of fishes consumed and the total length of each bass.

tion. Some individuals primarily consumed Bluntnose Minnows or Red Shiners, whereas other bass consumed individuals of all species approximately equally (Fig. 6).

DISCUSSION

In single species trials, all fishes except Common Shiners changed their behavior in the presence of Largemouth Bass. Both captive and wild Topeka Shiners, as well as Red Shiners, showed the strongest avoidance of Largemouth Bass by emigrating from the pool and moving into riffles. This represented an effective anti-predator behavior as Largemouth Bass occupied the pool a majority of the time (82% of all observations). When these three species were in the pool with bass, they moved to the water surface and had overall low activity levels. Common Shiners did not respond to Largemouth Bass as they continued to use the pool and remained active. Bluntnose minnows exhibited an intermediate response by migrating into riffles only when cover was unavailable in the pool, but, when cover was present, they were inactive and used the cover extensively. The disparity of responses among prey species may be related to the evolutionary history of these predator and prey species (Gilliam and Fraser, 1988). Although Largemouth Bass are a relatively recent addition to the fish assemblage of small prairie streams, other native predators (e.g., Creek Chub, Green Sunfish, Spotted Bass *Micropterus punctulatus*) have historically occurred in these systems (Cross, 1967; Cross and Collins, 1995). Such native predators would have been a more

substantial threat to small-bodied prey species than large-bodied prey species, like Common Shiners, which could have escaped predation from these gape-limited predators. If this had been the case, Common Shiners might not have perceived large-bodied fishes as representing a substantial predatory threat, even though the Largemouth Bass used in our study were capable of consuming adult Common Shiners. This lack of history with a large-gaped predator could explain the general lack of response of Common Shiners to Largemouth Bass in the experiments.

The large body size of Common Shiners also should result in greater swimming speed (Bainbridge, 1958) and perhaps greater ability to escape predation. Moreover, because these experimental trials were conducted during simulated daylight hours in clear water, prey fishes would likely be able to see the bass. Thus, Common Shiners may not have reacted to Largemouth Bass because they could easily escape. Alternatively, there is the possibility that Common Shiners reacted to Largemouth Bass in a manner not easily detected by this experimental design. Heczko and Seghers (1981) showed that Common Shiners reacted to conspecific alarm pheromones by increasing school cohesion and polarization and cover use. Although cover use was measured in our experiment, there was no analysis of group cohesion or polarization. Common Shiners could have reacted to bass through increased schooling behavior, but this response would not have been measured with our design. Based on behaviors measured with our design, we predicted that Common Shiners would be most susceptible to predation by Largemouth Bass if they were naïve prey or less susceptible if they had efficient escape behavior.

Largemouth Bass revealed a high degree of variability among individuals in their prey selection and no differences in consumption rates among species, suggesting random predation of stream minnows, regardless of individual prey avoidance behavior observed in our indoor experimental stream. However, there were differences in the behavior exhibited by prey species in the indoor and outdoor experimental streams. For instance, in the presence of bass, Common Shiners remained in the pool in the indoor stream but frequently were observed moving into riffles with the other species in the outdoor streams. Such behavior could be caused by a multispecies schooling effect (Moyle, 1973; Pitcher, 1986) or to the presence of Schreckstoff, an alarm substance released by minnows upon the wounding or death of an individual (Smith, 1982).

Conservation implications.—Our experimental results strongly suggest that Largemouth Bass do not preferentially prey on Topeka Shiners. Unless there is a large discrepancy in the habitat use of Topeka Shiners in the wild and in the experimental streams, this finding should translate into natural predator-prey dynamics. Although Largemouth Bass do not prefer to feed on Topeka Shiners, this does not negate the effects that bass could have on the persistence of Topeka Shiner populations in the wild. Predators can have indirect effects on prey by forcing them into suboptimal habitats (Mittlebach, 1986; Harvey, 1991), which can lead to poor growth and reproduction of prey (Werner et al., 1983; Fraser and Gilliam, 1992). In addition, the spawning aggregations of Topeka Shiners involve the establishment and maintenance of breeding territories for successful reproduction (Kerns and Bonneau, 2002; Stark et al., 2002). Largemouth Bass could present a nonlethal negative effect on Topeka Shiners by interrupting spawning or forcing them to use unsuitable breeding habitats. They also may cause Topeka Shiners to migrate out of large, deep pools and into habitats that are less profitable for feeding or more susceptible to desiccation during times of drought (i.e., riffles or shallow pools).

Largemouth Bass consume Topeka Shiners; thus, they would have a negative effect on Topeka Shiner populations in the wild. In our experiments, a single Largemouth Bass consumed on average 1.5 fish day⁻¹, 0.2 of which were Topeka Shiners. Although this may be trivial, Topeka Shiner populations are already at low densities in many areas, and even a small loss to predation would compound these effects and possibly cause extirpation of that population. This set of circumstances is constructed under the assumptions that predation rates are independent of a prey's relative availability and that Largemouth Bass continue to feed on a species even as it becomes rare. Alternatively, Largemouth Bass might ignore prey species occurring at low densities (i.e., switching behavior), thereby alleviating other biotic constraints (i.e., interspecific competition) and temporarily facilitating prey species occurring at low densities (Begon et al., 1996).

We propose that future experiments are designed to evaluate the functional response of Largemouth Bass to gain an understanding of how density-dependent consumption rates might influence the population dynamics of species at low densities, like the Topeka Shiner. It also may be informative to use bioenergetics data in conjunction with relative abundance estimates of prey fish assemblages in Flint Hills

streams to evaluate the effects that random predation by Largemouth Bass could have on the population dynamics of native prey species, including the endangered Topeka Shiner.

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