

Seasonal and Diel Habitat Selection by Bluegills in a Shallow Natural Lake

CRAIG P. PAUKERT*¹ AND DAVID W. WILLIS

Department of Wildlife and Fisheries Sciences,
South Dakota State University,
Brookings, South Dakota 57007, USA

Abstract.—Habitat use by bluegill *Lepomis macrochirus* may be dictated by the avoidance of predators and the availability of prey. Previous work suggests that bluegills large enough to avoid predators will select habitats based on foraging profitability. However, these studies focused on smaller fish (<150 mm standard length) in laboratory experiments or in natural systems with distinct vegetated and open-water habitats. Our objective was to use radio telemetry to determine monthly and diel vegetation selection by larger (>200 mm total length [TL]) bluegills in a shallow (mean depth = 1.2 m), 332-ha, natural lake (Pelican Lake, Nebraska) with both emergent and submergent vegetation distributed throughout. A total of 78 bluegills (200–273 mm TL) were implanted with radio transmitters and relocated daily for 6 d per month (April–September); up to 20 of the tagged fish were relocated every 2 h for a 24-h period once each month. Regardless of diel period, bluegills used open-water, emergent vegetation, submergent vegetation, and mixed emergent–submergent vegetation habitat types in similar proportions. During April, June, and July, male bluegills positively selected emergent vegetation, whereas female bluegills showed no vegetation selection preference during any month. Throughout the study period, bluegills never avoided open-water habitats, suggesting that larger individuals may continue to use open-water habitats in proportion to their availability. In addition, emergent vegetation appeared to be important, particularly for male bluegills. Although the mechanism for the positive selection of emergent vegetation by males was unclear, the protection or enhancement of such habitats may facilitate the preservation of quality bluegill populations in shallow lakes.

Habitat use by bluegill *Lepomis macrochirus* often depends on prey availability and predator avoidance (Savino and Stein 1982). Food habits studies suggest that bluegills consume benthic and epiphytic macroinvertebrates (Schramm and Jirka 1989; Keast and Fox 1992; Schneider 1999) and may also consume zooplankton when predation risk is limited and foraging efficiency is greater in open-water habitats (Mittelbach 1981). Invertebrate prey density usually increases with plant density (Schramm et al. 1987), and even large bluegills (i.e., >180 mm total length [TL]) may feed in submergent vegetation (Engel 1987).

Predation risk may also influence bluegill habitat use. In a natural lake in Michigan, bluegills smaller than 100 mm standard length (SL) avoided open-water habitats because of increased predation risk, whereas larger (101–150 mm SL) bluegills were unconstrained by predation and used the energetically more profitable open-water habitats (Mittelbach 1981). To minimize predation risk,

bluegills may use structurally more complex habitats (Savino and Stein 1982; Gotceitas and Golgan 1987), such as dense submergent vegetation. However, limited information exists on bluegill habitat use in different types of vegetation (e.g., submergent versus emergent). In a previous study of 30 Nebraska Sandhill lakes, increased emergent vegetation abundance was associated with higher-quality bluegill populations (Paukert et al. 2002). Therefore, both submergent and emergent vegetation may provide important habitat for bluegills in natural lakes.

Diel distribution and habitat use in fishes may be a function of foraging activity. Bluegills feed diurnally, although nocturnal foraging has also been documented (Keast and Welsh 1968; Sarker 1977). Because feeding may be a primary determinant of the diel distribution of fish (Helfman 1981; Keast and Fox 1992), bluegills may limit their habitat use to areas of high foraging profitability during diurnal periods. However, evidence of diel shifts in habitat use by bluegills has been limited to indirect estimates.

The objective of our study was to determine whether habitat preferences of larger (≥ 200 mm TL) bluegills differed diurnally and seasonally in a shallow natural lake. We wanted to determine

* Corresponding author: cpaukert@usgs.gov

¹ Present address: Southwest Biological Science Center, U.S. Geological Survey, 2255 North Gemini Drive, Flagstaff, Arizona 86001, USA.

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whether bluegills exhibited affinities for certain vegetation types so that future management efforts could focus on protection or enhancement of these habitats. We hypothesized that larger bluegills would use open-water habitats for foraging in the study lake due to their lower susceptibility to predation. We also expected bluegills to select areas of emergent vegetation because this habitat type was correlated with quality bluegill populations in Nebraska's Sandhill lakes (Paukert et al. 2002).

Methods

Study site.—Pelican Lake is a 332-ha, shallow (mean depth = 1.2 m), prairie lake located on the Valentine National Wildlife Refuge in the Sandhill region of north-central Nebraska. In midsummer 1999, submergent vegetation covered approximately 23% of the lake area, whereas emergent vegetation covered 14%; 63% of the lake was open water (Paukert and Willis 2000). Both submergent and emergent vegetation types were clustered throughout the lake. Pelican Lake is considered productive, with summer chlorophyll-*a* values of 2.6 mg/m³ and total alkalinity levels of 100 mg/L (Paukert and Willis 2000). Invertebrate sampling in 1998 revealed high summer benthic macroinvertebrate (1,377/m²) and zooplankton (1,178/L) densities (Paukert and Willis 2000) as compared with natural lakes in South Dakota (Brown and St. Sauver 2002).

The fish community in Pelican Lake is simple and contains primarily bluegills, largemouth bass *Micropterus salmoides*, yellow perch *Perca flavescens*, northern pike *Esox lucius*, and common carp *Cyprinus carpio*. Angling effort is relatively low for all fishes, with annual bluegill exploitation typically less than 5% of the population (Paukert et al., in press). Largemouth bass and northern pike are the primary predators in the Nebraska Sandhill lakes, including Pelican Lake (Paukert et al. 2002; Paukert and Willis, in press).

Lake mapping.—To determine random sample points for estimating available habitat, we digitized a satellite image of Pelican Lake into a geographic information system (ArcView; ESRI 1999) and recorded locations along the shoreline with a global positioning system (GPS) to verify the satellite image map. In the laboratory, we divided the lake map into 50-m × 50-m cells, which created a total of 1,370 cells. We randomly selected 137 (i.e., 10%) of the cells each month for vegetation sampling. To ensure even sample site distribution, the cells were selected with the criterion that no adjacent cells would be sampled during the same

month. In the field, we used a GPS to navigate to the center of each selected cell, and then visually classified vegetation by taxon. For emergent vegetation (i.e., bulrush *Scirpus* spp., common reed *Phragmites australis*, and cattail *Typha* spp.), we used a seven-tier classification system based on the proportion of the cell covered with that vegetation type (i.e., category 1 = <1%, 2 = 2–5%, 3 = 6–25%, 4 = 26–50%, 5 = 51–75%, 6 = 76–95%, and 7 = >95%; Daubenmire 1959). For submergent vegetation (i.e., long-leaf pondweed *Potamogeton nodosus*, floating-leaf pondweed *P. natans*, coontail *Ceratophyllum demersum*, and water milfoil *Myriophyllum verticillatum*), we used a three-tier classification (i.e., category 1 = zero plants attached to a wading rod scooped from the bottom, 2 = 1–3 plants, and 3 = >3 plants) because of the difficulty in determining underwater vegetation density. We assumed that the center of the cell was representative of the entire cell. Cells with category-1 designations for all vegetation taxa constituted open water. We then interpolated surface coverages of submergent and emergent vegetation with the spatial analyst extension in ArcView, based on a cell size of 10 m. Low light levels prohibited the measurement of vegetation at fish locations (see below) during the diel tracking; therefore, we used the interpolated coverage for areas of emergent vegetation, submergent vegetation, mixed vegetation types, and open water to obtain the proportion of the lake covered by each habitat type.

Surgery and transmitter implantation.—During 8–17 March 2000, 33 female and 27 male bluegills (range, 228–271 mm TL) were collected with double-throated, modified fyke nets with 16-mm-bar mesh. All bluegills were transported to Valentine State Fish Hatchery (Valentine, Nebraska), where they were held in raceways for 24 h prior to radio transmitter implantation. Transmitters averaged 0.85% (range, 0.74–1.4%) of body weight for females and 0.92% (range, 0.55–1.08%) for males, and were small enough to minimize transmitter loss and fish mortality (Paukert et al. 2001). Each fish was placed ventral side up into a trough that allowed water contact with the gills during surgery. We surgically implanted a transmitter into each bluegill through a small incision closed with two to three interrupted sutures (Paukert et al. 2001). Transmitters (PD-2, Holohil, Inc., Ontario) were rated for a battery life of 6 months.

Because of delayed mortality or transmitter expulsion, 18 transmitters were recovered from near-shore habitats and re-implanted into four females

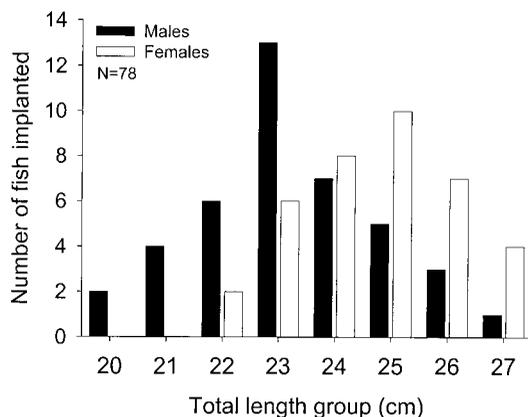


FIGURE 1.—Length distributions of 78 male and female bluegills implanted with radio transmitters in Pelican Lake, Nebraska, in March and May 2000. Sixty fish were implanted in March 2000, but 18 of those fish either died or expelled their transmitters, prompting collection of replacement fish that were implanted in May. All six males smaller than 22 cm were implanted in May.

(range, 243–273 mm) and 14 males (range, 200–255 mm) on 22–23 May 2000. The fish were collected with daytime electrofishing and with overnight sets of the same fyke nets used to collect fish in March 2000, and subsequent surgery was conducted on the banks of Pelican Lake. For bluegills implanted in March and May combined, implanted females averaged 14 mm longer than males (Kolmogorov–Smirnov [KS] two-sample test, asymptotic KS statistic [KSa] = 1.83, $P = 0.002$; Figure 1).

Telemetry tracking procedures.—We attempted to locate all bluegills daily for six consecutive days on 4–9 April, 10–15 May, 16–21 June, 18–23 July, 10–15 August, and 6–11 September 2000 during daylight hours with a four-element yagi antenna. We maneuvered the boat toward a fish until the signal strength was equal in all directions. At all relocation sites, GPS coordinates and vegetation were recorded by the methods previously described. We estimated that we were within 5 m of the actual fish locations, based on visual observations of four bluegills with transmitters. Fish appeared undisturbed by the boat, as few individuals swam away during our approach.

In addition to daily bluegill locations, we randomly selected up to 10 males and 10 females from the pool of all fish located in a given month for one 24-h tracking period on 21 April, 15 May, 20 June, 22 July, 14 August, or 9 September 2000. During the 24-h tracking period, fish were located every 2 h by methods similar to those of daily

tracking. We classified the 24-h period into four diel periods: dawn (2 h before to 2 h after sunrise), daytime, dusk (2 h before to 2 h after sunset), and night. We located each fish at least twice per diel period to obtain a minimum of one movement rate per period.

Statistical analysis.—To determine the accuracy of our vegetation coverage interpolations, we calculated the correct classification rate for each vegetation type by randomly selecting 50 points where habitat was measured and excluding them from the map creation process. The 50 points were overlain onto our created coverage to determine how many were correctly classified after the map interpolations (Paukert and Willis 2002).

The habitat selection analysis was four tiered. First, we used a two-way logistic regression to determine differences in the proportion of fish locations among diel periods and habitat types (Stokes et al. 1995). When no interaction was found between diel period and habitat type, we looked at the main effect of diel period to determine whether the proportion of fish locations differed among diel periods. Second, we used logistic regression to determine whether the proportion of fish locations differed between sexes or among habitat types. In the absence of an interaction between sex and habitat type, we looked at the main effect of sex to determine whether the proportion of fish locations differed between sexes. Third, logistic regression was used to determine whether bluegills selected open water or vegetated habitat (i.e., all vegetation habitats combined). In the logistic regression analysis, each of the 137 randomly selected vegetation measurement points was coded as zero, and the fish locations were coded as 1.0. Logistic regression determined the probability of fish presence at a location based the presence of vegetation (i.e., selection for vegetation). Finally, for those diel periods, sexes, and months where bluegills did select for vegetation, we again used logistic regression to determine selection for specific vegetation taxa based on vegetation density categories. Significant positive coefficients in the logistic regression model suggested positive selection of a taxon, whereas significant negative coefficients suggested negative selection.

Results

Lake Mapping

We correctly classified 70% (SE = 2%) of our vegetation coverages across vegetation types (submergent and emergent) and months. Classification

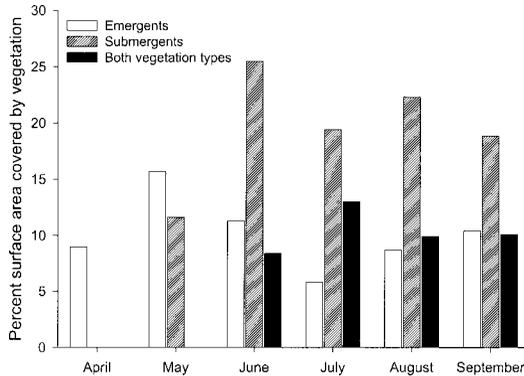


FIGURE 2.—Percentages of the Pelican Lake, Nebraska, surface area covered by emergent vegetation, submergent vegetation, and mixed vegetation from April to September 2000. Coverages are based on interpolated maps from a geographical information system.

rates did not differ between vegetation types ($F = 0.08$; $df = 1, 19$; $P = 0.79$) or across months ($F = 3.27$; $df = 4, 19$; $P = 0.06$). Data from April 2000 were excluded from the analysis due to the absence of submergent vegetation during that time. However, emergent vegetation coverage in April had an 80.5% ($SE = 4.5\%$) correct classification rate.

Vegetation coverage was clustered throughout the lake, particularly during midsummer. Emergent vegetation coverage peaked in September (20.5% of the water surface), and was lowest in April (9%) (Figure 2). Submergent vegetation coverage peaked in June (33.9%) and was lowest in April (0%).

Overall, the total vegetation surface coverage ranged from 9% in April to 45% in June. Vegetation did not substantially decline in September, as total vegetation coverage was still 39%.

Vegetation Use and Selection

Bluegill use of habitat types was similar across dawn, dusk, daytime, and nighttime periods for all months. No interaction between diel period and habitat type was found for any month sampled (Table 1). When the main effect of diel period was evaluated, no difference was found in the proportion of locations in the various habitat types for any month sampled. Bluegills used habitat types in similar proportions across diel periods; therefore, we combined all diel periods for further analyses. The analysis of bluegill locations by habitat type and sex indicated an interaction between the two factors (suggesting that males and females did not use habitat types similarly) from April to July, but not in August or September (Table 2).

Female bluegills used all vegetated and open-water habitats in proportion to their availability (Figure 3). However, male bluegills positively selected vegetation, particularly in spring and early summer. Males were three times more likely to be present in vegetated habitats than in open-water habitats in April ($\chi^2 = 8.11$, $df = 1$, $P < 0.001$) and June ($\chi^2 = 10.77$, $df = 1$, $P = 0.001$) and twice as likely to be in vegetated habitats in July ($\chi^2 = 6.81$, $df = 1$, $P = 0.01$). However, male bluegills used vegetated and open-water habitats in proportion to their availability in May ($\chi^2 =$

TABLE 1.—Logistic regression analysis testing whether the proportion of bluegill locations differed among habitats or diel periods during April–September 2000 in Pelican Lake, Nebraska. The four habitats consisted of open water and areas with emergent vegetation only, submergent vegetation only, and both emergent and submergent vegetation. The diel periods were dawn (2 h before to 2 after sunrise), daytime, dusk (2 h before to 2 h after sunset), and night.

Month	Source	χ^2	df	P
Apr	Diel period	0.001	3	0.99
	Habitat type	136.99	1	<0.001
	Diel period \times habitat type	1.41	9	0.70
May	Diel period	0.49	3	0.92
	Habitat type	55.02	2	<0.001
	Diel period \times habitat type	0.49	6	0.67
Jun	Diel period	0.26	3	0.97
	Habitat type	70.21	3	<0.001
	Diel period \times habitat type	10.17	9	0.34
Jul	Diel period	0.21	3	0.98
	Habitat type	88.43	3	<0.001
	Diel period \times habitat type	5.26	9	0.81
Aug	Diel period	0.84	3	0.84
	Habitat type	75.95	3	<0.001
	Diel period \times habitat type	5.88	9	0.75
Sep	Diel period	0.17	3	0.98
	Habitat type	45.30	3	<0.001
	Diel period \times habitat type	12.15	9	0.21

TABLE 2.—Logistic regression analysis testing whether the proportion of bluegill locations differed among habitats or between sexes during April–September 2000 in Pelican Lake, Nebraska. See the caption to Table 1 for habitat types.

Month	Source	χ^2	df	<i>P</i>
Apr	Sex	0.001	1	0.99
	Habitat type	84.40	1	<0.001
	Sex \times habitat type	27.83	1	<0.001
May	Sex	3.31	1	0.07
	Habitat type	43.66	2	<0.001
	Sex \times habitat type	13.74	2	<0.001
Jun	Sex	0.53	1	0.47
	Habitat type	78.05	3	<0.001
	Sex \times habitat type	27.25	3	<0.001
Jul	Sex	0.53	1	0.47
	Habitat type	93.06	3	<0.001
	Sex \times habitat type	8.90	3	0.03
Aug	Sex	0.50	1	0.48
	Habitat type	83.98	3	<0.001
	Sex \times habitat type	5.24	3	0.16
Sep	Sex	0.01	1	0.91
	Habitat type	47.60	3	<0.001
	Sex \times habitat type	1.81	3	0.61

1.02, *df* = 1, *P* = 0.31). Female bluegills showed no positive selection for vegetation or open water in April (χ^2 = 0.25, *df* = 1, *P* = 0.62), May (χ^2 = 2.91, *df* = 1, *P* = 0.09), June (χ^2 = 1.57, *df* = 1, *P* = 0.21), or July (χ^2 = 0.04, *df* = 1, *P* = 0.85). Bluegills used vegetated and open-water habitats in proportion to their availability in August (χ^2 = 1.21, *df* = 1, *P* = 0.27) and September (χ^2 = 0.092, *df* = 1, *P* = 0.76), the only months when males and females used habitat types similarly. Bluegills never positively selected open water over vegetation in any month sampled.

When bluegills selected any vegetation, they typically selected emergent vegetation taxa (Table 3). During April, male bluegills were two times more likely to be located among bulrushes than among other vegetation, but showed no positive or negative selection for cattails or common reeds (χ^2 = 12.54, *df* = 3, *P* = 0.006). During June, male bluegills positively selected bulrushes, common reeds, and cattails, and negatively selected coontails (χ^2 = 43.92, *df* = 5, *P* < 0.001). However, in July, male bluegills positively selected common reeds, cattails, and submergent long-leaf pondweeds, and negatively selected bulrushes (χ^2 = 56.82, *df* = 7, *P* < 0.001). Males in all other months and females in all months exhibited no positive or negative selection for any vegetation category. Although bluegill selection for particular vegetation types was not statistically detectable for August, we recorded only the lowest cattail density (i.e., category 1, virtually no cattails) at our ran-

dom sites, whereas 22% of fish locations were in cattail densities higher than category 1 (i.e., densities of at least 2%), suggesting that larger fish may have positively selected for cattails in August. Bluegills were only found in the lowest vegetation density category for cattails and floating-leaf pondweeds in September (i.e., virtually no cattails or floating-leaf pondweeds).

Discussion

We found no evidence that bluegills in Pelican Lake used vegetated and open-water habitats differently across diel periods. Because bluegills are sight feeders and feed during diurnal periods (Keast and Welsh 1968; Werner and Hall 1974), we expected them to select habitats that provided the greatest foraging profitability during diurnal periods. However, during this study, bluegills used the same habitats regardless of diel period, suggesting foraging profitability may be similar across diel periods. Because water clarity was limited (i.e., Secchi depth transparency was <0.5 m) in Pelican Lake, visual predators such as northern pike may not have had much advantage during daylight periods. Therefore, in this relatively turbid lake, diel period may not affect the habitat choice of potential prey (i.e., bluegills) as strongly.

Male bluegills in Pelican Lake positively selected emergent vegetation over submergent vegetation and open-water habitats during spring and early summer (except in May), whereas females used vegetated and open-water habitats in proportion to their availability during all months, suggesting random selection of habitat types. In general, bluegills in April and June positively selected for bulrushes and cattails, with selection of long-leaf pondweeds in July as the only instance of positive selection for submergent vegetation. The larger bluegills in our study neutrally selected for open-water habitats, suggesting that open water was still used by the bluegills, particularly the slightly larger females.

The positive selection of emergent vegetation by large bluegills in Pelican Lake may be attributed to predator avoidance. The minimum size of bluegills in our study was 200 mm TL, and some predators in Pelican Lake were large enough to consume bluegills of this size or larger. Gillen et al. (1981) suggested that a tiger muskellunge (muskellunge *Esox masquinongy* \times northern pike), which is morphologically similar to a northern pike, can consume prey sizes up to 30% of its total length. This would mean that northern pike larger than 677 mm TL could consume bluegills in our

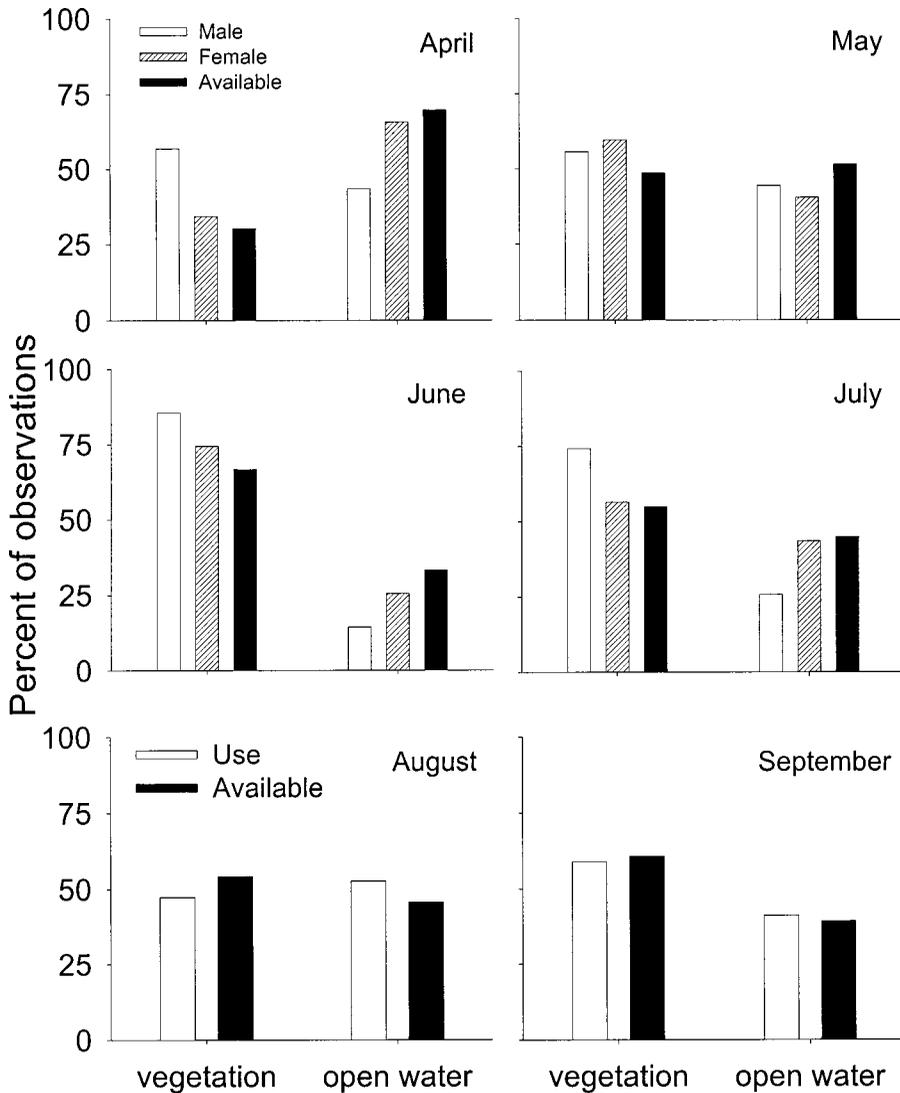


FIGURE 3.—Proportion of telemetry locations of radio-tagged bluegills observed in vegetated or open-water habitats in relation to the available habitat in Pelican Lake, Nebraska, from April to September 2000.

TABLE 3.—Vegetation selection by male bluegills implanted with radio transmitters in Pelican Lake, Nebraska, April–September 2000. Female bluegills did not select for vegetation during any month; males did not select for vegetation in May, August, or September. *P*-values for the coefficients of the logistic regression equation are provided.

Month	Positive		Negative		No preference	
	Taxon	<i>P</i>	Taxon	<i>P</i>	Taxon	<i>P</i>
Apr	Bulrush	<0.01			Cattail	0.18
					Common reed	0.11
Jun	Bulrush	<0.01	Coontail	<0.01	Long-leaf pondweed	0.47
	Cattail	0.04				
	Common reed	<0.01				
Jul	Cattail	<0.01	Bulrush	0.05	Long-leaf pondweed	0.33
	Common reed	<0.01			Coontail	0.39
	Floating-leaf pondweed	<0.01			Water milfoil	0.34

study. However, Margenau et al. (1998) found that northern pike up to 780 mm TL in Wisconsin lakes rarely consumed bluegills longer than 200 mm and typically consumed laterally-compressed prey smaller than the 30% of predator length reported by Gillen et al. (1981). Lawrence (1958) estimated that, based on mouth gape measurements, the minimum size of largemouth bass that could consume a 207-mm bluegill was 546 mm TL. At the end of our study in September 2000, annual sampling by the U.S. Fish and Wildlife Service found that the maximum size of northern pike collected was 780-mm TL, with 38% of northern pike exceeding 667 mm TL (USFWS 2000). However, the maximum length of largemouth bass sampled was only 520 mm (USFWS 2000).

Another possible explanation for the positive selection of emergent vegetation by bluegills may be prey preference or availability. In Cozad and Watts lakes, two other Nebraska Sandhill lakes, bluegills preferred chironomids and amphipods, while zooplankton contributed less than 7% (by weight) to the diet (Olson et al., in press). Bluegill diets consisting of macroinvertebrates have also been documented in Florida lakes (Schramm and Jirka 1989), the Mississippi River backwaters in Wisconsin (Dewey et al. 1997), and natural Michigan lakes (Schneider 1999). In a previous Pelican Lake study (Paukert and Willis 2000), densities of zooplankton (1,178 individuals/L) and benthic macroinvertebrates (1,377 individuals/m²) in both open water and combined vegetation suggested high invertebrate abundance, which may make foraging profitable in both habitat types. In addition, samples taken from Pelican Lake from April to September 2001 revealed that zooplankton and benthic macroinvertebrate densities did not differ between vegetated and open-water habitats (T. J. DeBates, South Dakota State University, unpublished data). Because both emergent and submergent vegetation were distributed in patches throughout Pelican Lake, vegetation refugia were close to open water, possibly making open-water foraging less risky. In addition, relative abundance of bluegills smaller than 80 mm TL in fall trapnet samples did not differ between nearshore and offshore samples (C. Paukert, unpublished data). Therefore, bluegill foraging patterns described in other studies for lakes with vegetated littoral zones and unvegetated limnetic zones (e.g., Keast 1978; Mittelbach 1981; Werner and Hall 1988) may not apply to bluegills in Pelican Lake.

The reason for positive selection of emergent vegetation by male bluegills in some months, in

contrast to the absence of notable habitat selection by females, is unclear. Although female bluegills in our study were, on average, larger than males, the difference was only 14 mm. Therefore, size was unlikely to have influenced bluegill habitat selection more than sex. The positive selection by males for emergent vegetation in June and July may be related to spawning. Avila (1976) reported bluegills spawning at depths less than 1.0 m over sand substrates, which describes the majority of Pelican Lake. Perhaps the male bluegills were guarding nests located near emergent vegetation during June and July, a behavior that would be similar to that of black crappies *Pomoxis nigromaculatus* in two South Dakota waters (Pope and Willis 1997). Because water clarity was low (typically <0.5 m), we could not visually document bluegill spawning or nesting behavior. Another possible reason for sexual differences in bluegill vegetation selection may be morphological differences in males and females. In a controlled study, Ehlinger (1999) found that male bluegills retained a deeper body morphology that was more efficient for foraging in vegetated environments, whereas female body morphology was adapted to either the open water or vegetated environments. Although the explanation for positive selection of emergent vegetation is unclear, bluegill size structure, growth, and body condition increased with increasing emergent vegetation coverage in 30 Sandhill lakes, indicating the importance of emergent vegetation to bluegills in these systems (Paukert et al. 2002). Protection or enhancement of emergent vegetation may benefit the maintenance or development of quality bluegill populations in these shallow, natural lakes.

Habitat selection by larger bluegills in Pelican Lake differed by sex and season but not diel period. However, it is unclear whether the mechanisms influencing vegetated habitat selection by smaller bluegills (e.g., Mittelbach 1981) are similar to those for the larger bluegills used in this study. Additional research is needed to determine the mechanisms for emergent and submergent vegetation selection by larger bluegills in systems with homogenous habitats.

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References

- Avila, V. L. 1976. A field study of nesting behavior of male bluegill sunfish (*Lepomis macrochirus* Rafinesque). *American Midland Naturalist* 96:195–206.
- Brown, M. L., and T. St. Sauver. 2002. An assessment of yellow perch, *Perca flavescens*, stocking contributions in eastern South Dakota lakes. *Fisheries Management and Ecology* 9:225–234.
- Daubenmire, R. F. 1959. A canopy coverage method of vegetational analysis. *Northwest Science* 33:43–64.
- Dewey, M. R., W. B. Richardson, and S. J. Zigler. 1997. Patterns of foraging and distribution of bluegill sunfish in a Mississippi River backwater: influence of macrophytes and predation. *Ecology of Freshwater Fish* 6:8–15.
- Ehlinger, T. J. 1999. Ecology, phenotype, and character evolution in bluegill sunfish. Pages 121–130 in S. A. Foster and J. A. Endler, editors. *Geographic variation in behavior: perspectives in evolutionary mechanisms*. Oxford University Press, New York.
- Engel, S. 1987. Impact of submergent macrophytes on largemouth bass and bluegills. *Lake and Reservoir Management* 3:227–234.
- ESRI (Environmental Systems Research Institute, Inc). 1999. *Getting to know ArcView GIS*. ESRI Press, Redlands, California.
- Gillen, A. L., R. A. Stein, and R. F. Carline. 1981. Predation by pellet-reared tiger muskellunge on minnows and bluegills in experimental systems. *Transactions of the American Fisheries Society* 110:197–209.
- Gotceitas, V., and P. Golgan. 1987. Selection between densities of artificial vegetation by young bluegills avoiding predation. *Transactions of the American Fisheries Society* 116:40–49.
- Helfman, G. S. 1981. Twilight activities and temporal structure in a freshwater fish community. *Canadian Journal of Fisheries and Aquatic Sciences* 38:1405–1420.
- Keast, A. 1978. Feeding interrelations between age groups of pumpkinseed (*Lepomis gibbosus*) and comparisons with bluegill (*L. macrochirus*). *Journal of the Fisheries Research Board of Canada* 35:12–27.
- Keast, A., and M. G. Fox. 1992. Space use and feeding patterns of an offshore fish assemblage in a shallow mesotrophic lake. *Environmental Biology of Fishes* 34:159–170.
- Keast, A., and L. Welsh. 1968. Daily feeding periodicities, food uptake rates, and dietary changes with hour of day in some lake fishes. *Journal of the Fisheries Research Board of Canada* 25:1133–1144.
- Lawrence, J. M. 1958. Estimated sizes of various forage fishes largemouth bass can swallow. *Proceedings of the Annual Conference Southeastern Association of Game and Fish Commissioners* 11(1957):220–225.
- Margenau, T. L., P. W. Rasmussen, and J. M. Kampa. 1998. Factors affecting growth of northern pike in small northern Wisconsin lakes. *North American Journal of Fisheries Management* 18:625–639.
- Mittelbach, G. G. 1981. Foraging efficiency and body size: a study of optimal diet and habitat use by bluegills. *Ecology* 62:1370–1386.
- Olson, N. W., C. P. Paukert, D. W. Willis, and J. A. Klammer. In press. Prey selection and diets of bluegill *Lepomis macrochirus* with differing population characteristics in two Nebraska natural lakes. *Fisheries Management and Ecology*.
- Paukert, C. P., P. J. Chvala, B. L. Heikes, and M. L. Brown. 2001. Effects of implanted transmitter size and surgery on survival, growth, and wound healing of bluegill. *Transactions of the American Fisheries Society* 130:975–980.
- Paukert, C. P., and D. W. Willis. 2000. Factors affecting panfish populations in sandhill lakes. Nebraska Game and Parks Commission, Federal Aid in Sport Fish Restoration Project F-118-R, Job 1, Segments 1 and 2, Completion Report, Lincoln.
- Paukert, C. P., and D. W. Willis. 2002. Bluegill habitat use in Pelican Lake, Nebraska. Nebraska Game and Parks Commission, Federal Aid in Sport Fish Restoration Project F-118-R, Job 1, Segment 4, Final Report, Lincoln.
- Paukert, C. P., and D. W. Willis. In press. Population characteristics and ecological role of northern pike in shallow Nebraska natural lakes. *North American Journal of Fisheries Management*.
- Paukert, C. P., D. W. Willis, and D. W. Gabelhouse, Jr. In press. Effect and acceptance of bluegill length limits in Nebraska natural lakes. *North American Journal of Fisheries Management*.
- Paukert, C. P., D. W. Willis, and J. A. Klammer. 2002. Effects of predation and environment on quality of yellow perch and bluegill populations in Nebraska sandhill lakes. *North American Journal of Fisheries Management* 22:86–95.
- Pope, K. L., and D. W. Willis. 1997. Environmental characteristics of black crappie (*Pomoxis nigromaculatus*) nesting sites in two South Dakota waters. *Ecology of Freshwater Fish* 6:183–189.
- Sarker, A. L. 1977. Feeding ecology of the bluegill, *Lepomis macrochirus*, in two heated reservoirs of Texas III. Time of day and patterns of feeding. *Transactions of the American Fisheries Society* 106:596–601.
- Savino, J. F., and R. A. Stein. 1982. Predator–prey interaction between largemouth bass and bluegills as influenced by simulated submersed vegetation. *Transactions of the American Fisheries Society* 111:255–266.

- Schneider, J. C. 1999. Dynamics of quality bluegill populations in two Michigan lakes with dense vegetation. *North American Journal of Fisheries Management* 19:97–109.
- Schramm, H. L., Jr., and K. J. Jirka. 1989. Epiphytic macroinvertebrates as a food resource for bluegills in Florida lakes. *Transactions of the American Fisheries Society* 118:416–426.
- Schramm, H. L., Jr., K. J. Jirka, and M. V. Hoyer. 1987. Epiphytic macroinvertebrates on dominant macrophytes in two central Florida lakes. *Journal of Freshwater Ecology* 4:151–161.
- Stokes, M. E., C. S. Davis, and G. G. Koch. 1995. Categorical data analysis using the SAS system. SAS Institute, Cary, North Carolina.
- USFWS (U. S. Fish and Wildlife Service). 2000. Results from the 2000 fishery assessment survey conducted on the Valentine National Wildlife Refuge. USFWS Great Plains Fish and Wildlife Management Assistance Office, Pierre, South Dakota.
- Werner, E. E., and D. J. Hall. 1974. Optimal foraging and the size selection of prey by the bluegill sunfish (*Lepomis macrochirus*). *Ecology* 55:1042–1052.
- Werner, E. E., and D. J. Hall. 1988. Ontogenetic habitat shifts in bluegill: the foraging rate–predation risk trade-off. *Ecology* 69:1352–1366.