

# Associations between hydrological connectivity and resource partitioning among sympatric gar species (Lepisosteidae) in a Texas river and associated oxbows

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**Abstract** – The middle Brazos River, located in east-central Texas, is a meandering lowland river with many oxbow lakes on its flood plain. Flood dynamics of the Brazos River are aseasonal, and faunal exchange during lateral connections of the main river channel and oxbows is pulse-like and occurs only during floods that may be months or years apart. Patterns of resource use among sympatric gar species (*Lepisosteus oculatus*, *Lepisosteus osseus* and *Atractosteus spatula*) associated with river–flood plain connectivity were studied for a period of 2 years (May 2003 to May 2005). The first year was relatively dry yielding few lateral connections, whereas the second year was relatively wet resulting in more frequent lateral connections. This study focused on habitat and diet partitioning among the three gar species in oxbow habitats with different connection frequencies and an active river channel site. Overall, 684 gars were collected with experimental gillnets: 19 *A. spatula* (alligator gar), 374 *L. oculatus* (spotted gar) and 291 *L. osseus* (longnose gar). There was strong partitioning of habitat between spotted and longnose gars, in which 98% of spotted gars were captured in oxbow habitats and 84% of longnose gars were captured in the river channel. Hydrology did not appear to affect habitat partitioning, although longnose gar abundance significantly increased in oxbows during the wet year. Diet overlap was high between spotted and longnose gars. Temporal variation in diet was significantly influenced by flood pulses that connected oxbows with the river channel, and which allowed predators and their prey to move between habitats.

Key words: diet; flood pulse; habitat partitioning

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## Introduction

Despite their unique morphological characteristics, ancient origins and broad distributions in North America, fishes in the order Lepisosteiformes have received relatively little attention in the ecological literature. The seven living gar species of the family Lepisosteidae are found in North America, Central America and Cuba (Helfman et al. 1999). Most studies on the ecology of this ancient lineage of fishes have

focused on the impact of gars on recreationally important species, by either directly consuming them or competing with them for prey (Lagler & Hubbs 1940; Bonham 1941; Lagler et al. 1942; Crumpton 1971). The paucity of ecological research on gars may be associated with their history of classification as ‘rough’ or ‘trash’ fish by many natural resource agencies.

Three sympatric gar species occur in the Middle Brazos River, Texas, and its associated oxbow lakes:

alligator gar (*Atractosteus spatula*), spotted gar (*Lepisosteus oculatus*) and longnose gar (*Lepisosteus osseus*). The Middle Brazos River maintains a dynamic channel and flood plain, allowing for river–oxbow connections during stochastic flood events. These hydrologic connections allow piscivores, such as gars, to move between flood plain and river habitats to exploit abundant prey, or to consume prey as they move between habitats (Ross & Baker 1983; Kwak 1988; Winemiller 1996, Zeug et al. 2005).

Here, we investigate resource use among the three sympatric gar species in the Middle Brazos River during a year with relatively few river–oxbow connections and a year with frequent river–oxbow connections. We compared both habitat use (oxbow vs. river channel) and diet during periods of isolation and following periods of flood connection.

## Methods

### Study site

The Brazos River originates in north-west Texas, and flows south-east across the state entering the Gulf of Mexico near Freeport, TX. Our study focused on the middle Brazos River (between 30°25'N and 30°37'N), a meandering lowland reach with a broad floodplain dominated by forest and agricultural lands. Aerial surveys identified more than 40 oxbow lakes on the flood plain of the middle Brazos River (Winemiller et al. 2000). Our sampling was conducted monthly from June 2003 to May 2005 at two oxbows (Big Bend and Moehlman's) and the Brazos River channel at the Texas State Highway 21 bridge. For more detailed descriptions of the study sites, refer to Winemiller et al. (2000) and Zeug et al. (2005).

Big Bend and Moehlman's oxbows differ geomorphologically (Winemiller et al. 2000). Big Bend oxbow is located closer to the active channel than Moehlman's oxbow, and lower flows are required to connect Big Bend oxbow with the river channel (Zeug et al. 2005). Figure 1 shows the daily stream flow hydrograph during the 2-year study period. The first year of the study was relatively dry with few connection events (dry year). In the second year, river–oxbow connection events were relatively frequent (wet year), yielding multiple connections of Moehlman's oxbow which, on average, connects with the river channel only once every 1.93 years (TWDB, 2004).

### Fish collection

Gars were collected using experimental multifilament gillnets consisting of three 16.5-m × 2-m panels of 2.54-, 5.1- and 7.6-cm bar meshes. Gillnets were set from approximately 16:00–08:00 hours. The duration

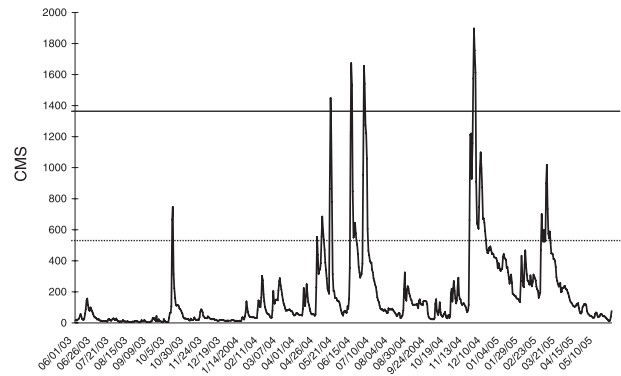


Fig. 1. Hydrograph of daily stream flow [ $\text{m}^3/\text{s}$  (CMS)] of the Brazos River at the Texas State Highway 21 bridge from June 2003 to May 2005. The lower line represents the minimum flow required to connect Big Bend oxbow, and the upper line is the minimum flow to connect Moehlman's oxbow. Connectivity estimates provided by the Texas Water Development Board (TWDB 2004).

of each gillnet set was recorded for calculations of catch-per-unit effort (CPUE). Gars captured in gillnets were transported to the laboratory on ice, measured to the nearest 0.1-cm standard length (SL), and weighed to the nearest gram. Stomachs were removed and fixed in a 10% formalin solution. Some studies have indicated that piscivores may regurgitate stomach contents when captured using gillnets (e.g., Sutton et al. 2004), but little evidence of regurgitation (few fully distended but empty stomachs) was encountered during this study.

To estimate prey abundance, small fishes and grass shrimp (Palaemonidae) were collected during each survey using a 10-m × 2-m bag seine with a 0.64-cm mesh in the wings and a 0.32-cm mesh in the bag, following Winemiller et al. (2000). The seine was hauled perpendicular to shore at different locations until three consecutive hauls yielded no additional species to the cumulative list. The distance of each seine haul was estimated for calculations of prey species CPUE. Fish and grass shrimp collected in the seine were preserved in 10% formalin and returned to the laboratory where they were identified to species, counted and weighed to the nearest 0.1 g. Based on comparisons with data from electrofishing and experimental gillnetting, seining was determined to be a highly effective method of surveying fish assemblages in oxbow lakes (Winemiller et al. 2000). Oxbows were uniformly shallow (0.5–2 m), and the 10-m × 2-m seine efficiently captured small and intermediate size classes of all fish species that were the principal prey of gar.

### Diet analysis

Fishes were identified to the lowest possible taxonomic level, and invertebrates were identified to order. Each prey item was counted, measured (SL for fishes and total length for all other prey items) to the nearest

1 mm, and its volume determined by water displacement (Winemiller & Pianka 1990) to the nearest 0.01 ml. For analysis, prey items were grouped by family for fish and order for invertebrates. Resource categories that consisted of unidentified or miscellaneous fish were not included in the calculation of indices. Diets were compared among gar species between seasons and years. Seasonal groupings were designated as summer (June–August), autumn (September–November), winter (December–February) and spring (March–May).

Diet overlap was estimated with Pianka's (1974) symmetrical niche overlap:

$$\phi_{jk} = \frac{\sum p_{ij}p_{ik}}{\sqrt{\sum p_{ij}^2 \sum p_{ik}^2}}$$

where  $p_{ij}$  and  $p_{ik}$  represent the volumetric proportion of prey category  $i$  in the diet of consumer species  $j$  and  $k$  respectively. Values for this symmetrical overlap index range from zero, which indicates no overlap in diet, to 1, indicating an identical diet or complete overlap between consumer species  $j$  and  $k$ , respectively.

Resource preferences were calculated using Lawlor's (1980) electivities ( $e_{ij}$ ). For each consumer species  $j$ , electivities were calculated for each prey category  $i$  as:

$$e_{ij} = \frac{p_{ij}}{R_i}$$

where  $p_{ij}$  is the volumetric proportion of prey category  $i$  in the diet of consumer species  $j$ , and  $R_i$  is the relative proportion of prey species (fish and grass shrimp)  $i$  in the habitat (seine samples). To make comparisons, all electivities were standardised as a percentage of the totals.

An index of relative importance (IRI) (Pinkas et al. 1971) also was calculated for each prey category  $i$  found in the diet of each consumer species  $j$ :

$$\text{IRI}_{ij} = (\% \text{ by number} + \% \text{ by volume}) \\ \times \% \text{ frequency of occurrence}$$

As with the electivities, to make comparisons between seasons, sites and species, the IRIs were standardised as per cent IRI.

Niche breadth ( $B_j$ ) for each consumer species  $j$  was calculated using Levins (1968) measure:

$$B_j = \frac{1}{\sum p_{ij}^2}$$

where  $p_{ij}$  is the volumetric fraction of prey item  $i$  in the total diet of consumer species  $j$ . Values of  $B_j$  range from 1, indicating a minimum niche breadth or maximum specialisation, to  $n$ , where  $n$  is equal to the total number of resource states (or prey categories)

indicating a maximum niche breadth and minimum specialisation. For this study, there was a total of 20 prey categories (Appendix I). Niche breadth was standardised to make comparisons between species and habitat using Hurlbert's (1978) method:

$$B_A = \frac{B_j - 1}{n - 1}$$

where  $B_A$  is Levins' standardised niche breadth for consumer species  $j$ , with values ranging from 0 to 1, indicating minimum and maximum niche breadth, respectively.

To assess resource partitioning by prey size, predator weight (g) and prey SL (mm) were log transformed and plotted against each other. Predator weight was used, as spotted gars and longnose gars differ in morphology. A linear regression was used to determine the relationship between gar weight and prey SL.

### Statistical analysis

Chi-square tests were calculated to test for significant ( $\alpha < 0.05$ ) differences in gar abundance in river and oxbow habitats between years, as well as for differences between average gar SLs across habitats. A principal components analysis (PCA) was performed on matrices of volumetric proportions of prey items according to species, sites and seasons using CANOCO (version 4; Microcomputer Power, Ithaca, NY, USA).

## Results

### Habitat

During the 2-year study, 693 gars were collected in gillnets. In the dry year, 411 gars were collected, and in the wet year 282 gars were collected. Gar CPUE was greater in the Brazos River and Moehلمان's oxbow than Big Bend oxbow (Table 1). Overall, 89.4% of alligator gars and 98.1% of spotted gars were captured from oxbow habitats (Table 1). By contrast, 84.3% of longnose gars were collected from the river channel.

Distributions of spotted gar captures did not vary much between years. During the dry year, 98.7% of spotted gars were collected in oxbows and only three individuals were collected from the river channel (Table 1). During the wet year, 96.9% of spotted gars were collected from oxbows and four individuals were collected from the river channel. Spotted gar abundance in oxbows significantly decreased during the wet year ( $\chi^2 = 315.1$ , d.f. = 1,  $P < 0.001$ ). During the dry year, 97.0% of longnose gars were collected from the river channel and only five individuals were collected from oxbow habitats. Captures of longnose gars from oxbow habitats significantly increased from 3.0%

		<i>Atractosteus spatula</i> N (%)	<i>Lepisosteus oculatus</i> N (%)	<i>Lepisosteus osseus</i> N (%)	Total CPUE
Dry year	Brazos River	1 (50.0)	3 (1.2)	161 (97.0)	0.42
	Big Bend	1 (50.0)	65 (26.7)	3 (1.8)	0.25
	Moehlman's	–	175 (72.0)	2 (1.2)	0.44
Wet year	Brazos River	1 (5.9)	4 (3.1)	93 (68.9)	0.44
	Big Bend	9 (52.9)	45 (34.6)	23 (17.0)	0.22
	Moehlman's	7 (41.2)	81 (62.3)	19 (14.1)	0.31
Total	Brazos River	2 (10.5)	7 (1.9)	254 (84.3)	0.43
	Big Bend	10 (52.6)	110 (29.5)	26 (8.6)	0.23
	Moehlman's	7 (36.8)	256 (68.6)	21 (7.0)	0.38
Stomachs examined (% empty)	Brazos River	2 (50.0)	7 (57.1)	215 (69.8)	
	Big Bend	10 (50.0)	110 (29.1)	26 (34.6)	
	Moehlman's	7 (42.9)	254 (26.8)	21 (42.9)	
	Total	19 (47.3)	371 (28.0)	262 (64.1)	

Table 1. Total catches of gar species by year and sample site, and total stomachs examined for diet content analysis by site and species.

during the dry year to 31.1% during the wet year ( $\chi^2 = 442.3$ , d.f. = 1,  $P < 0.001$ ). Longnose gar abundance in the river channel was not significantly different between years ( $\chi^2 = 1.1$ , d.f. = 1,  $P = 0.29$ ). During the dry year, only two alligator gars were collected, one from an oxbow (Big Bend) and one from the river channel. During the wet year, 17 alligator gars were collected, with 94.1% captured from oxbows and only one individual captured from the river channel. Alligator gar abundance was significantly greater in oxbows during the wet year ( $\chi^2 = 202.5$ , d.f. = 1,  $P < 0.001$ ). All alligator gars captured from oxbows were juveniles that ranged in size from 409 to 810 mm, whereas both of the alligator gars captured in the river channel were adults (1474 and 1850 mm).

### Diet

From the 693 gars collected, a total of 652 stomachs was removed for analysis (Table 1). Gars in both Big Bend and Moehlman's oxbows had a low occurrence of empty stomachs (37.9% and 37.5% respectively), whereas gars in the river channel had a high occurrence of empty stomachs (59.0%). Between species, longnose gar had the highest occurrence of empty stomachs and spotted gar had the lowest occurrence of empty stomachs (Table 1).

### Diet breadth

Gar diet breadth was highly variable between sites and years (Fig. 2). During the dry years, longnose gars in the river channel had higher diet breadth than spotted gars in oxbows, but longnose gars had lower diet breadth than spotted gars during the wet year. Spotted gars in Big Bend oxbow had higher diet breadth than those in Moehlman's. Spotted gar diet breadth in both oxbows increased during the spring of the dry year which coincided with over-bank flooding of both habitats (Fig. 1). During the autumn and winter of the dry year when Big Bend oxbow was drying out and fish

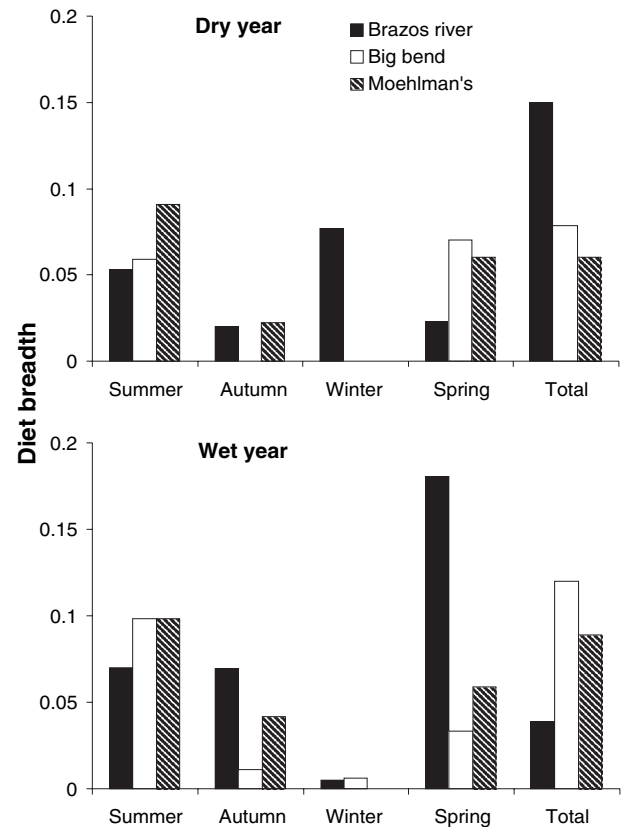


Fig. 2. Seasonal diet breadths, based on 15 prey categories during the dry year and 20 prey categories for the wet year for *Lepisosteus oculatus* in Moehlman's and Big Bend oxbows and *Lepisosteus osseus* in the Brazos River.

abundances had declined, spotted gars in that habitat consumed only crayfish (Cambaridae). Spotted gars in Moehlman's oxbow consumed only shad (Clupeidae) during the winter of both the dry and wet years.

### Diet composition

Overall, shad and sunfish (Centrarchidae) were the most important prey items for spotted gars in oxbow habitats, whereas mayflies (Ephemeroptera) and

Table 2. Standardised index of relative importance (IRI) for dominant food items consumed by gar species by year, season and habitat.

			Dry year					Wet year				
			Summer	Autumn	Winter	Spring	Annual	Summer	Autumn	Winter	Spring	Annual
<i>Lepisosteus oculatus</i>	Big Bend	Catfish	–	–	–	7.1	4.8	23.3	7.1	–	–	13.8
		Crayfish	–	100	100	55.0	42.4	2.3	–	19.3	38.0	6.1
		Grasshopper	1.9	–	–	–	0.9	61.1	–	–	–	37.4
		Shad	48.5	–	–	–	15.6	13.2	76.5	80.7	–	32.2
		Sunfish	39.2	–	–	35.4	30.7	–	16.4	–	62.0	10.5
	Moehlman's	Catfish	–	–	–	–	–	23.6	–	–	–	11.3
	Shad	66.2	87.3	100	56.9	74.6	37.2	77.9	100	37.7	58.0	
	Sunfish	14.1	3.8	–	–	8.8	39.3	22.1	–	46.5	28.6	
<i>Lepisosteus osseus</i>	Brazos River	Catfish	45.5	17.8	25.2	6.3	20.4	31.5	39.6	64.6	13.9	41.1
		Mayflies	7.8	–	–	–	3.0	57.2	–	–	7.9	44.7
		Minnows	30.2	–	9.1	29.3	19.9	11.3	48.3	–	13.9	6.9
		Shad	–	54.3	–	46.4	21.6	–	–	18.0	–	1.1
		Sunfish	–	–	44.6	–	14.3	–	–	–	–	–

catfish (Ictaluridae) were the most important prey items for longnose gars in the river channel (Table 2). Based on electivities, catfish were the most selected prey item for longnose gars in the river channel ( $%e_{ij} = 67.3\%$ ) and spotted gars in oxbow habitats (81.0%). For spotted gars in Big Bend oxbow, crayfish (27.7%) were the most important prey item, and shad were the most important prey item for spotted gars in Moehlman's oxbow. Sunfish were also an important prey for spotted gars in both oxbows (Big Bend: 22.3%, Moehlman's: 16.5%). Based on a limited sample size, shad (37.5%) and suckers (Catastomidae, 31.7%) were the most important prey for alligator gars.

Variation in the relative importance of other prey taxa in gar diets also was observed between habitats and years. During the wet year, shad were the most important prey, followed by catfish and minnows (Cyprinidae), for longnose gars in the river channel (Table 2). During the dry year, mayflies and catfish were the most important prey items for longnose gars, while shad importance decreased. Crayfish and sunfish were the most important prey items for spotted gars in Big Bend oxbow during the dry year, but during the wet year, shad and grasshoppers (Orthoptera) increased in importance along with catfish. For spotted gars in Moehlman's oxbow, sunfish and catfish importance increased during the second (wet) year, whereas shad importance decreased.

For the statistical analysis of the diet composition data, the first two axes of PCA combined to explain 65.3% of the variation in diet (Fig. 3). Axis 1 loadings from low to high include crayfish (0.11), minnows (0.16), catfish (0.41) and shad (3.65). Axis 2 loadings from low to high include shad (–0.44), crayfish (0.25), sunfish (0.64) and catfish (2.71). In Big Bend oxbow, crayfish were important in the diet of spotted gars during the dry year when fish prey items were declining in abundance (total prey fish CPUE:

summer: 62.1, autumn: 19.7, winter: 5.8 and spring: 19.8). After the river connected with the oxbow during the summer of the dry year and spring of the wet year, there were shifts toward greater shad consumption. Similarly, catfish were the most important prey item for longnose gars in the Brazos River, and after the river connected with the oxbow during the autumn and spring floods of the dry year, shad became the most important prey item (Fig. 3). Shad abundance was low in the river prior to oxbow connection events (Fig. 4). Moehlman's oxbow had low frequencies of hydrological connections, and spotted gars in this oxbow had a relatively stable diet dominated by shad. Following flood connections during the spring of the dry year and summer of the wet year in Moehlman's oxbow, spotted gar diets included more catfish, but later switched back to shad (Fig. 3).

*Dietary overlap*

Dietary overlap between the two most common gar species, longnose and spotted combined across all habitats and years was high: 72.7% during the dry year and 90.1% during the wet year. Dietary overlap between longnose and alligator gars was 41% and between spotted and alligator gars was 43% during the wet year (alligator gar diet data were only analysed for the wet year). Dietary overlap between longnose and spotted gars varied seasonally. During the dry year, dietary overlap was the highest in autumn, which coincided with a hydrological connection with Big Bend oxbow (Fig. 1). During the wet year, summer and winter had higher dietary overlaps, which coincided with hydrologic connections between the river and both oxbows.

*Predator–prey size relationships*

Predator–prey size relationships (Fig. 5) were examined based on 311 measurable prey items for spotted

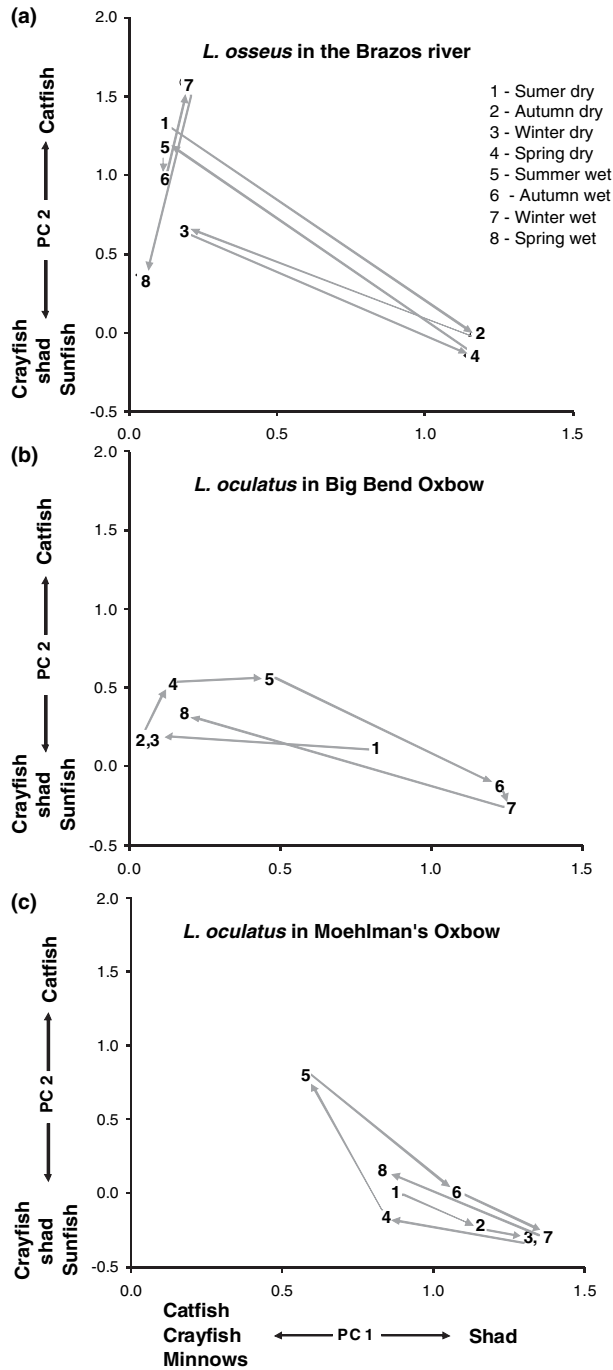


Fig. 3. PCA ordination plots based on seasonal volumetric proportions of diet items by gar species and habitat. (a) *Lepisosteus osseus* in the Brazos River, (b) *Lepisosteus oculatus* in Big Bend Oxbow and (c) *L. oculatus* in Moehlman's oxbow.

gars and 123 measurable prey items for longnose gars. Most of the prey consumed by longnose and spotted gars were 30–80 mm. The average size of prey consumed by spotted and longnose gars was 55.0 and 65.7 mm, respectively. Based on a linear regression, prey size significantly increased as predator weight increased for both longnose and spotted gars

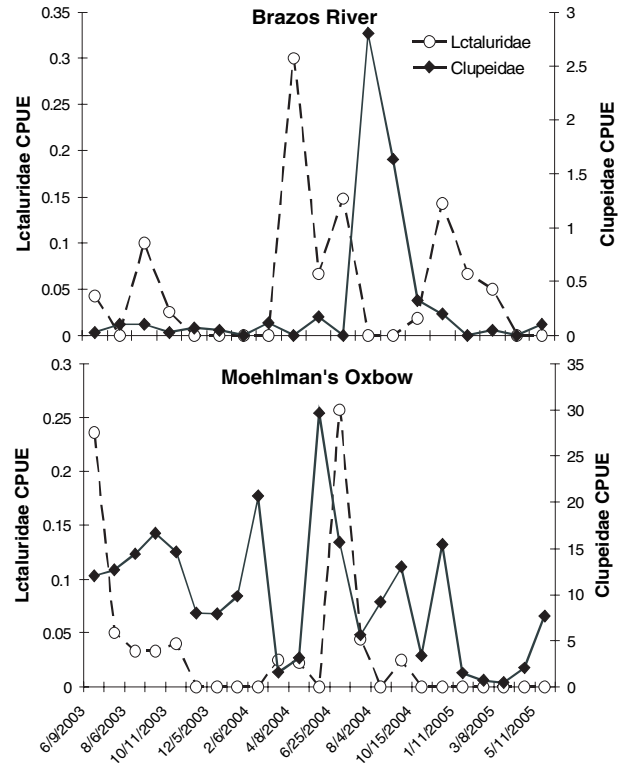


Fig. 4. Changes in abundance of shad (*Clupeidae*) and catfish (*Ictaluridae*) during the 2-year sampling period in the Brazos River and Moehlman's oxbow. CPUE for shad and catfish are at different scales on the Y-axis.

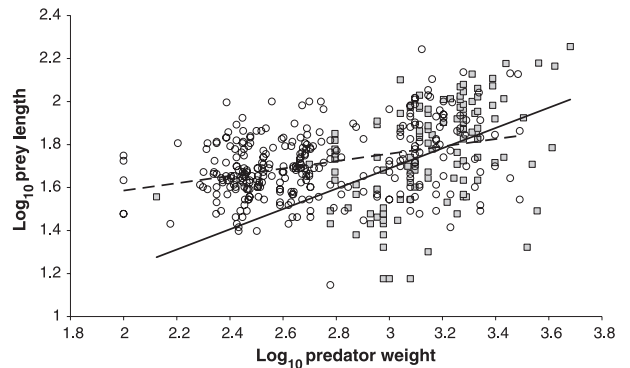


Fig. 5. Relationship between log-transformed prey length and log-transformed gar weight. (○ = *Lepisosteus oculatus*, □ = *Lepisosteus osseus*).

(longnose gar:  $SL_{prey} = 0.47[W_{gar}] + 0.27$ ,  $r^2 = 0.21$ ,  $F_{1,310} = 45.3$ ,  $P < 0.001$ ; spotted gar:  $SL_{prey} = 0.17[W_{gar}] + 1.24$ ,  $r^2 = 0.13$ ,  $F_{1,122} = 32.19$ ,  $P < 0.001$ ). Interspecific difference in the slope of the predator–prey relationship could not be determined due to a significant interaction between gar species and weight (ANCOVA:  $F_{2,434} = 35.7$ ,  $P < 0.001$ ).

## Discussion

### Habitat partitioning

Gar CPUE values suggest strong habitat partitioning between spotted and longnose gars in the Brazos River, with spotted gars most abundant in oxbows and longnose gars most abundant in the river channel. Similar habitat preferences in gars have been reported from other systems (Holloway 1954; Goodyear 1967; Snedden et al. 1999). Even during the wet year, with frequent lateral connections that provided corridors for gars to move between habitats, spotted gars remained within oxbow habitats (spotted gar CPUE did significantly decrease between years, but this likely was due to a doubling of water volume in oxbow habitats during the wet year). Longnose gars, however, significantly increased in abundance in oxbow habitats during the wet year.

Movement of riverine species into floodplain habitats during lateral connections has been well documented (Ross & Baker 1983; Kwak 1988; Miranda & Lucas 2004; Miranda 2005; Zeug et al. 2005). Many channel-dwelling fishes move onto floodplain habitats to spawn (Hohausová et al. 2003; Penczak et al. 2003) or to exploit the abundant food resources associated with off-channel habitats (Winemiller & Kelso-Winemiller 1994; O'Connell 2003). Longnose gars apparently enter oxbows to forage opportunistically on abundant prey rather than for spawning, as longnose gars seem to be stream spawners that require flow (Netsch & Witt 1962; Johnson & Noltie 1996). Conversely, spotted gars seem to prefer backwaters or areas with little or no flow for spawning (Echelle & Riggs 1972; Love 2004).

Alligator gars appeared to move into oxbow habitats during flood connections. Although based on a limited sample ( $N = 19$ ), alligator gar abundance significantly increased in oxbow habitats during the wet year, and all were juveniles. The alligator gar size distribution probably was skewed due to gear sampling bias. Throughout the study, there was evidence of large fish escaping capture (large holes in the multifilament gillnet), and a large alligator gar was observed in Big Bend oxbow during a flood connection. Adult alligator gars may move into oxbow habitats during floods to exploit abundant prey, and subsequently return to the river channel. By contrast, juvenile alligator gars appear to remain in oxbows for extended periods. There was no evidence that juvenile longnose gars moved into, or remained within oxbow habitats, based on average SL of longnose gars in the two habitats (river = 727 mm, oxbow = 700 mm,  $\chi^2 = 0.511$ , d.f. = 1,  $P = 0.48$ ). A potential advantage of juveniles remaining in oxbow habitats is enhanced foraging,

growth and survival, which have been shown in other species (Sommer et al. 2001).

### Diet partitioning

Based on high diet overlap, spotted and longnose gars do not seem to partition food resources. Other studies of piscivorous fishes in rivers have shown that diets often are similar for species that partition habitats (Jepsen et al. 1997, Sala & Ballesteros 1997; Wheeler & Allen 2003). Diet partitioning may be more prevalent among species that co-occur in the same habitat (Winemiller 1989; Bacheler et al. 2004; Pelicice & Agostinho 2006). Fishes comprised a major portion of the diet of both spotted and longnose gars, but they were not strict piscivores (Appendix I). The two species consumed both aquatic and terrestrial invertebrates, and longnose gars consumed terrestrial vertebrates as well.

Gars tend to consume prey in proportion to their availability (Holloway 1954; Goodyear 1967; Dugas et al. 1976; Seidensticker 1987; Snedden et al. 1999). Physical and environmental characteristics of oxbows have been shown to determine fish assemblage structure, and fish assemblages in Big Bend and Moehlman's oxbow differ, especially during periods of isolation (Winemiller et al. 2000; Zeug et al. 2005). These differences in fish assemblage structure were reflected in the diets of spotted gars in the two habitats. In Big Bend, sunfish were the most abundant fish (46.1% of total prey fish CPUE) and also were the most important fish in the diets of spotted gars. Crayfish, however, were the most important food item overall for spotted gars in Big Bend oxbow. Crayfish were abundant (C. R. Robertson and S. C. Zeug, personal observation) during the autumn and winter of the dry year when Big Bend oxbow was desiccating and fish abundances decreased. For a 6-month period (autumn and winter of the dry year), spotted gars in Big Bend consumed only crayfish until a flood connection in the spring refilled the oxbow. In Moehlman's oxbow, shad were the most abundant fish (38% of total prey fish CPUE), and also were the most important prey in spotted gar diets.

Longnose gars in the Brazos River did not seem to follow this trend of consuming the most abundant food resource in their habitat. In the Brazos River, minnows were the most abundant fish, but comprised only a small portion (8.5%) of longnose gar diets. Based on electivities, longnose gars were strongly selecting against minnows. Similarly, spotted gars selected against the second most abundant fish in both oxbows, mosquitofish (Poeciliidae), with only one individual consumed during the entire 2-year study. Gars probably select against minnows and mosquitofish because of their small size. Minnows and mosquitofish are

among the smallest fishes in the system and are probably not easily detected or captured by gars (Lundvall et al. 1999; Dörner & Wagner 2003).

In tropical floodplain systems, fishes have been shown to increase their diet breadth during flood periods (Winemiller & Kelso-Winemiller 1994; Balcombe et al. 2005). Spotted gars in both Big Bend and Moehlman's oxbows (Fig. 2) followed this pattern, with greater diet breadth during the wet year. Moreover, seasonal increases in diet breadth within years coincided with connections with the river channel. However, the opposite was observed for the longnose gar. Longnose gar diet breadth decreased during the wet year. Seasonal decreases in diet breadth within years also coincided with river channel connections. Thus, longnose gars seem to forage opportunistically on pulses of abundant prey according to flood dynamics. During flood connections (Fig. 1), shad were an important component in diets of longnose gars in the river channel. Shad abundances are typically low in the river channel, and high in oxbows and floodplain lakes (Winemiller et al. 2000; Miranda 2005; Barko et al. 2006; Pegg et al. 2006). Shad abundance increased in the Brazos River channel following flood connections (Fig. 4). This difference in prey spatial distributions creates a pulsed food subsidy (Winemiller & Jepsen 2004; Hoeinghaus et al. 2006) for longnose gars in the river channel. Based on electivity values, longnose gars selected shad when their abundance in the river channel increased following river-oxbow connections (dry year-autumn: 51.5%, spring: 73.1%; and wet year-summer: 95.9%, winter: 99.5%). The relative size (Lundvall et al. 1999; Dörner & Wagner 2003; Gill 2003) and mobility (Savino & Stein 1989; Ostrand et al. 2004) of shad probably make them vulnerable to large sit-and-wait predators such as gars.

Spotted gars in Brazos River oxbow habitats probably benefited from pulsed subsidies from the river channel. In both oxbows, floods were followed by an increased abundance of juvenile catfish, probably originating from the river channel. Catfish were the most selected prey for spotted gars in oxbows, as well as longnose gars in the river channel. Allochthonous food resources also were found in the diets of spotted gars. Grasshoppers were the most important diet item for spotted gars in Big Bend during the summer flood of the wet year when numerous grasshoppers were observed on the water surface of an inundated pasture.

The physical characteristics of oxbows (connection frequency) influence gar diets as well. Among the three habitats sampled, the river channel is the most dynamic habitat, followed by Big Bend oxbow which connects frequently with the river channel. Moehlman's oxbow requires higher flow rates for lateral

connections with the river channel and therefore is a relatively stable environment. This pattern was strongly reflected in the diet ordination (Fig. 3). In Big Bend oxbow, diets shifted from crayfish during 6 months when the oxbow was desiccating, to a diet dominated by fishes brought into the oxbow during a flood. In the Brazos River, catfish were the most important prey of longnose gars, but the diet shifted toward greater shad consumption following floods. Spotted gars in Moehlman's oxbow had a relatively stable diet comprised mostly of shad and sunfish, but they consumed more catfish after floods. Thus, relatively unpredictable flood pulses seem to be an important factor controlling upper food web dynamics in this temperate lowland river.

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## Appendix I.

Total volumes (ml) of prey items from stomach contents of the three gar species.

	<i>Lepisosteus oculatus</i>	<i>Lepisosteus osseus</i>	<i>Atractosteus spatula</i>
Fishes			
Clupeidae			
<i>Dorosoma cepedianum</i>	492.0	480.0	66.0
<i>Dorosoma petenense</i>	32.6	3.8	–
<i>Dorosoma spp.</i>	22.2	18.9	3.0
Centrarchidae			
<i>Lepomis cyanellus</i>	39.0	15.0	–
<i>Lepomis gulosus</i>	45.0	6.1	–
<i>Lepomis humilis</i>	6.0	–	–
<i>Lepomis megalotis</i>	53.0	–	–
<i>Lepomis spp.</i>	69.5	4.0	–
<i>Pomoxis annularis</i>	121.3	21.0	11.0
Centrarchidae	24.3	63.6	–
Ictaluridae			
<i>Ameiurus melas</i>	114.4	2.1	–
<i>Ameiurus natalis</i>	–	0.2	–
<i>Ictalurus furcatus</i>	–	19.9	18.2
<i>Ictalurus punctatus</i>	19.6	76.6	5.6
<i>Ictalurus spp.</i>	–	14.2	–
<i>Pylodictis olivaris</i>	–	20.0	–
Ictaluridae	1.2	14.2	–
Cyprinidae			
<i>Cyprinella lutrensis</i>	–	6.9	–
<i>Cyprinella venusta</i>	–	0.6	–
<i>Cyprinus carpio</i>	48.7	–	–
<i>Notropis buchanani</i>	–	0.4	–
<i>Notropis shumardi</i>	–	5.8	–
<i>Pimephales vigilax</i>	0.8	3.1	–
Cyprinidae	–	1.7	–
Catastomidae			
<i>Carpoides carpio</i>	–	48.8	–
<i>Ictiobus bubalus</i>	14.8	–	148.0
Lepisosteidae			
<i>Lepisosteus spp.</i>	–	–	25.0
Percidae			
<i>Percina sciera</i>	–	2.7	–
<i>Percina spp.</i>	–	1.1	–
Percidae	–	0.3	–
Atherinopsidae			
<i>Menidia beryllina</i>	–	2.1	–
Poeciliidae			
<i>Gambusia affinis</i>	1.0	–	–
Aquatic Invertebrates			
Cambaridae	272.3	0.1	–
Ephemeroptera larva	–	4.8	–
Macrobranchium	–	1.7	–

## Appendix I. (continued)

	<i>Lepisosteus oculatus</i>	<i>Lepisosteus osseus</i>	<i>Atractosteus spatula</i>
Odonata Anisoptera larva	–	0.6	–
Palaemonidae	1.4	2.9	–
Terrestrial Invertebrates			
Diptera Tipulidae	0.1	–	–
Orthoptera	47.6	1.5	–
Hymenoptera	–	0.1	–
Lepidoptera	–	0.7	–
Terrestrial Vertebrates			
Amphibia Anura	–	2.8	–
Rodentia	–	0.5	–