

## Habitat segregation in stream crayfishes: implications for conservation

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**Abstract.** Three-quarters of the world's crayfish fauna are found in the US and Canada. Small natural ranges, habitat disturbance, and introduced crayfish species threaten many species, and nearly ½ are imperiled. Naturally small ranges are considered the leading factor for crayfish vulnerability to loss, yet species with small ranges have received little research attention. *Orconectes saxatilis* is a rare crayfish species with a range restricted to the upper Kiamichi River watershed in southeastern Oklahoma. We examined the distribution, habitat use, and life-history characteristics of *O. saxatilis* and 2 sympatric crayfish species in the upper Kiamichi River watershed to determine factors that might limit its distribution. Surveys for *O. saxatilis* expanded its known range and confirmed its restriction to tributaries of the upper Kiamichi River. *Orconectes saxatilis* showed a strong affinity for riffles, contrary to previous data, whereas *Orconectes palmeri longimanus*, a regionally abundant sympatric species, showed an equally strong affinity for pools. Tributaries of the upper Kiamichi River are intermittent, and surface flow typically ceases in late summer and early autumn. During dry periods when habitat was limited to disconnected pools, *O. saxatilis* aestivated beneath cobbles and boulders in dry riffles. The strict use of riffles by *O. saxatilis* and its need for habitat conducive to aestivation probably contribute to its small range and put this species at risk. Year-round monitoring of populations susceptible to imperilment is needed to make informed conservation decisions. For *O. saxatilis* and other imperiled crayfish species, conservation efforts should emphasize identification of habitat types required for species survival, avoiding alterations to those habitat types, and protecting natural flow regimes.

**Key words:** crayfish, *Orconectes*, conservation, habitat segregation, aestivation, life history, intermittent, endemic species, Kiamichi.

The >540 described species of crayfish make up a globally diverse assemblage of invertebrates that plays a key role in freshwater ecosystems. Crayfish inhabit a wide range of habitats including streams, lakes, wetlands, ditches, caves, and sloughs (Bouchard 1978). As omnivores, they influence multiple trophic levels by feeding on algae (Luttenton et al. 1998), macrophytes (Nyström and Strand 1996), fish (Guan and Wiles 1997), amphibians (Gamradt and Kats 1996), invertebrates (Perry et al. 2000), and detritus (Schofield et al. 2001). Crayfish are important prey items for fish, wading birds, and mammals. As a result, crayfish play an integral role in the community structure of freshwater ecosystems (Momot et al. 1978, Creed 1994, Lodge et al. 1994, Nyström et al. 1996, Usio

and Townsend 2001, 2004) but, like many other aquatic species, they have been adversely affected by the wide array of anthropogenic alterations inflicted globally upon freshwater systems (Malmqvist and Rundle 2002).

Current North American extinction rates for crayfish, mussels, fish, gastropods, and amphibians are higher than historical rates and are predicted to increase substantially (Ricciardi and Rasmussen 1999). This loss of biodiversity is a direct result of anthropogenic changes to rivers and lakes (Richter et al. 1997). Habitat destruction and the introduction of nonnative species are leading causes of extinction and reduced abundances of aquatic taxa including fish (Miller et al. 1989, Warren et al. 2000, Cambrey 2003), mussels (Williams et al. 1993, Ricciardi et al. 1998, Vaughn and Taylor 1999), and crayfish (Master 1990, Taylor et al. 1996, Lodge et al. 2000). Moreover, species with small ranges have a higher risk of extinction from

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habitat alterations, pollution, or nonnative species introductions than species with wide ranges.

Crayfish in North America have not experienced the massive population declines facing European stocks (reviewed in Gherardi and Holdich 1999), but threats against North American species are growing. The major factors threatening crayfish in North America are habitat loss and degradation, the introduction of nonnative species, and small natural ranges of some species (Master 1990, Taylor et al. 1996). Approximately 348 known species and subspecies of crayfish occur in North America north of Mexico (Taylor 2002), representing ~75% of the world's crayfish diversity (Lodge et al. 2000). Of this number, only 52% have populations that are considered stable; the remaining species are classified as possibly extinct, endangered, threatened, or of special concern (Taylor et al. 1996).

A major issue facing crayfish conservation is the lack of information regarding specific habitat requirements for nearly 1/3 of North American crayfish species with small natural ranges (C. Taylor, Illinois Natural History Survey, personal communication). Most crayfish studies focus on common species, species of commercial value, or nonnative species. For example, ecological research has focused on species such as *Orconectes rusticus*, *Procambarus clarkii*, and *Pascifastiscus leniusculus* that invade and displace native species (Light et al. 1995, Gamradt et al. 1997, Hill and Lodge 1999, Vorburger and Ribic 1999, Westman et al. 2002). The impact of habitat alterations on crayfish has also been investigated (Light et al. 1995), but to a lesser extent. Research on nonnative species and habitat alterations is critically important, but it largely fails to address the habitat use, ecology, and life-history characteristics of species with small natural ranges. This research is also critical for addressing the conservation needs of rare and potentially imperiled crayfishes. Furthermore, crayfish species restricted to highly localized areas face a significantly greater probability of extinction from habitat alterations and nonnative species introductions than do widely distributed species.

We examined the distribution, habitat use, and life-history characteristics of a narrowly endemic crayfish species, *Orconectes saxatilis*, from southeastern Oklahoma. Growing demands for water resource development and a thriving silviculture industry have raised concerns about possible impacts on the aquatic fauna of southeastern Oklahoma, especially the Kiamichi River watershed. Like many crayfish species in the US and Canada, very little is known about *O. saxatilis*. Although not federally listed, *O. saxatilis* is considered an endangered species because of its highly restricted distribution (Taylor et al. 1996), and

the Natural Heritage Inventory has given this species Global 1 and State 1 (G1 S1) ranks (NatureServe, version 4.6; NatureServe, Arlington, Virginia; <http://www.natureserve.org/explorer>). Our goal was to determine the primary factors that limit the distribution of this species and use this information to make conservation recommendations for *O. saxatilis*.

## Methods

### Background

*Orconectes saxatilis*, the Kiamichi crayfish, is the most narrowly endemic crayfish species in Oklahoma. It was first described from Pigeon Creek at Oklahoma State Highway 63 in LeFlore County, Oklahoma (Bouchard and Bouchard 1976). In 1996 and 1997, a crayfish survey was conducted within the Ouachita National Forest (Robison 1997). This survey encompassed the type locality of *O. saxatilis*, but no individuals were found. A directed survey for *O. saxatilis* was conducted subsequently from September 2000 through November 2001 (Robison 2001). This survey resulted in the first known collections of *O. saxatilis* since its description in 1976. Aside from collections within Pigeon Creek and its tributaries, specimens were collected from only 2 other nearby streams, Corral Creek and Little Pigeon Creek. These 2 streams were not previously known to harbor this species, but these collections did not significantly increase the known range of *O. saxatilis*. Thus, the known range of *O. saxatilis* remained highly restricted with no information on life history or factors that limit its distribution.

### Study sites

The Kiamichi River, a tributary of the Red River, drains 471,765 ha in southeastern Oklahoma. The watershed originates between the Kiamichi Mountains and Rich Mountain, within 31,484 ha of the Ouachita National Forest. This region is mountainous (relief ranges from 245 to 860 m asl) and is characterized by formations of sandstone and shale, well-drained, highly weathered acidic soils, and a mixture of pine, oak, and hickory forests with pastureland and cropland in lowland areas (USDAFS 1999).

Most of the tributaries in the upper Kiamichi River watershed are shallow 1<sup>st</sup>- to 3<sup>rd</sup>-order intermittent streams dominated by cobble, boulder, and gravel substrates. Maximum stream depths are rarely >1 m under typical flow regimes and mean widths range from 6 to 10 m. The mean discharge of the upper Kiamichi River (US Geological Survey gauging station 07335700) for December to May (data from 1965 to

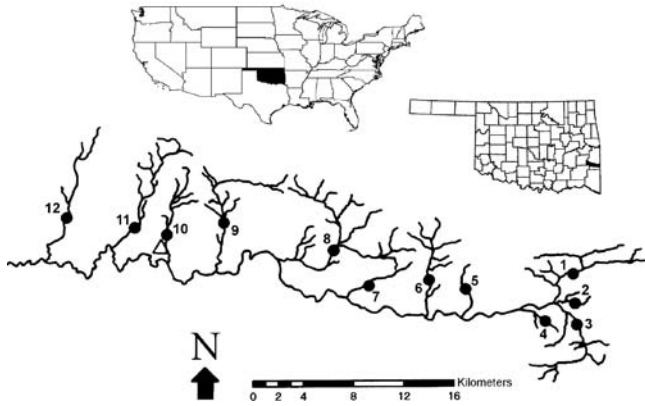


FIG. 1. Upper Kiamichi River and its tributaries in LeFlore County, Oklahoma. 1 = Kiamichi River above main tributaries, 2 = Little Pigeon Creek, 3 = Pigeon Creek, 4 = Corral Creek, 5 = Big Branch Creek, 6 = Big Cedar Creek, 7 = Little Cedar Creek, 8 = Billy Creek, 9 = Sycamore Creek, 10 = Woods Creek, 11 = Bohannon Creek, and 12 = Birney Creek. The open triangle indicates Whitesboro, Oklahoma. Closed circles are labeling tags and do not represent study sites.

2004) is  $3.5 \text{ m}^3/\text{s}$  and provides sufficient flow to cover most of the streambed. Flow rates decline in June, and by August, the mean discharge is only  $0.18 \text{ m}^3/\text{s}$ . These flows leave many areas of the streambed dry and create a series of disconnected pools. Discharge remains low throughout September and increases in October and November.

#### *Orconectes saxatilis* range determination

A 2-wk survey of Kiamichi River tributaries (Fig. 1) from Pigeon Creek, the uppermost tributary in the watershed, to Birney Creek, 60 km downstream of Pigeon Creek, was conducted in July 2002. Coral Creek and Little Pigeon Creek, a small tributary of Pigeon Creek, were known to harbor *O. saxatilis* and were not surveyed at this time because the survey was aimed at identifying previously unrecognized tributaries that harbored *O. saxatilis*. Crayfish were collected by kick netting and with hand nets by searching under cobbles and boulders during mid-July when water levels were low and allowed easy access to large areas of the streams. Surveys were done in watersheds adjacent to the Kiamichi River watershed in spring 2004.

#### Habitat surveys

Pool and riffle habitats in 5 streams in the upper Kiamichi River watershed with populations of *O. saxatilis* (Kiamichi River, Pigeon Creek, Big Cedar Creek, Billy Creek, and Sycamore Creek) were surveyed monthly for 15 mo from July 2002 to October 2003. A single reach,  $\sim 400 \text{ m}$  long containing distinct

riffle and pool sequences with occasional runs, was chosen in each stream based on accessibility. Bridges crossed the Big Cedar Creek and Sycamore Creek sites, but nearly all samples were taken upstream of the bridge at the Big Cedar Creek site. All samples at the Sycamore Creek site were taken downstream of the bridge because of constraints on accessibility.

A randomly selected  $1\text{-m}^2$  quadrat plot was sampled from a riffle (if present) and a pool monthly at each site (127 samples; riffles were not always present during summer months). Riffles were characterized as shallow water with surface turbulence and mean flow velocity  $\geq 0.6 \text{ cm/s}$ , whereas pools had a mean flow velocity  $< 0.6 \text{ cm/s}$  and no surface turbulence. Riffles were considered present only when surface flow was sufficient to cover the streambed. However, riffles retained features that distinguished them from pools even after they dried during late summer and early autumn. Riffles tended to have smaller substrate sizes, fewer boulders, narrower widths, and very little detritus compared to pools. Backwater and side-channel habitats were not present during any part of the year, and aquatic vegetation was scarce.

Before sampling, substrate composition was estimated visually as % bedrock, boulder ( $> 256 \text{ mm}$ ), cobble ( $64\text{--}256 \text{ mm}$ ), gravel ( $2\text{--}64 \text{ mm}$ ), sand ( $0.06\text{--}2 \text{ mm}$ ), silt ( $0.004\text{--}0.03 \text{ mm}$ ), clay ( $< 0.004 \text{ mm}$ ), detritus (coarse particulate organic matter), mud/muck (fine particulate organic matter), and marl within each plot (Barbour et al. 1999). Monthly % substrate composition of riffles and pools was averaged across all months and pooled by stream. Averaging was done because of unequal sample sizes; pools retained water longer and were measured more times than riffles. Differences in substrate composition were assessed with nonmetric multidimensional scaling (NMDS) and hierarchical cluster analysis using Primer (version 5; PRIMER-E, Plymouth Marine Laboratory, Plymouth, UK). A 1-way analysis of similarity (ANOSIM) was used to test for differences in substrate composition among streams with riffle and pool substrate data pooled within each stream. A second ANOSIM was used to test for differences between riffles and pools independent of stream. SIMPER was used to characterize substrate differences between pools and riffles.

Discharge was calculated monthly at the same location within each of the 5 streams. pH, dissolved  $\text{O}_2$ , temperature, minimum depth, and maximum depth were measured at every sample plot. Dependent *t*-tests were used to assess differences between riffles and pools with respect to temperature, dissolved  $\text{O}_2$ , pH, depth, and flow velocity during wet (November–June) and dry (July–October) months. Data were paired by sampling date and stream. During dry

months, riffles were compared with pools for the dates on which riffles were present. Means were calculated for pools when no riffles were present.

After substrate composition was estimated, rocks within each plot were removed individually until only gravel and sand remained. Crayfish were captured with hand nets. Capture with hand nets was chosen based on sampling effectiveness during preliminary surveys. Other studies have used kick netting successfully to quantify crayfish densities (Mather and Stein 1993, DiStefano et al. 2003, Flinders and Magoulick 2003), but kick netting yielded a lower capture rate than hand netting on a per area basis across both habitats in our study. Crayfish were identified to species and form, sexed, and measured (see below). Individuals that were observed but not captured (2.6% of all individuals encountered) were counted and their species was noted if possible. All rocks were replaced, and the crayfish were released.

Measurements were made with digital vernier calipers to the nearest 0.01 mm and included total carapace length (TCL; tip of rostrum to posterior margin of carapace), chela width (maximum width), and chela length (base to tip of the finger). Females displaying glair (milky white substance on the uropods and abdomen used in egg attachment) and males with corneous pleopods (Form I) were considered reproductively active. Measurements of size were used to determine growth patterns, age class, and size at maturity. Densities were compared between riffles and pools with *t*-tests within each stream. A *G*-test of independence with a Williams correction was used to determine whether the proportions of each species caught differed between habitats (Sokal and Rohlf 1995).

## Results

### Distributions

*Orconectes saxatilis* was collected from Pigeon Creek, Kiamichi River, Big Branch Creek, Big Cedar Creek, Little Cedar Creek, Billy Creek, and Sycamore Creek (Table 1). With the exception of Pigeon Creek, these streams were new localities for *O. saxatilis* and increased the known range by 25.6 km downstream in the Kiamichi River watershed.

Two sympatric species were collected in addition to *O. saxatilis*. *Orconectes palmeri longimanus* was collected from all surveyed streams, whereas *Procambarus tenuis* was collected only from the 5 streams that were sampled monthly. Based on our collections, *P. tenuis* inhabits streams that support *O. saxatilis* populations within the upper Kiamichi watershed. *Orconectes palmeri longimanus* was captured frequently during

TABLE 1. Presence/absence of *Orconectes palmeri longimanus* (PAL), *O. saxatilis* (SAX), and *Procambarus tenuis* (TEN) in streams of the upper Kiamichi River watershed. River length above is the length of the Kiamichi River above the confluence of the stream with the Kiamichi River. Kiamichi River is the headwater section of the river above its first tributary, Pigeon Creek. X = presence, blank = absence.

Stream	River length above (km)	PAL	SAX	TEN
Kiamichi River	10.6	X	X	X
Pigeon Creek	10.6	X	X	X
Big Branch Creek	15.4	X	X	
Big Cedar Creek	18.6	X	X	X
Little Cedar Creek	28.2	X	X	
Billy Creek	39.4	X	X	X
Sycamore Creek	45.8	X	X	X
Woods Creek	52.2	X		
Bohannon Creek	60.2	X		
Birney Creek	69.8	X		

surveys of adjacent watersheds, but no *O. saxatilis* or *P. tenuis* individuals were caught during those surveys.

### Habitat characteristics

Flow patterns in the 5 streams were characterized by sufficient water to cover the streambed channel from November through early July. Water levels declined beginning in mid-July, and surface flow ceased by mid-August, leaving only isolated pools in the deepest areas of each stream. These pools diminished in volume throughout late September and early October. Precipitation increased by mid- to late October, and water levels were sufficient to cover the channel beds by early to mid-November. This pattern was consistent with historical data on annual flow patterns of the upper Kiamichi River watershed.

Depth and flow velocity differed between riffles and pools, but temperature, dissolved O<sub>2</sub>, and pH did not. Mean depth was greater in pools than riffles, whereas mean flow velocity was higher in riffles than pools (Table 2). During the driest period of the year, when riffles were absent, mean pool depth decreased to 14.3 cm, a value similar to mean riffle depths (15.7 cm) during the wet months (Table 2). Mean temperature was identical between riffle and pools throughout the year, but differed by 11.4°C between wet and dry months (Table 2). Dissolved O<sub>2</sub> and pH were nearly identical between the 2 habitat types. Dissolved O<sub>2</sub> was higher in wet than in dry months, but pH showed little temporal variation.

The substrate of all streams was predominantly cobble and boulder underlain by coarse gravel.

TABLE 2. Mean ( $\pm 1$  SE) depth, flow velocity, temperature, dissolved O<sub>2</sub>, and pH in riffle and pool habitats in streams in the upper Kiamichi River watershed during wet (November–June) and dry (July–October) periods. Dependent *t*-tests were used to test for differences with data paired by sampling date and stream. *p*-values correspond to probabilities (2-tailed) associated with dependent *t*-tests comparing riffles and pools. – indicates no water in riffles.

Abiotic factor	Period	Riffles	Pools	<i>p</i>
Depth (cm)	Wet	15.7 $\pm$ 0.8	23.0 $\pm$ 1.3	<0.001
	Dry	12.4 $\pm$ 2.0	23.8 $\pm$ 4.2	0.006
Flow velocity (cm/s)	Dry	–	14.3 $\pm$ 1.2	
	Wet	11.4 $\pm$ 0.08	3.1 $\pm$ 0.04	0.008
Temperature (°C)	Dry	8.2 $\pm$ 0.05	1.4 $\pm$ 0.02	0.008
	Dry	–	0.1 $\pm$ 0.01	
Dissolved O <sub>2</sub> (mg/L)	Wet	13.6 $\pm$ 1.0	13.6 $\pm$ 1.0	0.852
	Dry	25.0 $\pm$ 1.6	25.0 $\pm$ 1.4	0.920
pH	Dry	–	24.8 $\pm$ 0.8	
	Wet	9.1 $\pm$ 0.4	8.9 $\pm$ 0.4	0.554
pH	Dry	4.2 $\pm$ 0.9	4.6 $\pm$ 1.0	0.089
	Dry	–	3.8 $\pm$ 0.4	
pH	Wet	7.3 $\pm$ 0.1	7.2 $\pm$ 0.1	0.538
	Dry	7.0 $\pm$ 0.2	6.9 $\pm$ 0.3	0.830
pH	Dry	–	7.4 $\pm$ 0.1	

Substrate composition did not differ among streams (ANOSIM, *p* = 0.695), but substrate composition differed significantly between riffles and pools (ANOSIM, *p* = 0.008). Riffles and pools formed 2 distinct clusters in NMDS plots (90% Bray–Curtis similarity level), but Big Cedar pools formed a cluster separate from the pools in other streams (Fig. 2). The greatest contributor to dissimilarity between the habitat types (>50%) was the differential distribution of boulder and cobble substrates (SIMPER). Boulders were more common in pools (11.9% of the substrate) than in riffles (5.5%), whereas cobble and gravel were more common in riffles (71.3% and 21.3%, respectively) than in pools (66.2% and 16.0%, respectively). Detritus was more common in pools (4.5%) than in riffles (1.3%).

Habitat use

A total of 696 *O. saxatilis*, 725 *O. palmeri longimanus*, and 28 *P. tenuis* individuals were captured during our study. Mean total crayfish densities did not differ between riffles and pools within streams in wet months when both habitat types were present (*p* > 0.05 for all *t*-tests), but densities tended to be higher in riffles than in pools, except in Big Cedar Creek, where the densities were similar between habitats (Fig. 3A).

*Procambarus tenuis* was not included in the analysis of habitat use because this species was rarely collected

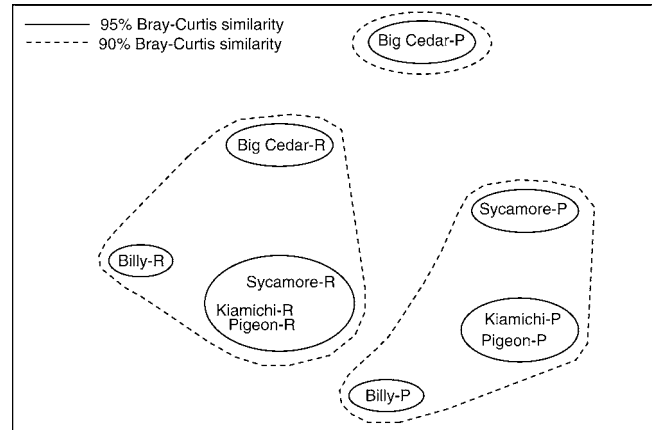


FIG. 2. Nonmetric multidimensional scaling ordination plot based on % substrate composition in riffle and pool habitats in Kiamichi River, Pigeon Creek, Big Cedar Creek, Billy Creek, and Sycamore Creek. Bray–Curtis similarity of substrate composition among streams and habitats was used to cluster sites. Stress = 0.05 for the analysis. P = pools, R = riffles.

(13 from riffles and 15 from pools). When both habitat types were present, >90% of *O. saxatilis* captures were in riffles, and ~79% of *O. palmeri longimanus* captures were in pools (Fig. 3B). Proportional habitat use differed significantly between species (*G* = 480.66, *df* = 1, *p* < 0.0001). When both habitat types were present, proportional habitat use by adult and young-of-the-year (YOY) individuals was similar within species (Fig. 3C). For *O. saxatilis*, 92.7% of YOY (*n* = 262, TCL = 6.4–16.5 mm) and 84.0% of adults (*n* = 106, TCL > 16.5 mm) were captured in riffles. For *O. palmeri longimanus*, 71.8% of YOY (*n* = 149, TCL = 5.8–22.4 mm) and 77.7% of adults (*n* = 103, TCL > 22.4 mm) were captured in pools. A time-restricted search for crayfish at night on 18 December 2002 in Pigeon Creek yielded 25 *O. saxatilis*, 2 *P. tenuis*, and 0 *O. palmeri longimanus* from riffles and 7 *O. palmeri longimanus* and 1 *O. saxatilis* from pools.

*Orconectes saxatilis* habitat use changed between wet and dry months. When both pools and riffles were present, 19 of 262 YOY and 17 of 106 adults were caught in pools. When riffles were not present, 159 YOY and 36 adults were caught in pools (Fig. 3C). Densities of *O. saxatilis* were lower than densities of *O. palmeri longimanus* in pools during dry months in all streams except Pigeon Creek (Fig. 3D).

In August 2003, *O. palmeri longimanus* individuals were observed in dried pools within shallow burrows (5–10 cm deep) under small boulders. Some of the burrows contained small amounts of water, whereas other burrows were without standing water, but were moist. *Orconectes saxatilis* individuals were observed in

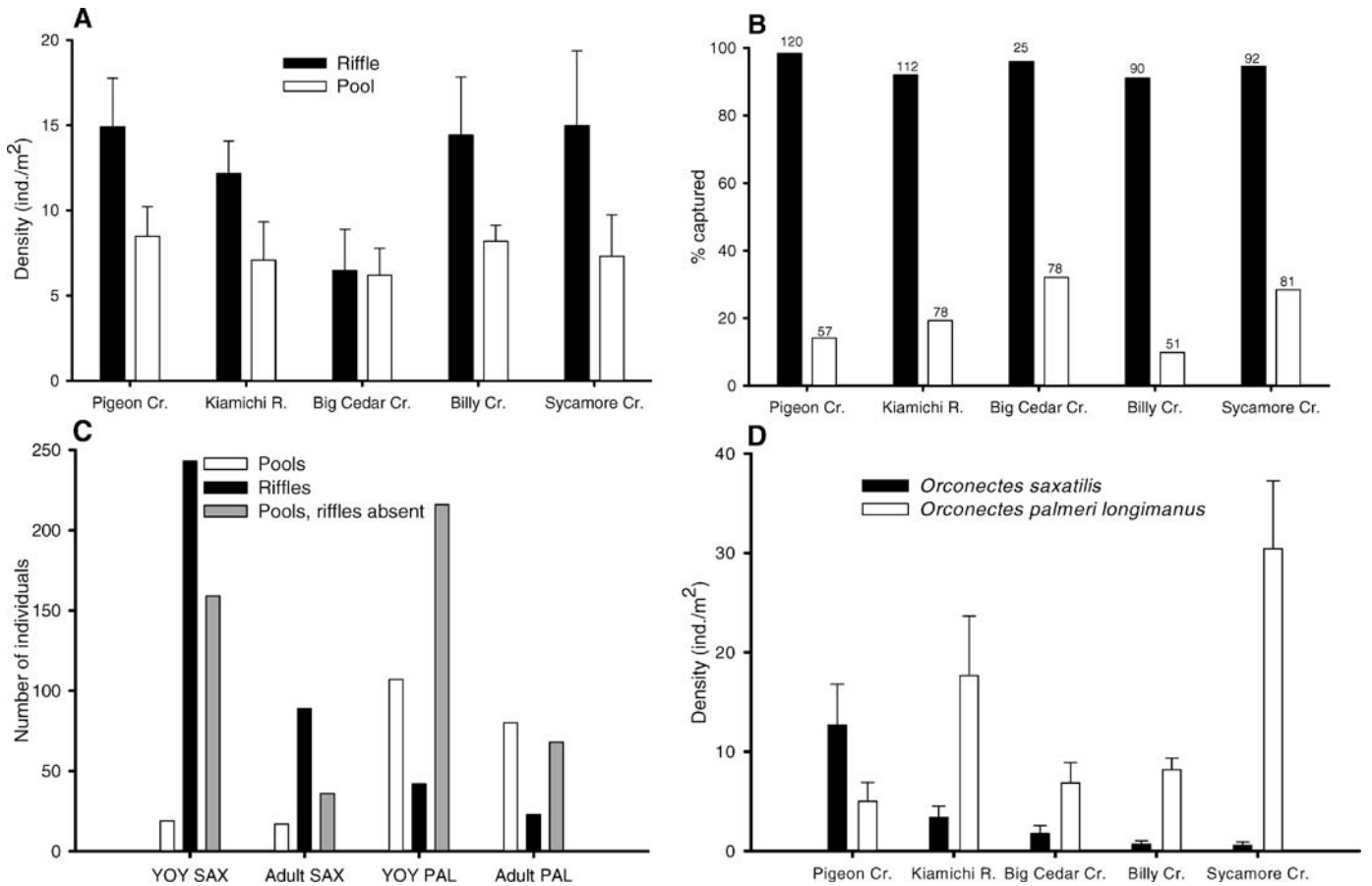


FIG. 3. A.—Mean (+1 SE) density of crayfish in riffle and pool habitats for 5 streams in the upper Kiamichi River watershed during months when surface flow was sufficient to form riffles and pools. B.—Percentage of total crayfish caught in riffle habitats during months when both riffle and pool habitats were present. Numbers above bars are the total number of individuals collected. C.—Number of young-of-the-year (YOY) and adult *Orconectes saxatilis* (SAX) and *O. palmeri longimanus* (PAL) caught in pools and riffles when surface flow was sufficient to form riffles and pools and in pools when riffles were absent. D.—Mean (+1 SE) density of *O. saxatilis* and *O. palmeri longimanus* in pools when riffles were absent.

dried riffles within shallow burrows devoid of water under large boulders that maintained a tight seal against the substrate. When exposed, these crayfish remained almost completely motionless within their burrows. On 2 separate occasions when the distance between pools was <2 m, individuals of both species were observed crawling across dry portions of the streambed between pools.

*Life-history characteristics*

*Orconectes palmeri longimanus* adults were significantly larger than *O. saxatilis* adults (Table 3). The 2 species also differed in size at maturity, with *O. saxatilis* generally maturing at a smaller size than *O. palmeri longimanus* (Table 3).

The 2 species had similar patterns of reproductive timing and growth. Both species became reproductively active in September and October. Females

TABLE 3. Mean ( $\pm 1$  SE) total carapace length (TCL), size at sexual maturity, chela length, and chela width of adult *Orconectes palmeri longimanus* (PAL) and *O. saxatilis* (SAX).

Characteristic	PAL	SAX
TCL	32.96 $\pm$ 1.20	23.43 $\pm$ 0.40
Male TCL at sexual maturity	23.56 $\pm$ 1.03	20.61 $\pm$ 0.57
TCL of smallest sexually mature male	22.46	16.50
Female TCL at sexual maturity	24.58 $\pm$ 1.80	21.40 $\pm$ 0.29
TCL of smallest sexually mature female	20.99	20.74
Chela length	28.16 $\pm$ 2.15	18.36 $\pm$ 0.64
Chela width	10.27 $\pm$ 0.74	7.54 $\pm$ 0.27

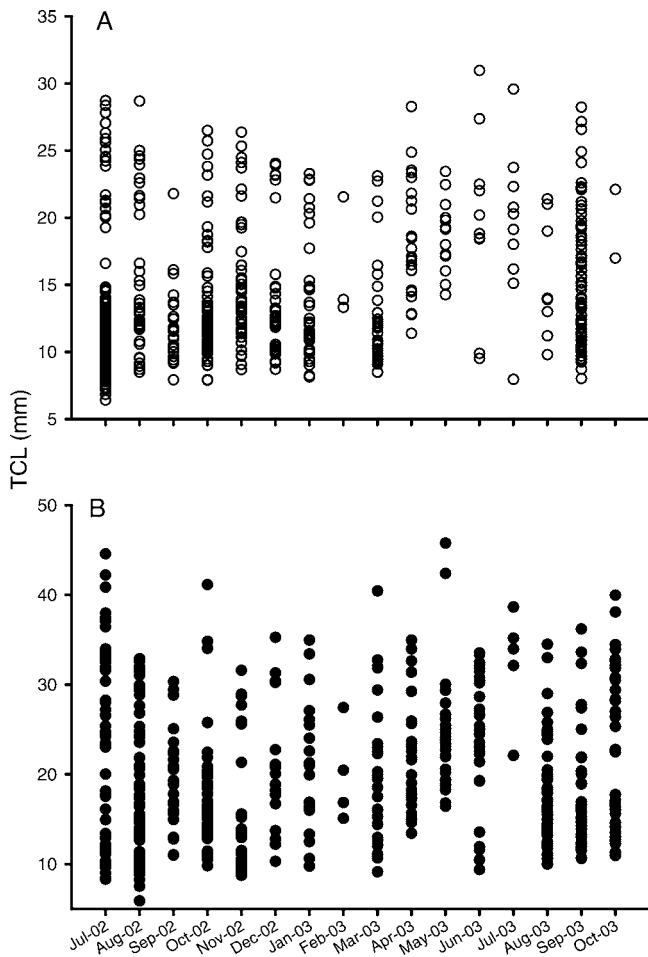


FIG. 4. Total carapace lengths (TCL) for *Orconectes saxatilis* (A) and *O. palmeri longimanus* (B) individuals collected monthly from July 2002 to October 2003.

continued to display glair through January, and the only females in berry (carrying eggs) were observed in March. Three *O. palmeri longimanus* females displayed glair in March, indicating that they might be capable of producing young late in the year. YOY individuals that were independent of their mothers began to appear in June, became very prevalent in August, and remained prevalent for the rest of the year in both species. Several Form I males were observed between March and August, but they were typically large adults, which occasionally remain in Form I throughout the year.

TCL measurements suggested that growth of both species was greatest from March to June (Fig. 4). Growth probably continued throughout autumn, but the presence of YOY individuals and the possibility that individuals might have mated in spring to produce offspring in autumn made shifts in distributions of size classes difficult to detect and to interpret.

Insufficient sample size precluded the use of size-frequency data in the analysis of age-class structure and growth (France et al. 1991).

**Discussion**

*Habitat use and factors limiting distribution*

Our study provided new information on the distribution of 3 species of crayfish in the upper Kiamichi River watershed. The known range of *O. saxatilis* was increased from 3 to 9 tributaries, but surveys of 5 tributaries of the Kiamichi River downstream of Sycamore Creek and 9 streams in the 3 adjacent watersheds to the upper Kiamichi River watershed failed to find *O. saxatilis*. The range of *O. saxatilis* is estimated to be the upper 45 km of the Kiamichi River and its associated tributaries above Whitesboro, Oklahoma, based on our collections.

The direct mechanism(s) limiting the distribution of *O. saxatilis* is unknown, but the availability of riffle habitats dominated by cobble and gravel substrate appears to be a key factor. Adult and YOY *O. saxatilis* individuals were captured consistently in riffles when surface flow was present. Use of pools was moderate and occurred mostly during dry months when riffles were absent. However, densities in pools during dry months were lower than densities in riffles during wet months. Our results suggest that *O. saxatilis* has a strong affinity for riffle habitat when it is available. In contrast, the sympatric species *O. palmeri longimanus* has a strong affinity for pools throughout the year.

The discovery of this affinity for riffles is a key finding of our study because it largely contradicts the findings of Bouchard and Bouchard (1976) and Robison (2001). *Orconectes saxatilis* was originally described as inhabiting pool areas that had little current, thus differing from its closest relative, *Orconectes menae*, which inhabits deeper, faster riffles and runs (Bouchard and Bouchard 1976). Robison (2001) agreed with Bouchard and Bouchard, stating that *O. saxatilis* individuals were taken only from shallow pool areas with little or no current. We believe this discrepancy can be attributed to the months when specimens were collected. Robison (2001) noted that *O. saxatilis* was most commonly collected in late July and August when water flow is strictly subsurface and all surface water is present in isolated pools. Bouchard and Bouchard (1976) collected the type specimens on 11 August, at which time they described flow as sluggish with visible water confined to isolated pools connected only by subsurface flow. Thus, *O. saxatilis* was incorrectly labeled a pool species because only pool habitats were surveyed.

The availability of riffle habitat probably contributes

to the restricted range of *O. saxatilis*. It is not known whether *O. saxatilis* inhabits the mainstream of the Kiamichi River between Big Cedar and Whitesboro, Oklahoma (a distance of ~22.5 km), because of the relative inaccessibility of this reach of the river. *Orconectes saxatilis* does not appear to inhabit the Kiamichi River or any of its tributaries downstream of Whitesboro, where the substrate is predominantly sand and gravel with a low abundance of cobbles, water is deep, and riffles are widely separated. These factors may prevent migration of *O. saxatilis* further downstream, limiting it to the upper 45 km of the Kiamichi River and its associated tributaries. Two downstream tributaries, Bohannon Creek and Woods Creek, near Whitesboro, appeared to have habitat characteristics sufficient to maintain *O. saxatilis*, but no individuals were captured in these streams. A lack of appropriate habitat in the main stream may limit the ability of *O. saxatilis* to reach downstream tributaries that could potentially support them. A 3<sup>rd</sup> tributary downstream of Whitesboro (Birney Creek) also did not harbor *O. saxatilis*, but appears to have undergone siltation from surrounding agricultural land use. Thus, it appears that *O. saxatilis* is restricted to the upper Kiamichi River watershed and should retain its endangered conservation status (Taylor et al. 1996) and Heritage Inventory G1 S1 rank because of its limited distribution within a single watershed.

In addition to *O. saxatilis*, 2 sympatric species (*P. tenuis* and *O. palmeri longimanus*) were collected. Collections of *P. tenuis* from tributaries of the upper Kiamichi River were novel, although the sites are within the known range of this rare species. However, a more intensive study is needed to determine the mechanisms that restrict its populations. *Orconectes palmeri longimanus* has a widespread distribution and occurs in Kansas, Oklahoma, Texas, Arkansas, and Louisiana (Hobbs 1989). Our study confirmed its widespread distribution in the Kiamichi River and adjacent watersheds.

#### *Life-history characteristics*

*Burrowing behavior.*—Orconectids, including *O. saxatilis* and *O. palmeri longimanus*, are not known for their burrowing ability. However, all crayfish have the ability to burrow (Berrill and Chenoweth 1982, Cooper and Braswell 1995) and may do so when water levels recede. Burrowing may be an important adaptation to survival in these intermittent streams. In late summer, *O. saxatilis* and *O. palmeri longimanus* construct small burrows under large boulders and cobbles where moisture and cool temperatures provide suitable conditions for crayfish aestivation. When observed in

burrows, crayfish remained essentially motionless and did not display typical escape responses when disturbed, behavior that suggests aestivation. It is possible that crayfish are subjected to physiological stress in burrows and must conserve energy while reducing O<sub>2</sub> consumption.

*Growth and longevity.*—Growth rates for *O. saxatilis* and *O. palmeri longimanus* appeared to be similar. However, *O. saxatilis* mature at a smaller size than *O. palmeri longimanus*. *Orconectes saxatilis* reaches sexual maturity at 20.6–21.4 mm TCL and *O. palmeri longimanus* at ~23.6–24.6 mm. Thus, for both species, YOY that are produced in June and July could become reproductively mature within a year. Reliable estimates of life span could not be made for either species. However, similar species live 2 to 3 y on average, and may live up to 5 y (Hamr 2002).

#### *Threats and conservation considerations*

*Orconectes saxatilis* is just one of >100 crayfish species with a small natural range in the US and Canada. These species are often at increased risk of decline or even extinction if faced with habitat destruction or the introduction of nonnative species. Moreover, very few reliable data are available on the life histories, habitat use, and distributions of these species. These basic data are essential to making sound conservation decisions.

Our surveys revealed that the rare endemic crayfish *O. saxatilis* was more widely distributed than previously believed, although still restricted in range. In addition, *O. saxatilis* was strongly associated with riffle habitats, counter to previous belief. Flinders and Magoulick (2005) made similar discoveries with *Orconectes marchandi*, a rare endemic crayfish of the Ozarks in southern Missouri and northern Arkansas. Surveys conducted over 2 y increased the known distribution of this species from 3 streams to 20 streams (Flinders and Magoulick 2005). *Orconectes marchandi* was originally believed to inhabit fast-flowing riffle habitats, but was found almost exclusively in shallow slow-moving water (Flinders and Magoulick 2005). These results exemplify the need for basic research on the distributions and habitat use of crayfish. Many data on crayfish distributions and habitat use are based on short-term surveys and collections of the type specimens, and such data must be interpreted with caution.

The strong affinity of *O. saxatilis* for riffles and *O. palmeri longimanus* for pools was striking because crayfish are considered generalists. However, other studies of stream-dwelling crayfish that examined habitat use have found similar species–habitat associ-



ations based on flow velocity and depth (DiStefano et al. 2003, Flinders and Magoulick 2005). Habitat preferences and associations maybe an under-recognized attribute of crayfish ecology and may warrant further investigation, especially for endemic crayfish species that often have narrow distributions and may be strongly affected by local changes in abiotic conditions. Therefore, habitat preference should be addressed carefully when gathering data.

Urbanization, industrial development, landuse changes, and hydrological alterations continue to affect lotic ecosystems worldwide (Malmqvist and Rundle 2002). In the Kiamichi River watershed, surface water is the primary source of human drinking water, and 5 sites supply >22,000 people (USDAPS 1999). Additional water resource development projects have been proposed to meet the demands of growing populations in neighboring states. Water resource development and associated stream drying has been cited as a cause of serious declines in mussel, fish, and crayfish diversity (Miller et al. 1989, Richter et al. 1997, Vaughn and Taylor 1999, Light 2003). Long dry periods (2–12 mo) significantly decrease taxa richness and density of macroinvertebrates in intermittent streams (Boulton 2003, Fritz and Dodds 2004). Any water resource development that alters surface water availability, connectivity, permanence, and periodicity poses serious threats to lotic ecosystems and endemic crayfish.

Landuse practices also have direct effects on lotic ecosystems. A significant proportion of the range of *O. saxatilis* occurs within the Ouachita National Forest in LeFlore County, Oklahoma, where silviculture is an important industry. At least 70% of the length of every stream that harbors *O. saxatilis* lies within the Ouachita National Forest. National forests often provide protection from urbanization and pollutants. However, siltation resulting from poor tree-harvesting techniques, road construction, or large-scale changes in land use poses a potential threat to stream organisms, particularly habitat specialists like *O. saxatilis*, *O. luteus*, *O. punctimanus*, and *O. marchandi*. Increased sedimentation and turbidity resulting from landuse changes negatively affect fish and macroinvertebrates (McClelland and Brusven 1980, Gurtz and Wallace 1984, Vuori and Joensuu 1996, Sutherland et al. 2002). Moreover, increased sedimentation enhances the ability of some nonnative species of fish (Jones et al. 1999) and crayfish (Light et al. 1995) to invade new areas. Nonnative crayfish introductions pose a real threat to sustaining biodiversity (Richter et al. 1997, Lodge et al. 2000), although they are not currently known to threaten the faunas of Oklahoma's aquatic systems.

We believe that it is crucial to identify species

requirements and sensitive areas where habitat alterations and nonnative species introductions would be most devastating. Even in our short-term study, we were able to expand greatly the known range of *O. saxatilis* and show that previous data on habitat use were incorrect and misleading. With reliable pre-disturbance data on hand, conservation strategies can be preemptive, rather than reactive.

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