OBSERVATIONS OF FLUCTUATIONS IN POPULATION DENSITY OF TWO SPECIES OF CRAYFISH IN A TALLGRASS PRAIRIE STREAM

by

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Introduction

This is a report of an investigation into mechanisms that influence the distribution and abundance of two species of crayfish in a pristine tallgrass prairie stream in eastern Kansas. "The richness and complexity of benthic communities in streams has long been recognized, but very few factors that influence these patterns are understood" (McAuliffe 1981). 1) Organisms in streams are limited ultimately to specific ranges of physical environments (temperature, water chemistry, etc.) by their physiological tolerances. 2) Within suitable ranges of these physical limitations, organisms may be restricted to particular sub-ranges of current velocities, substrate types, or food availability within which they can successfully procure food resources. 3) Predation, interspecific competition, and many kinds of physical disturbances may further restrict the distribution and abundance of individuals within otherwise suitable microhabitats (McAuliffe ibid.).

Freshwater crayfish are found in virtually every North American aquatic habitat. They are the largest and longest lived members of the freshwater crustacea in North America and are of interest to scientists, fishermen, and aquaculturists. Crayfish, as opportunistic omnivores, play an important role in determining the fate of energy and nutrients in aquatic ecosystems (Abrahamson 1966, Rickett 1974, Flint and Goldman 1975, Momot et al. 1978).

An extensive review by Momot et al. (1978) documents crayfish as polytrophic (primary consumer, primary carnivore, decomposer). They not only convert detritus from a wide range of sources into available energy, but they play an additional role by ingesting material that ordinarily is slowly decomposed (e.g. wood) and reducing it to finer particles more easily attacked by other decomposers. Thus, crayfish may make sources of energy (e.g. detrital material, decaying wood, and periphyton) available to higher trophic levels that, in the absence of crayfish, would be unavailable.

Stream ecosystems are driven by external environmental factors such as temperature, light, etc. Streams are also influenced by terestrial inputs and the most frequent agent of stream disturbance is flooding (Fisher et al. 1982). Large floods denude stream substrate and may produce change in the channel morphology. Benthic organisms recolonizing an area are thought to come from three sources: 1) drift from unaffected areas upstream, 2) migration from downstream, and 3) migration from within the substrate (Williams and Hynes 1976).

The particulate organic resources in Kings Creek, Riley Co., Kansas, a typical tallgrass prairie stream, vary widely with the hydrologic regime. The organic matter imported to the stream from riparian vegetation may accumulate during dry periods, (Gurtz et al. 1982), instream primary production may be high during base flow periods (Tate 1985) yet storm discharges may erode organic materials in channel storage and either deposit them on the floodplain or export them downstream. The characteristic unpredictability of the hydrologic regime thus influences the predictability of resource availability (quality and quantity) and provides an environment in which the omnivory and burrowing habits of crayfish confer distinct adaptive advantages.

Upstream migration among crustacea, especially amphipoda, is not uncommon (Minckley 1964) and the seasonal migration of crayfish in lakes is well documented (Flint 1977, Fast and Momot 1974). Crayfish migration in streams is less well understood. Merkle (1969) reported no directional movements, Henry (1951), reported seasonal migrations in response to temperature change, and Momot (1966) and Black (1963) reported upstream movements and suggested that they were possibly a compensatory behavior in response to downstream displacement by floods. Information concerning daily movements and home range is incomplete (Merkle 1969, Camougis and Hichar 1959, Black 1963).

Hall et al. (1970) stressed the importance of 'keystone' predators (Paine 1966) in aquatic communities. This type of predator switches between various species depending on prey abundance. The predator, therefore, produces stability in the system and influences community structure and diversity. Crayfish easily fulfill this position with their role as a benthic predator and can influence the nature and extent of interactions among a subweb of invertebrate and vertebrate species (Rickett 1974, Momot et al. 1978).

Crayfish also serve as an important prey animal to fish, birds, reptiles, and mammals (Lorman and Magnuson 1978). Crayfish are nocturnal, cryptic invertebrates and in continual need of refuge from predators. They occupy crevices and natural burrows under rocks or create burrow systems of their own. Burrowing behavior is commonly associated with intermittent aquatic systems. Hobbs and Hart (1959) distinguished between species that never leave their burrows (primary burrowers), species that may burrow under drought conditions, or during their breeding seasons (secondary burrowers), and species that typically inhabit swifter water and have not been observed to burrow. Berril and Chenoweth (1982), however, predicted that the ability to excavate and seal a burrow is a characteristic shared by all crayfish and that nonburrowing species do not exist.

Crayfish are benthic organisms, swimming only rarely when threatened. Their benthic foraging movements frequently bring them in contact with one another. Interspecific and intraspecific aggressive encounters are common and well documented (Bovbjerg 1953 1956, Penn and Fitzpatrick 1963, Capelli 1982, Capelli and Munjal 1982). The crayfish of any particular aquatic habitat generally are limited to one or very few species, even if many species occur in the geographical region (Williams 1954). The ecological isolation and competitive exclusion between a stream/lake species and a pond/slough species has been documented by Bovbjerg (1970). Rabeni (1985) claims that, given their aggressive tendencies, different species existing in proximity is more surprising than is the exclusion of one species by another.

Two species of stream dwelling crayfish, (*Orconectes nais* and *Orconectes neglectus*) were observed in King's Creek, and their relative abundance appeared to vary from the headwater channels to the lower reaches of the stream. The primary objectives of this study, therefore, was to measure the distribution and abundance of the two species of stream dwelling crayfish in King's Creek. Secondary objectives were to monitor the effects of drought on the population structure and to examine some of the environmental variables that might have been affecting crayfish movement.

Due to unusually heavy precipitation in the Fall of 1986, it was impossible to study the effects of the streams drying up. However, the study design was flexible enough that it allowed the examination of flood effects on movements and population structure. This study therefore addresses the subjects of crayfish density, migration, and response to stream intermittency.

Literature Review / Study Animals

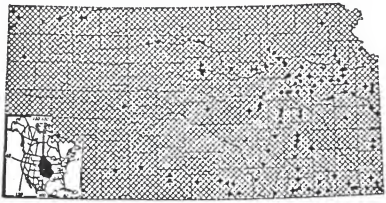
More crayfish species (322) are found on the North American continent than any other region in the world (Bouchard 1978). The species of crayfish that are most commonly studied in North America are those associated with aquaculture and used for human food and for fish bait. The areas of heaviest research are located in the southern United States. Crayfish species found further north have not been so thoroughly studied, with the exception of *Orconectes virilis* (Momot 1967; Momot and Gowing 1977).

The two crayfish species that were examined during this study were *Orconectes nais* and *O. neglectus*. *Orconectes nais* is widely distributed throughout the Great Plains and Ozark region, while *O. neglectus* has a very limited and restricted distribution (Fig. 1), especially in Kansas (Williams 1954). Only general information concerning life history is known for either species (Williams and Leonard 1952).

Orconectes nais is found in streams (Hobbs 1974), but is also found in ponds and ditches (Williams and Leonard 1952). *Orconectes neglectus* has never been found in any habitat but clear, fast flowing, rocky bottom streams (Hobbs 1974). During several studies of crayfish growth in the Manhattan, Kansas area, the only species that was found to inhabit farm ponds was *O. nais* (Ingelin 1984). Both species, however, are found in various densities in the Kings Creek watershed (Riley County, Kansas) and apparently coexist sympatrically.

One of the earliest references to stream crayfish is found in a

Orconectes nais



Orconectes neglectus

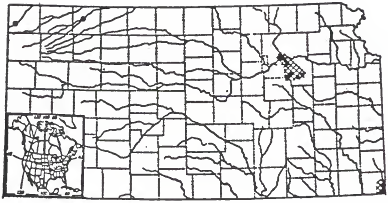


Figure 1. Distribution of Orconectes nais and Orconectes neglectus in Kansas and North America (Williams and Leonard, 1952).

371 page monograph by T. H. Huxley (1880). Huxley had chosen the crayfish as the organism to 'exemplify the general truths respecting the development of zoological science'. He made several observations on the general life history and burrowing habits of stream crayfish but did not give specific information on distributions of sympatric species of stream-dwelling crayfish.

Densities of *Orconectes nais* have been found to reach $89/m^2$ in Kansas farm pond situations (Ingelin 1984). Reports of stream crayfish densities are not abundant in the literature. Momot (1966), however, reports that a population of *Orconectes nais* was found in an Oklahoma stream in densities of $2/m^2$. Wickleff (1940) reports that an unidentified adult crayfish population reached densities of $22/m^2$ in riffle sections of an Ohio stream.

Rhoades (1962) dealt with *Orconectes propinquis* and *O. rusticus*, the major stream species in Ohio. He found that within a given stream system, the relative abundance of these two species of crayfish would change dramatically. *Orconectes propinquis* was most abundant in the lower stream reaches (shale and sandstone bottoms) while *O. rusticus* was most prevalent in the headwater channels (limestone bottoms). He concluded that transition zones were associated with geological features, specifically the Niagaran Limestone escarpment.

Capelli and Capelli (1980) suggested that hybridization may play an important role in the distribution of some species of *Orconectes*. No evidence was presented, however, that *O. nais* and *O. neglectus* hybridize.

Stream intermittency affects distributions of benthic organisms (Meffe and Minckley 1987, Fend 1986, Gurtz 1986, Williams and Hynes 1976, Fisher et al. 1982). Momot (1966) reported that periodic floods displaced members of an O. nais population downstream, and that they responded with an upstream migration. Merkle (1969), however, found that populations of the crayfish O. juvenalis were not drastically reduced by flooding and no upstream migration occurred.

Taylor (1983) showed that drought also altered local stream population distributions of a burrowing species (Cambarus latimanus) and a nonburrower (Procambarus spiculifer). Many crayfish respond to drought conditions by burrowing (Larimore et al. 1959, Williams et al. 1974, Grow and Merchant 1980, Berril and Chenoweth 1982, Hamr and Sinclair 1985). O. nais and and O. neglectus, however, are not considered to be even secondary burrowers (Williams and Leonard 1952).

There are virtually no reports on the effects of stream intermittency on crayfish density and abundance. Different investigators have found conflicting results when studying the effects of flood on migration. These differences could be attributed to species differences, but only future research can determine this.

Study Site

The Kings Creek drainage basin is part of the Konza Prairie Research Natural Area (KPRNA), in Riley and Geary Counties, Kansas (Fig. 2); see Hulbert 1985 for details. This native tallgrass prairie site was purchased by The Nature Conservancy in the period 1971 to 1979. The site is leased to Kansas State University for ecological research. The Kings Creek watershed drains 1060 ha and is the largest drainage on the 3487 ha site. The drainage network is composed of first- through fifth-order stream channels (Strahler 1957) that exhibit a variable flow regime. Headwater channels are ephemeral, while other stream reaches are intermittent or perennial.

The KPRNA site is typical of the Flint Hills Uplands which extend north and south through east-central Kansas. It is a dissected upland with hard chert- and flint-bearing Permian limestone and shale layers. The ridges are characteristically flat, and wider valleys have deep, permeable soils (Gurtz et al. 1982).

There are three fairly distinct zones of riparian vegetation in the watershed. Grasses such as big bluestem (*Andropogon gerardii*), little bluestem (*A. scoparius*), and Indiangrass (*Sorghastrum nutans*) dominate the upland headwater channels. Mid-reach channels are composed mainly of grasses, shrubs such as smooth sumac (*Rhus glabra*), and buckbrush (*Symphoricarpos orbiculatus*), and small trees such as the American Elm (*Ulmus americana*). The fourth- and fifth-order channels flow through a gallery forest that is dominated by bur and chinquapin oaks (*Quercus macrocarpa* and *Q. muehlenbergii*), hackberry (*Celtis occidentalis*), American Elm (*Ulmus americana*), and

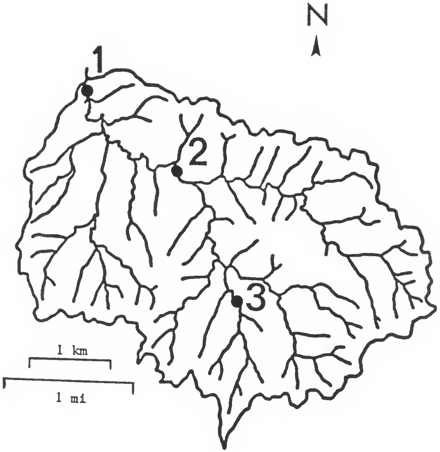


Figure 2. Study site locations within the King's Creek watershed, on the Konza Prairie Research Natural Area.

sycamore (*Platanus occidentalis*).

Limestone outcroppings occur along the channel where the stream has cut through the bed-rock strata. Stream sediments are dominated by angular pieces of limestone and chert that vary from sand-size to boulder-size. The presence and percentage of silt and clay is dependent upon parent material at that point, channel morphology, and hydrologic regime (Hooker 1987). The riffle-pool arrangement that is formed from erosional and depositional activity during periods of high flow is typical. Stream discharge is quite variable from year to year and within years (Koelliker et al. 1985)

The site of the short term habitat study is labelled 1 in Figure 2. This is a 100 m fifth-order reach of the main channel just before Kings Creek leaves the KPRNA. Steep banks and a partially closed canopy are typical of this gallery forest site. The average stream depth and width of this site during the study period were 34 cm and 340 cm respectively. Stream dimensions and habitat characteristics at 5 m intervals are given in Table 1.

The long-term migration study was conducted at sites labeled 2 and 3 in Figure 2. Site 2 is in the gallery forest in a fifth-order channel and consists of two pools. The upper pool is located about 50 m below the United States Geological Survey (USGS) water gaging station. The lower pool is about 125 m further downstream. They are separated by a long, shallow riffle area. Both pools are characterized by rocky bottoms with no visible crayfish burrows. Crayfish burrows are plentiful, however, in areas just above and below site 2 in erosional areas of cut banks. The morphometry of the

Table 1. Stream dimensions and habitat characteristics at each trap used in the habitat association study. (location 1 in figure 2)

Trap Site	Mean Depth(cm)	Width(cm)	Burrows Present	Pool/Run /Riffle
1	32	230	few	pool
2	41	220	few	run
3	19	210	few	riffle
4	31	335	few	run
5	38	247	intermediate	pool
6	49	510	intermediate	pool
7	71	525	many	run
8	27	253	intermediate	riffle
9	43	248	many	run
10	36	200	many	run
11	13	568	few	riffle
12	33	382	intermediate	run
13	45	370	many	pool
14	41	374	intermediate	pool
15	43	365	many	pool
16	39	405	many	run
17	26	340	intermediate	riffle
18	21	337	intermediate	riffle
19	22	358	few	riffle
20	19	341	few	riffle
21	16	327	few	riffle

pools is presented in Table 2.

Site 3 is located on the South Branch of Kings Creek in the channel draining the watershed designated N4 by the KPRNA management plan (Hulbert 1985) and consists of two pools, a lower pool and an upper pool. This site is located in the grass/shrub transition zone, on a third order stream. The lower pool is about 60 m upstream from the concrete gaging flume. The upper pool is about 125 m further upstream, separated by 2 riffle areas and one long shallow pool area. The bottom of both pools is rocky with no visible crayfish burrows.

Table 2. Average baseflow pool morphometry during the crayfish movement study.

Site	Pool	Length(m)	Width(m)	Depth(cm)
Forest	Lower	7.0	4.0	80.0
	Upper	6.0	4.0	60.0
Prairie	Lower	5.5	1.5	50.0
	Upper	6.0	2.0	60.0

Methods

Crayfish Habitat Association Study

A 100 m reach of gallery forest stream at site 1 was blocked at the upper and lower ends with .635 cm (1/4") hail screen. The "fence" extended about 0.5 m above the water surface and 1 m to either side of the active channel boundary. Twenty-one trap stations, 5 m apart, were established at mid-channel. Trap 1 was at the lower end and trap 21 was at the upper end. Stream width and depth were recorded as continuous variables but were given categorical assignments (i.e. shallow, wide, etc.) for analysis purposes. These definitions are presented in Table 3. Trap sites were characterized as being riffles, runs, or pools. The presence of crayfish burrows was quantified as the number of visible burrows per square meter. Areas of less than 5 burrows per square meter were defined as few burrows. Intermediate burrow areas were those areas that had from 5 to 10 burrows per square meter. Stream areas that had more than 10 burrows per square meter were described as being areas of many burrows.

The traps were constructed of .635 cm (1/4") hail screen, were cylindrical (about 60 cm long and 20 cm in diameter) and had removable funnels in each end. The funnels had a narrow diameter of 5 cm and a wide diameter of 25 cm. The traps were constructed (after Fitch 1951) for a previous herpetofauna study (Heinrich 1984).

The traps were set nine times between July 23, 1986 and August 13, 1986 (Table 4). The setting and recovery of traps was done at various times to determine when the largest numbers of crayfish were

Table 3. Categorical assignments of habitat variables used in the habitat association study.

Depth	
< 30 cm	Shallow
30-40 cm	Medium
> 40 cm	Deep

Width	
< 325 cm	Narrow
325-450 cm	Intermediate
> 450 cm	Wide

Crayfish Burrows	
< 5 burrows per square meter	Few
5-10 burrows per square meter	Intermediate
> 10 burrows per square meter	Many

Riffle/Run/Pool	
Shallow, fast current velocity	Riffle
Medium depth, intermediate flow	Run
Deep, slow current velocity	Pool

Table 4. Trapping schedule during the habitat association study.

	Traps set		Traps Checked	
Day	Date	Time	Date	Time
1	7/23	1700	7/24	1430
2	7/25	1600	7/26	1000
3	7/27	1900	7/28	0700
4	7/30	0830	7/30	1730
5	8/01	1900	8/02	1100
6	8/04	1800	8/05	1400
7	8/05	1700	8/06	1430
8	8/06	1730	8/07	1700
9	8/12	1800	8/13	1200

caught. Each trap was baited with one medium 'Milkbone' dog biscuit on all trap dates except for August 1st. No bait was used on this occasion to examine the effectiveness of the traps without bait.

The species and sex of each captured individual were recorded, and carapace length was measured to the nearest mm with vernier calipers. Individuals that were captured in the lower 50 m (traps 1-11) were marked by clipping the left fourth pereiopod. Individuals that were captured in the upper 50 m (traps 12-21) were marked by clipping the right fourth pereiopod. Individuals were then released at the trap site where they were captured. Traps were set and recovered in a downstream to upstream sequence.

Crayfish Movement Study

A second study was conducted to examine some factors that potentially influenced crayfish movement. This study was conducted at sites 2 (a gallery forest site) and 3 (a prairie site) (Fig. 2). Traps were set 29 times between August 24, 1986 to November 6, 1986, on Sundays, Tuesdays, and Thursdays at 1700 hr each week. Traps were recovered on Mondays, Wednesdays, and Fridays at 0900 hr of that same week. Six weekly trapping events were recorded from November 11th to December 17th. Each trap was baited with one medium 'Milkbone' dog biscuit. Four traps were set in each of the four pool sites. Traps were placed at mid-channel, evenly spaced along the thalweg in each pool, but oriented at 45 degrees to the flow.

Data on available moonlight and cloud cover were obtained for each trap night (Table 5). Temperature, oxygen, and stream stage were measured at mid-pool before the traps were removed and examined

Table 5. Variables affecting the available moonlight during the crayfish movement study.

Day	Date	+ % Of Full Moon Shining	+ % Of Night That Moon Is Out	++ % Of Cloud Cover
1	8/24	76	95	20
2	8/26	59	85	70
3	8/28	40	75	0
4	8/31	14	50	85
5	9/02	4	30	50
6	9/04	1	0	60
7	9/07	12	0	0
8	9/09	30	0	60
9	9/11	52	25	0
10	9/16	96	75	100
11	9/18	100	100	10
12	9/21	89	100	50
13	9/23	74	95	60
14	9/25	56	80	35
15	9/28	29	65	100
16	10/05	4	0	20
17	10/07	18	0	30
18	10/09	38	15	100
19	10/12	71	35	100
20	10/14	88	65	45
21	10/16	98	85	10
22	10/19	97	100	0
23	10/21	87	100	100
24	10/23	73	100	100
25	10/26	45	65	0
26	10/28	25	55	0
27	11/02	0	0	100
28	11/04	7	0	100
29	11/06	24	0	0
30	11/11	77	55	100
31	11/18	96	100	100
32	11/25	42	65	90
33	12/02	2	0	0
34	12/09	62	45	30
35	12/16	100	100	100

\+ Local Climatological Data, National Weather Service Topeka, Kansas.

++ The Astronomical Almanac, 1986. Washington, D.C., United States Government Printing Office.

(Table 6 and Table 7). Temperature and oxygen were measured with a portable oxygen meter (Yellow Springs Instrument Co., Inc., Model 54A). Stream stage was measured with a 2 meter length of 1/2" rebar that had been driven into the stream bottom at the lower end of each pool. The length of rebar that extended above the water surface was measured as the stream stage.

Crayfish found in the traps were identified to species and sex, and carapace length (tip of rostrum to the posterior edge of the cephalothorax) was measured to the nearest mm with a vernier caliper. Crayfish from each pool were given unique marks using a combination of leg and telson clipping. Individual marking was not attempted. Marking remained the same for each site for the first five weeks. The marks were changed on a weekly basis after that, so that rate of movement could be evaluated.

The marking technique was chosen for its ease of use and prior success (Jackson 1972, Ingelin 1984). Crayfish with similar marks were maintained under various laboratory conditions and showed no difference in behavior or mortality from unmarked crayfish.

Table 6. Weekly mean temperature, oxygen, and stream stage at the two forest pools during the crayfish movement study.

Week	Samples/ Week	Temperature	Oxygen	Stream Stage
1	3	14.9	7.9	29.9
2	3	15.6	6.9	30.3
3	3	15.3	7.5	30.2
4	2	17.1	8.1	27.3
5	3	17.6	8.3	27.5
6	1	18.6	8.7	14.4
7	3	15.3	9.3	14.9
8	3	12.7	10.9	15.0
9	3	14.3	11.3	12.1
10	2	13.1	9.7	12.8
11	3	11.8	10.0	15.7
12	1	7.7	10.9	18.0
13	1	9.0	10.5	19.0
14	1	9.0	10.7	20.0
15	1	8.3	10.8	20.5
16	1	5.9	11.5	20.5
17	1	9.0	11.0	20.5

Table 7. Weekly mean temperature, oxygen, and stream stage at the two prairie pools during the crayfish movement study.

Week	Samples/ Week	Temperature	Oxygen	Stream Stage
1	3	17.7	7.7	56.2
2	3	17.4	8.1	57.7
3	3	15.9	9.7	56.6
4	2	18.3	9.5	56.4
5	3	19.9	9.3	57.2
6	1	18.7	9.1	45.2
7	3	14.7	10.2	50.1
8	3	12.5	11.5	50.3
9	3	13.7	12.1	50.3
10	2	12.6	9.7	47.8
11	3	11.4	10.4	49.7
12	1	8.5	11.1	52.5
13	1	6.8	11.5	53.0
14	1	6.2	11.9	54.0
15	1	4.9	12.1	54.5
16	1	2.5	12.5	54.0
17	1	6.6	12.0	54.0

Results

Habitat Association Study

A total of 1,636 crayfish were captured between July 23, 1986 and August 13, 1986 (Table 8). Recapture rates were 23% for *Orconectes neglectus* and 31% for *O. nais*. Population estimates were calculated using Schnabel's Weighted Mean estimate (Begon 1979) (Table 9). Density estimates were calculated using population estimates and the average stream area (100m X 3.6m). A total of 2,482 crayfish were estimated to be living in the 100 m section of stream during the study period. Eighty-eight percent of the crayfish present were represented by *O. neglectus*. The sex ratios of *O. nais* and *O. neglectus* were 1.2:1 and .86:1 respectively. Crayfish population densities were estimated at about $1/m^2$ for *O. nais* and $6/m^2$ for *O. neglectus*.

The number of crayfish captured ranged from 78 on July 30th (8 hour day-time set) to 266 on July 25th (Table 10). The most crayfish were caught when traps were set at ca. 1700 and checked at ca. 0900 the following day. Traps set on August 1st, when no bait was used, yielded a low number of crayfish but was not significantly different (X^2, $p < .05$) from August 5th and 6th. The size distribution and the proportion of species and sex was not different between crayfish caught in baited traps and crayfish caught in unbaited traps(X^2, $p < .05$). This indicated that all crayfish responded to the biscuit type bait in the same manner. No differences were found among species, sex, or size in crayfish captured for the first time versus crayfish that were recaptured. Crayfish were, therefore, not

Table 8. Numbers, of each sex and species captured in the habitat association study.

Total Captured	Male	Female	Total
Orconectes nais	159	113	272
Orconectes neglectus	768	596	1364

Total Recaptured	Male	Female	Total
Orconectes nais	52	32	84
Orconectes neglectus	203	112	315

Table 9. Population estimates and density estimates at Site 1 during the habitat association study.

	Male	Female	Total
Orconectes nais	159	130	289
	$.44/m^2$	$.36/m^2$	$.8/m^2$
Orconectes neglectus	1014	1179	2193
	$2.8/m^2$	$3.3/m^2$	$6.1/m^2$

Table 10. Number of crayfish caught on each day during the habitat association study.

Day	*O. nais*	*O. neglectus*	Totals
1	36	164	200
2	47	219	266
3	40	210	250
4	12	66	78
5	23	101	124
6	34	141	175
7	26	121	147
8	19	113	132
9	35	229	264

responding in a 'trap-happy' or a 'trap-shy' manner (Begon 1979).

The number of crayfish caught per trap site varied from 1 (Trap 3) to 202 (Traps 6 and 15) (Table 11). Orconectes neglectus were captured more often at every trap site but Trap 3 and Trap 11. The ratio of O. nais to O. neglectus captured at each trap site varied from 50% at trap 11 to 0% at trap 21. Description of the stream habitat at the individual trap sites are given in Table 1. The categorical assignments for the continous habitat variables are given in Table 3.

No differences were noted between the two species in regard to their distribution within the stream (Table 12). This was also true for sex differences within each species.

The length frequency distributions for both species are shown in Fig. 3 and Fig. 4. The carapace lengths of O. nais ranged from 15.6 mm to 47.8 mm with a mean carapace length of 30.9 mm. Carapace lengths of O. neglectus ranged in size from 10 mm to 40.1 mm with a mean carapace length of 26.3 mm. Categorical size classes were subjectively assigned to each species to aid in analysis. Orconectes nais were labeled as small if they were less than 25 mm in carapace length, medium if their carapace length was 25 mm to 35 mm, and large if their carapace length was over 35 mm. Orconectes neglectus were labeled small if they were less than 20 mm in carapace length, medium if their carapace length was 20 mm to 30 mm, and large if their carapace length was greater than 30 mm. The categorical size distributions for both species are given in Fig. 5 and Fig. 6. Large and medium sized individuals were most prevalent in the O.

Table 11. Number of crayfish caught in each trap during the habitat association study.

Trap	*O. nais*	*O. neglectus*	Total
1	2	7	9
2	6	34	40
3	1	0	1
4	4	36	40
5	17	104	121
6	38	164	202
7	20	94	114
8	14	49	63
9	12	99	111
10	9	104	113
11	1	1	2
12	2	36	38
13	21	139	160
14	7	46	53
15	39	163	202
16	53	133	186
17	7	48	55
18	11	40	51
19	6	23	29
20	2	30	32
21	0	14	14

Table 12. Percentage of crayfish captured in association with various habitat variables (*O. nais*, n= 272; *O. neglectus*, n= 1364).

Habitat variable - stream width

	Narrow	Medium	Wide
O. nais	22%	56%	22%
O. neglectus	29%	52%	19%

Habitat variable - stream depth

	Shallow	Intermediate	Deep
O. nais	15%	32%	53%
O. neglectus	15%	31%	54%

Habitat variable - Riffle/Run/Pool

	Riffle	Run	Pool
O. nais	15%	39%	46%
O. neglectus	15%	39%	46%

Habitat variable - Crayfish Burrows

	Few	Intermediate	Many
O. nais	8%	35%	57%
O. neglectus	10%	36%	54%

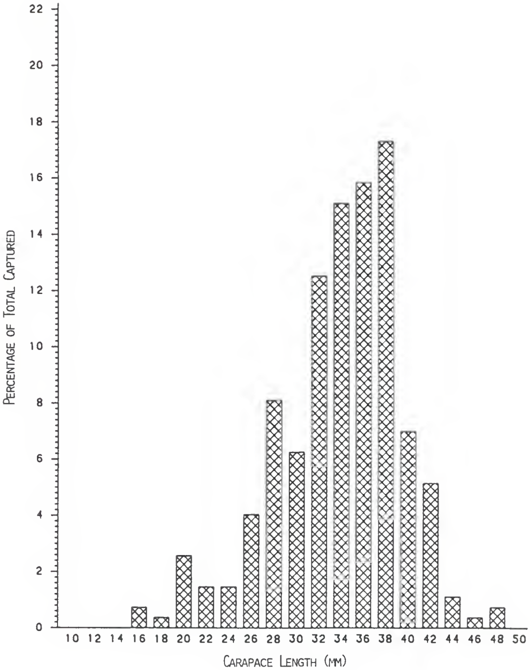


Figure 3. Length frequency distribution of Orconectes nais in the habitat association study (n = 272).

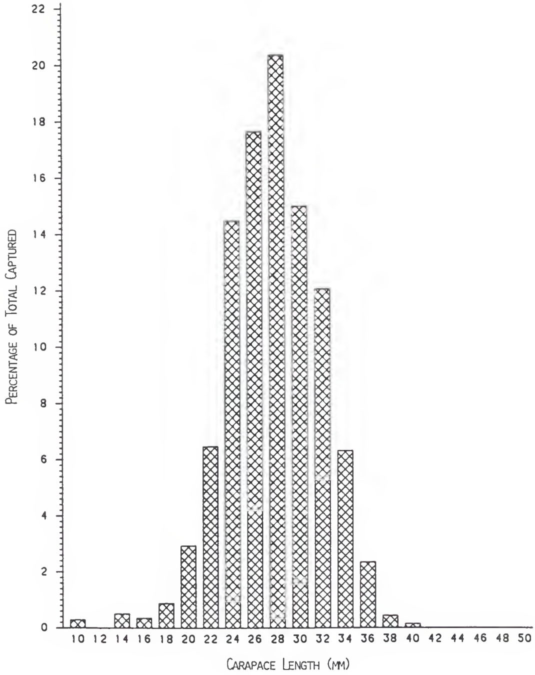


Figure 4. Length frequency distribution of Orconectes neglectus in the habitat association study (n = 1364).

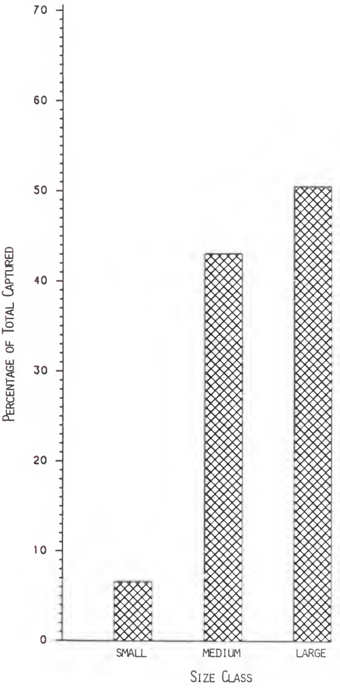


Figure 5. Categorical size distribution of Orconectes nais in the habitat association study (n = 272).

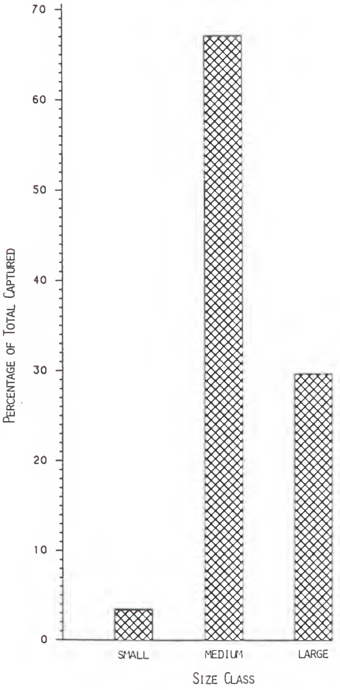


Figure 6. Categorical size distribution of Orconectes neglectus in the habitat association study (n = 1364).

nais population; whereas medium sized individuals were most abundant in the O. neglectus population. Categorical size distribution was not different between males and females for the small and medium size class for either species. However, the large size class showed sex differences for O. nais ($X^2 = 8.9$, $p < .05$) and O. neglectus ($X^2 = 83.5$, $p < .001$). Sixty-four percent of the large O. nais were males and 73% of the large O. neglectus were males (Table 13).

A relationship was sought between the size distribution of crayfish within the stream and the four habitat variables, using the SAS statistical analysis package (SAS Institute Inc. 1985). Nominal cross-classification tables were constructed using size classes and habitat variables. The tables were then analyzed with a chi-square test of independence for each stratum. Male and female size distributions were not different in relation to the four habitat variables for O. nais or O. neglectus. Size distribution was closely associated (X^2, $p < .001$) with all four habitat variables for O. neglectus. Size distribution was less closely associated (X^2, $p < .05$) with all four habitat variables for O. nais. These differences between the two species may be a function of the different sample size. The cross-tabulation tables for the four habitat variables in relation to size class are given in Tables 14-17.

Small crayfish of either species were caught in about equal numbers regardless of stream depth, stream type, or presence of burrows. Small crayfish of both species were never captured at wide (> 450cm) stream sites. Orconectes neglectus was found more often at intermediate widths than narrow width sections ($X^2 = 10.3$, $p < .01$).

Table 13. Categorical size distribution of each sex and species captured in the habitat association study.

Orconectes nais

	Small	Medium	Large
Male	7	70	82
Female	11	55	47

Orconectes neglectus

	Small	Medium	Large
Male	19	462	287
Female	28	463	105

Table 14. Categorical size distribution of crayfish captured at Site 1, associated with stream width.

	Orconectes nais		
	Small	Medium	Large
Narrow	7 (39%)	18 (14%)	36 (28%)
Intermediate	11 (61%)	85 (68%)	56 (43%)
Wide	0 (0%)	22 (18%)	37 (29%)

	Orconectes neglectus		
	Small	Medium	Large
Narrow	12 (26%)	238 (26%)	147 (38%)
Intermediate	35 (74%)	546 (59%)	127 (32%)
Wide	0 (0%)	141 (15%)	118 (30%)

Table 15. Categorical size distribution of crayfish captured at Site 1, associated with stream depth.

Orconectes nais

	Small	Medium	Large
Shallow	5 (28%)	29 (23%)	8 (6%)
Medium	5 (28%)	33 (26%)	49 (38%)
Deep	8 (44%)	63 (51%)	72 (56%)

Orconectes neglectus

	Small	Medium	Large
Shallow	14 (30%)	163 (18%)	28 (7%)
Medium	18 (38%)	269 (29%)	133 (34%)
Deep	15 (32%)	493 (53%)	231 (59%)

Table 16. Categorical size distribution of crayfish captured at Site 1, associated with riffle/run/pool characteristics.

Orconectes nais

	Small	Medium	Large
Riffle	5 (28%)	29 (23%)	8 (6%)
Run	6 (33%)	38 (30%)	62 (48%)
Pool	7 (39%)	58 (47%)	59 (46%)

Orconectes neglectus

	Small	Medium	Large
Riffle	14 (30%)	163 (18%)	28 (7%)
Run	21 (45%)	329 (36%)	186 (47%)
Pool	12 (25%)	433 (46%)	178 (46%)

Table 17. Categorical size distribution of crayfish captured at Site 1, associated with presence of crayfish burrows.

Orconectes nais

	Small	Medium	Large
Few	6 (33%)	14 (11%)	2 (2%)
Intermediate	8 (44%)	43 (34%)	45 (35%)
Many	4 (23%)	68 (55%)	82 (63%)

Orconectes neglectus

	Small	Medium	Large
Few	16 (34%)	117 (13%)	12 (3%)
Intermediate	18 (38%)	330 (36%)	139 (35%)
Many	13 (28%)	478 (51%)	241 (62%)

The majority of O. nais and O. neglectus in the medium size class were found in deep pools of intermediate width in the presence of many crayfish burrows. The fewest numbers of medium sized O. nais and O. neglectus were captured in shallow, riffle areas with few burrows present.

The smallest habitat differences between O. nais and O. neglectus, esp. stream type and presence of crayfish burrows), were observed in the large size class. Large crayfish were captured less than 3% of the time in areas of few crayfish burrows and 82.5% of the time in areas of many burrows. Large individuals were captured in shallow, riffle areas only 7% of the time. The majority of large O. nais and O. neglectus were captured in deep runs and pools. Large crayfish were caught at narrow, intermediate, and wide stream sections in about equal numbers .

Of the 272 O. nais captured in the lower and upper sections, only 2 individuals were found to have migrated (a 31.1 mm female and a 27.2 mm male) (Table 18). Both crayfish were recaptured in the lower section after having been marked in the upper section. Of the 1364 O. neglectus caught in both sections, a total of 25 were found to have moved downstream and 14 had moved upstream. Two percent of the recaptured O. nais were found to migrate, and 12% of the recaptured O. neglectus were found to migrate. No difference in up or downstream migration was found for either species. Only members of the medium size class were found to move for both species. The first crayfish marked and released in the lower section to reach the far end of the upper section was an O. neglectus male (22.8 mm) by

Table 18. Summary of movement data used in the habitat association study.

	Orconectes nais	
	Lower 50m	Upper 50m
Total Captured	124	148
Total Recaptured	44	40
Number Recaptured From Opposite Stream Section	2	0

	Orconectes neglectus	
	Lower 50m	Upper 50m
Total Captured	692	672
Total Recaptured	206	109
Number Recaptured From Opposite Stream Section	25	14

day 2. The first crayfish marked and released in the upper section to reach the far end of the lower section was an O. neglectus male (24.4 mm) by day 4.

Crayfish Movement Study

The analysis of the crayfish movement study is based on the capture of 3005 individuals (Table 19.) About 25% (852) of these were recaptured. O. nais composed 55% of the total crayfish caught, and varied from 66% in the forest to 42% in the prairie. The numbers caught in each pool varied from 598 (Forest upper pool) to 985 (Forest lower pool). The numbers of crayfish caught by week are summarized in Table 20. Weeks were composed of from one to three trap nights. The first eleven weeks of the study had 3 trap nights per week except for weeks 4 and 10 which had 2 trap nights, and week 6 which only had 1 trap night. Numbers of crayfish captured diminish with time at both sites. O. nais numbers decreased the most, particularly in the forest.

Pearson correlation coefficients were used to examine the relationship between numbers of crayfish caught per night and the following environmental variables: temperature, dissolved oxygen, stream stage height, percentage fullness of the moon, percentage of night that moon is out, and the percentage of cloud cover (Table 21). Temperature, dissolved oxygen, and stream stage were found to be closely correlated with number of crayfish caught on any given night for both sites. The factors affecting available moonlight were not found to be correlated with the numbers caught per night.

The greatest change in numbers caught per night occurred after

Table 19. Number of crayfish captured during the crayfish movement study at each study site.

		Total Captured		Total Recaptured	
Site		Male	Female	Male	Female
Forest Lower Pool	*O. nais*	423	293	88	85
	O. neglectus	117	152	17	50
Forest Upper Pool	*O. nais*	297	165	55	23
	O. neglectus	85	51	19	10
Prairie Lower Pool	*O. nais*	213	247	55	91
	O. neglectus	60	101	15	33
Prairie Upper Pool	*O. nais*	261	174	91	62
	O. neglectus	151	215	55	103

Table 20. Weekly summary of numbers captured during the crayfish movement study at Site 2 and Site 3.

		Site 2		Site 3	
Trap Nights	Week	*O. nais*	*O. neglectus*	*O. nais*	*O. neglectus*
3	1	205	72	120	75
3	2	220	55	144	72
3	3	181	49	138	54
2	4	121	24	91	40
3	5	226	66	244	101
1	6	47	20	53	24
3	7	79	31	35	49
3	8	32	31	13	26
3	9	37	40	18	29
2	10	5	6	14	18
3	11	14	7	9	15
1	12	0	0	0	4
1	13	3	0	5	3
1	14	2	1	3	7
1	15	2	2	2	5
1	16	2	1	2	1
1	17	2	0	4	4

Table 21. Correlation coefficients between the number of crayfish caught per day and the measured environmental variables during the crayfish movement study. * = significant at the .05 level. ** = significant at the .01 level.

Stream Variables	*Orconectes nais* Site 2	*Orconectes nais* Site 3	*Orconectes neglectus* Site 2	*Orconectes neglectus* Site 3
Water Temperature	.682**	.714**	.623**	.760**
Dissolved Oxygen	-.723**	-.503**	-.477**	-.620**
Stream Stage	.723**	.084	.437*	.446**

Moonlight Variables	*Orconectes nais* Site 2	*Orconectes nais* Site 3	*Orconectes neglectus* Site 2	*Orconectes neglectus* Site 3
% Fullness of Moon	-.098	.027	.124	-.077
% Of Night That Moon Is Above The Horizon	.049	.138	.235	.118
% Cloud Cover	-.134	-.043	.039	-.116

week 6. This was after a storm flow which occured from September 29th to October 3rd. Preflood and postflood density estimates are given in Table 22. Preflood density was calculated using data from weeks 1-6. Postflood density was calculated using dat from weeks 7-11.

Male and female O. nais densities were highest in the prairie pools reaching densities of $34/m^2$ and $25/m^2$ respectively. Male and female O. neglectus densities were highest in the prairie also, reaching densities of $9/m^2$ and $13/m^2$ respectively. The flood reduced the O. nais population by 84% at the forest site and by 91% at the prairie site. O. neglectes populations were reduced by 69% at the forest site and 28% at the prairie site. Males of both species were reduced in numbers more than females at all sites except the upper forest pool. At this site O. neglectus males experienced a 50% reduction, while O. neglectus females exhibited a 33% increase in numbers.

The flood also caused changes in the size structure of both species (Fig. 7 to Fig. 10). The greatest reduction in numbers was a ten fold decrease in small O. nais individuals in the forest pools. The smallest reduction in numbers was shown by large O. neglectus in the prairie pools. The smallest change in size class structure was observed at the forest site in the O. neglectus population. No differences between sexes were noted in either species with regard to reduction of the different size classes.

Of the 852 crayfish that were recaptured, 8% were recaptured in the opposite pool from where they had been marked (Table 23). The

Table 22. Density estimates during the crayfish movement study before and after the flood event.

Site		Preflood Density Estimates		Postflood Density Estimates	
		Male	Female	Male	Female
Forest Lower Pool	*O. nais*	$24/m^2$	$12/m^2$	$2/m^2$	$2/m^2$
	O. neglectus	$7/m^2$	$6/m^2$	$2/m^2$	$2/m^2$
Forest Upper Pool	*O. nais*	$26/m^2$	$15/m^2$	$4/m^2$	$5/m^2$
	O. neglectus	$1/m^2$	$2/m^2$	$.5/m^2$	$3/m^2$
Prairie Lower Pool	*O. nais*	$34/m^2$	$25/m^2$	$3/m^2$	$2/m^2$
	O. neglectus	$7/m^2$	$13/m^2$	$1/m^2$	$2/m^2$
Prairie Upper Pool	*O. nais*	$21/m^2$	$14/m^2$	$2/m^2$	$2/m^2$
	O. neglectus	$9/m^2$	$10/m^2$	$4/m^2$	$5/m^2$

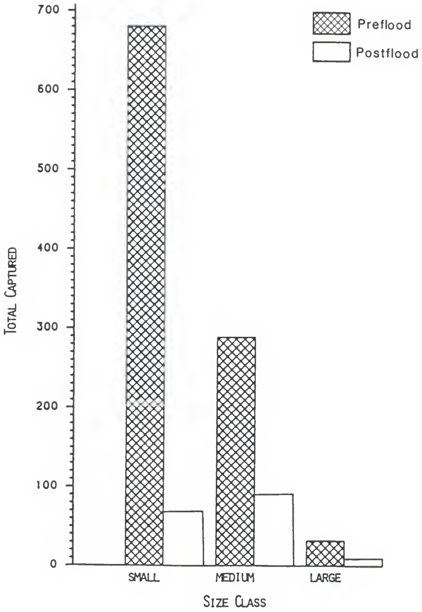


Figure 7. Preflood and postflood size distribution of <u>Orconectes nais</u> during the movement study at Site 2.

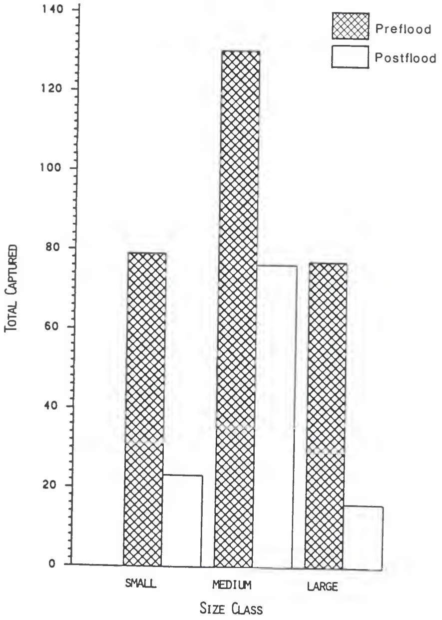


Figure 8. Preflood and postflood size distribution of <u>Orconectes neglectus</u> during the movement study at Site 2.

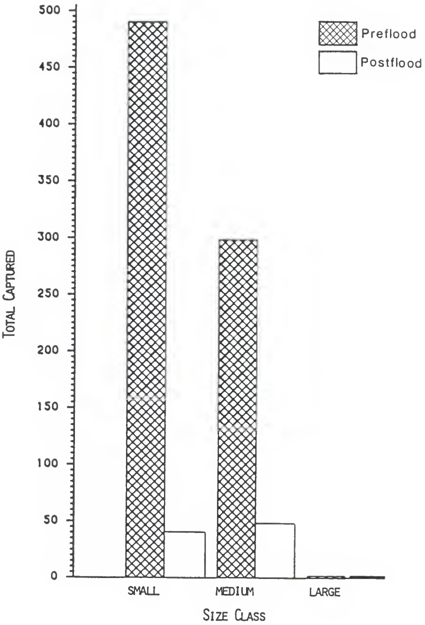


Figure 9. Preflood and postflood size distribution of Orconectes nais during the movement study at Site 3.

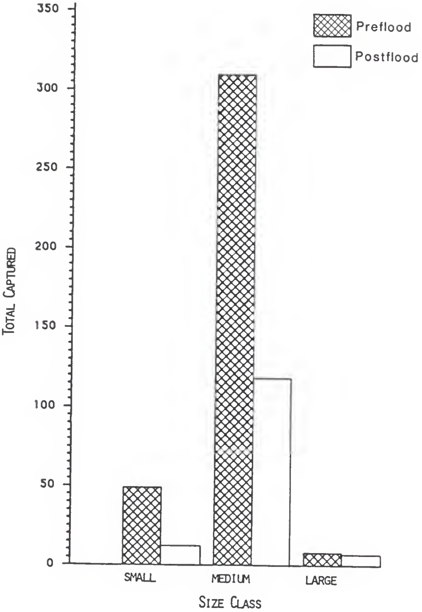


Figure 10. Preflood and postflood size distribution of Orconectes neglectus during the movement study at Site 3.

Table 23. Summary of movement data used in the crayfish movement study. The numbers recorded at the lower pools had been marked and released at the upper pools and the numbers recorded at the upper pools had been marked and released at the lower pools, indicating a 125 m migration in either direction.

Site		*O. nais*	*O. neglectus*
Prairie Lower Pool	Preflood	6	1
	Postflood	5	2
Prairie Upper Pool	Preflood	8	0
	Postflood	12	3
Forest Lower Pool	Preflood	3	1
	Postflood	6	1
Forest Upper Pool	Preflood	5	3
	Postflood	5	7

fastest verified migration was from Pool 3 to Pool 4 by an _O. nais_ female. This individual was marked on September 22, 1986 and captured on September 24, 1986. The percentage of crayfish found migrating in relation to the total number that were recaptured was 2% for both _O. nais_ and _O. neglectus_. No difference in upstream or downstream movement was indicated for either species at either site. No differences were found between preflood and postflood movements for either species.

Discussion

Orconectes neglectus is a stream dweller exclusively and has a very limited range (Williams 1954). *Orconectes nais*, on the other hand, is found throughout the Midwest and Great Plains in streams and permanent ponds (ibid). The exclusion of *O. neglectus* from ponds is a function of its requirement for high oxygen concentrations (Plaskett et al. 1980), in contrast to the low oxygen tolerance of *O. nais* (Rice and Armitage 1973, Wiens and Armitage 1961). Hynes (1970) and Williams (1954) believe that the restricted range of *O. neglectus* is a response to agricultural development and the associated turbidity of farmland streams. The different oxygen tolerances may explain the distribution and abundance of the two species in King's Creek.

The most dramatic differences in crayfish abundance occurred in response to a storm flow. Other authors have reported this phenomenon in benthic invertebrates (Williams and Hynes 1976, Fisher et al. 1982, Gurtz et al. 1982). *Orconectes nais* populations showed a more dramatic reduction in numbers, in response to flood than *O. neglectus* populations.

The tallgrass prairie streams on KPRNA experience two major natural disturbances on a seasonal basis; floods and droughts. *Orconectes nais* and *O. neglectus* can respond to these conditions in one of two ways, 1) emigration followed by recolonization when conditions become more favorable or 2) remaining and surviving by various physiological or behavioral responses.

Momot (1966) suggested that upstream migration by crayfish acted as a compensating redistribution mechanism to offset the effects of flood. He documented the removal of _O. nais_ by a summer flood in Oklahoma and found a significant upstream migration by _O. nais_. The current study, however, did not document significant upstream migration for either _O. nais_ or _O. neglectus_, before or after a flood.

Many crayfish respond to adverse environmental conditions, especially drought, by burrowing (Larimore et. al. 1959, Mobberly and Pfrimmer 1967, Williams et. al. 1974). Burrows often penetrate several meters to ground water. Even if dissolved oxygen drops to nearly zero, some crayfish species survive by exposing their gills above the water line and extracting oxygen directly from the air (Grow and Merchant 1980).

Both _O. nais_ and _O. neglectus_ have been regarded as non-burrowers (Hobbs 1974), but _O. nais_ was reported to construct burrows in banks of streams and ponds during drought conditions (Williams 1954). Other non-burrowing species are known to burrow during times of drought (Payne 1978, Berril and Chenoweth 1982, Hamr and Sinclair 1985). _O. neglectus_ has been found by the author in dry stream beds in short vertical burrows under rocks that retained moisture.

The highest densities of _O. neglectus_ were found in the perennial reaches (Site 1 and 3) and the lowest densities in the intermittent reach (Site 2). The highest densities of _O. nais_ were found in an intermittent reach (Site 2) and in areas of slow current flow (Site 3). The lowest densities of _O. nais_ were found after the flood and in the lowest reach where discharge is greatest.

Orconectes nais, therefore, was found to dominate in areas of slow current velocity and in areas where the stream regularly dries up. O. neglectus was found more often in areas where flow rate was high and perennial.

The physiological and behavioral differences between O. nais and O. neglectus provide a possible explanation for the differences in abundance and distribution in King's Creek. Orconectes neglectus is less tolerant of oxygen deficient water and was restricted to areas of perennial water and high flow rates that retain high oxygen concentrations year round. O. nais was less apt to maintain its position in high rates of flow (esp. the small sized individuals) and was therefore removed in large numbers from certain areas regularly, and restricted in numbers and size class at other areas on a regular basis.

It is important to note that the four pools that were studied during the flood events are rubble-bottomed with little evidence of burrows. The prairie pools were situated in bed-rock channels where evidence of burrowing was not noticeable. However, the gallery forest stream supports areas with extensive crayfish burrows above and below the study pools. These are most often associated with areas where the stream curves. The burrows are located on outside curves in erosional areas and were probably constructed by O. nais during drought periods.

Densities of the two species of crayfish were found to differ widely depending on what type of stream habitat was sampled, where in the watershed sampling was conducted, and when sampling was conducted.

Floods had the most dramatic effects on population densities, but no upstream migrations after the floods by either O. nais or O. neglectus were observed. The intermittency of King's Creek (flooding and drought) may well act as a 'resetting' mechanism (Cummins 1979) to control population densities of O. nais and O. neglectus. This study documented the effects of flood on the abundance and density of the two species of crayfish. Future studies regarding specific use of the crayfish burrow systems during drought conditions may provide useful information in understanding the response of Orconectes nais and Orconectes neglectes to stream intermittency.

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OBSERVATIONS OF FLUCTUATIONS IN POPULATION DENSITY OF TWO SPECIES OF CRAYFISH IN A TALLGRASS PRAIRIE STREAM

by

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ABSTRACT

This is a report of observations of two species of crayfish that coexist in a tallgrass prairie stream. The objectives of this study were to measure the distribution and abundance of Orconectes nais and O. neglectus in Kings Creek, on the Konza Prairie Research Natural Area in Riley and Geary Counties, Kansas. O. nais is a widely distributed, hardy crayfish that is tolerant of low oxygen conditions and is usually found in ponds, streams, and ditches. O. neglectus is a species with a restricted distribution, found only in clear, fast flowing well-oxygenated streams.

Two aspects of their coexistence were studied during the fall of 1986. Both studies employed the use of baited traps. The first examined the relationship of their distribution to the characteristics of the stream. Even though O. neglectus and O. nais were found in densities of about $6/m^2$ and $1/m^2$ respectively, both species were found in similar proportions in the various habitats. The size of the crayfish was found to be closely associated with the type of habitat that they were captured in.

The second study examined population response to hydrologic events. Unexpected heavy precipitation kept one site flowing for the entire study period. It was, therefore, impossible to study the effects of drought. The heavy rains, however, allowed the observations of the effects of a flooding event. The abundance and size structure of both populations were significantly altered by the flood. The O. nais population was more adversely affected than the population of O. neglectus. No upstream or downstream movement before or after the flood was observed. Orconectes nais and O. neglectus were found to reach densities of $59/m^2$ and $20/m^2$ respectively.