SPECIES DISTRIBUTIONS AND TRAIT-ENVIRONMENT CORRELATIONS: IMPLICATIONS FOR THE EVOLUTIONARY ECOLOGY OF CRAYFISH (DECAPODA: CAMBARIDAE)

By

REID LANDEN MOREHOUSE

Bachelor of Science in Fisheries and Aquatic Sciences
Purdue University
West Lafayette, IN
2006

Master of Science in Zoology
Oklahoma State University
Stillwater, OK
2010

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SPECIES DISTRIBUTIONS AND TRAIT-ENVIRONMENT CORRELATIONS: IMPLICATIONS FOR THE EVOLUTIONARY ECOLOGY OF CRAYFISH (DECAPODA: CAMBARIDAE)

Dissertation Approved:

Dr. Michael Tobler

Dissertation Adviser

Dr. Punidan Jeyasingh

Dr. Monica Papeş

Dr. Andrew Dzialowski

Dr. Shannon Brewer

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Abstract: Crayfish occur on every continent, except for Antarctica and Africa excluding Madagascar, and are a very diverse group of freshwater crustaceans with over 600 species. Crayfish are keystone species, ecosystems engineers, and make up the majority of invertebrate biomass in the systems they inhabit. In Oklahoma, there are 30 known species from six genera, with representatives from the three general ecological morphs that are defined by their burrowing behavior (burrowing types). In the first chapter, I provide a general overview and a synthesis of the questions addressed in my dissertation. The second chapter provides an in-depth account of Oklahoma's crayfish and their biology, including an illustrated dichotomous key for species identification, individual species descriptions with color photographs, and detailed distribution maps. This chapter provided the foundation for research on crayfish biology in my subsequent chapters. Specifically, my studies focused on the 27 epigean species of Oklahoma to address questions regarding the effects of climate change and land use on species distributions (Chapter 3), quantifying morphological variation among taxa to test of the role of evolutionary convergence among burrowing types (Chapter 4), and investigating whether and how trophic resource partitioning can mediate the coexistence of sympatric species (Chapter 5). In Chapter 3, my results suggested that different crayfish burrowing types were affected by distinct bioclimatic variables. Crayfish distributions, however, did not appear to be negatively affected by climate change, and habitat destruction is likely a driving factor in the decline of crayfish. Differences among burrowing types were also highlighted in Chapter 4, which indicated consistent morphological trait variation in species of the same burrowing type, irrespective of taxonomic affiliation, providing evidence for convergent evolution in crayfish morphology. Finally, in Chapter 5, stable isotope analyses indicated that some crayfish species pairs partition their food resources, but there is also evidence for overlap in dietary niches. Overall, my dissertation provides a foundation for the study of crayfish within Oklahoma and surrounding states and provides a basis of better understanding the evolutionary and ecological mechanisms that have lead to and contributed to maintaining crayfish diversity in North America.

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CHAPTER I

INTRODUCTION AND SYNTHESIS

For my dissertation, I was interested in illuminating the vast diversity of crayfish and their interactions with the environment and conspecifics. I focused on the crayfish fauna of Oklahoma to specifically address questions regarding their distribution in context of bioclimatic (temperature and precipitation) variables and climate change; explore morphological variation among taxonomic groups, between sexes and among burrowing types; and test for the role of trophic niche partitioning in facilitating the coexistence of sympatric species. In this chapter, I first introduce pertinent concepts, review available empirical data on the ecology of crayfish, and highlight current gaps of knowledge. I then provide an overview and synthesis of my dissertation research by highlighting the major questions I addressed in the subsequent chapters.

Crayfish diversity, identification, and threats

Crayfish are native to every continent except Antarctica and Africa, excluding Madagascar (Hobbs 1989). There are more than 600 described crayfish species in three families (Astacidae, Cambaridae, and Parastacidae) recognized worldwide. The greatest diversity occurs in North America, where approximately 77% (~400 species and subspecies) of species are found (Taylor et al. 2007). Two families are native to North America: the Astacidae are restricted to the far northwest, and the Cambaridae occur east of the Rocky Mountains.

The Cambaridae is the most diverse family worldwide, with 99% of its members occurring in North America (Taylor 2002), with the rest occurring in East Asia (Holdich 2002).

In North America, two subfamilies of Cambaridae have been described. The Cambarellinae includes a single genus (*Cambarellus*), and the Cambarinae contains ten genera. Three of the ten genera of the Cambarinae (*Cambarus, Orconectes,* and *Procambarus*) encompass 85% of all crayfish species and subspecies known in North America (Taylor 2002). With approximately 163 species, *Procambarus* is the most species rich genus worldwide, and its members are ecologically diverse, occurring in most freshwater habitats. To date, there is no robust phylogeny for crayfish. The phylogenetic relationships of crayfish have been debated for over a century, and there is currently a consensus that crayfish represent a monophyletic group with two distinct clades either occurring in the northern or southern hemisphere (Crandall 2006). The phylogenetic relationships remain unclear within the family Cambaridae where morphological and molecular techniques provide different results and studies so far had relatively limited taxon sampling (Fetzner and Crandall 2002, Crandall 2006, Crandall et al. 2009, Taylor et al. 2014).

Generally, crayfish species can be identified based on multiple morphological characters (Hobbs 1972, 1989). However, the structures of the gonopods, which are copulatory appendages in reproductive males, are often the defining traits that allow for the differentiation of closely related species (Bouchard 1978). Male crayfish appear in two different morphological forms depending on their reproductive state: form I (reproductive) and form II (non-reproductive). Positive identification of cambarids relies heavily on form I males; hence, morphological and taxonomic studies have largely focused on investigating variation in these copulatory structures.

Worldwide, crayfish populations have been declining primarily from loss, degradation, and/or alteration of habitats, pollution, introduction of non-indigenous species, and over-exploitation (Richter et al. 1997, Wilcove et al. 2000, Taylor et al. 2007, Wigginton and Birge 2007, Imhoff et al. 2012, Lodge et al. 2012). Accordingly, many crayfish are highly imperiled, with approximately 50% of all known species listed as threatened or endangered (Taylor et al. 2007). Despite solid background knowledge about species level diversity patterns and current conservation issues, the evolutionary ecology of crayfish remains understudied, and much of the current knowledge is often qualitative or based on observations from studies focusing on other aquatic organisms (but see Wigginton and Birge 2007, Lodge et al. 2012, Collen et al. 2014).

Current paradigms of crayfish ecology: burrowing behavior and trophic generalists

Crayfish are considered "keystone species" or "ecological dominants" by many ecologists (Momot et al. 1978, Parkyn et al. 1997) and inhabit a wide variety of aquatic habitats including wet pastures and fields, streams, rivers, lakes, reservoirs, swamps, subterranean streams, springs, ephemeral pools, and roadside ditches (Bouchard 1978). Two key ideas dominate our current understanding of crayfish ecology: (1) burrowing behavior determines largely what habitats a particular species inhabits, and (2) crayfish generally are omnivorous with an intermediate trophic position.

Crayfish vary in their propensity to burrow and construct tunnel systems, and burrowing behavior varies among species. Accordingly, crayfish have been classified into three broad ecological groups (burrowing types) based on their behavior: primary, secondary, and tertiary burrowers (Figures 1 and 2; Hobbs 1942). Primary burrowers excavate elaborate burrows, spending most of their lives underground. They usually dig vertically into the substrate until they reach the water table, which allows them to persist in habitats with semi-permanent standing water (i.e., wet fields, ditches, and shallow ponds). These burrows can reach up to 3 meters in depth, be composed of multiple chambers, and have tunnels with multiple surface openings (Taylor and Schuster 2004). Primary burrowers will emerge from their burrows to forage and mate during wet spring and fall months, and on warm humid nights (Walls 2009).

Secondary burrowers spend a considerable portion of their lives in burrows, but will frequently visit streams and other permanent water sources throughout the year. Their burrows are less complex than primary burrowers and usually have a tunnel that is connected to a permanent water body (Hobbs 1942). Secondary burrowers occur in areas that are inundated seasonally or within close proximity to permanent water bodies (Gherardi 2002). Tertiary burrowers are species that intermittently retreat into simple burrows (e.g., under large rocks in streams) during periods of drought, cold temperatures, and egg brooding (Taylor and Schuster 2004). Tertiary burrowers are always associated with permanent water bodies, usually with gravel, cobble, and boulder substrates (e.g., streams, rivers, ponds). Within the different genera of crayfish, there is observational evidence that different burrowing types have evolved multiple times independently. For example, within the genus *Procambarus*, there are closely related species (based on gonopod morphology) belonging to different burrowing types. There is also evidence of this within *Cambarus*, where some species are obligate cave dwellers, while others are primary burrowers.

The second theme in the current understanding of crayfish ecology is that crayfish are generally considered omnivorous with little variation across species. Crayfish are an important component in many freshwater ecosystems. Multiple species often co-exist in the same habitat and can comprise a significant proportion of invertebrate biomass within streams and lakes (Momot et al. 1978, Rabeni et al. 1995). As a group, they have been documented to consume a variety of food sources such as fine particulate organic matter (Momot et al. 1978, Parkyn et al. 1997), detritus (Schofield et al. 2001), algae (Luttenon et al. 1998), macrophytes (Nystrom and Strand 1996), invertebrates (Whitledge and Rabeni 1997, Perry et al. 2000), fish (Taylor and Soucek 2010, Thomas and Taylor 2013), and amphibians (Axelsson et al. 1997). Most of these dietary assessments were based on direct observations, the examination of gut contents (e.g., Momot 1995), or laboratory feeding experiments (e.g., Nystrom and Strand 1996, Axelsson et al. 1997). More recent studies using stable isotope analysis supports the general idea that crayfish function as omnivores and have a trophic position between fish and other primary consumers (Parkyn et al. 2001, Taylor and Soucek 2010). Furthermore, crayfish appear to digest and assimilate animal tissue better than plant material and other organic matter (Whitledge and Rabeni 1997, Taylor and Soucek 2010).

Testing and refining current paradigms: a synthesis of subsequent chapters

The current paradigms in crayfish ecology, which largely have been based on observational data, provide a unique opportunity to develop testable hypotheses geared towards refining our current knowledge of this group. For my dissertation, I used crayfish species occurring Oklahoma and surrounding states to embark on this task. As a foundation, Chapter 2 provides an overview of the current state of knowledge about Oklahoma's crayfish. It includes an updated and illustrated dichotomous key for the identification of all known species occurring in the state, provides detailed descriptions of each species, and contains distributional analyses for each species as well as crayfish biodiversity patterns in general.

In Chapters 3 and 4, I focus on questions surrounding the different burrowing types of crayfish. As different burrowing behaviors largely affect which habitats a particular species inhabits, I predicted that the distributions of the different burrowing types – irrespective of taxonomic affiliation – would be shaped by different environmental variables. Since burrowing types have evolved multiple times independently, I also investigated the potential role of convergent evolution in shaping variation in eco-morphological traits among species, which could contribute to developing an eco-morphological paradigm for crayfishes. If morphological traits have evolved convergently, there should be shared variation in traits of species belonging to the same burrowing type, irrespective of whether they are closely related or not.

In Chapter 3, I used ecological niche modeling and climate change scenarios based on bioclimatic variables to identify climatic drivers of crayfish distributions and predict the potential impacts of climate change. My results suggested that the distributions of the different burrowing types are shaped by different environmental variables. This represents an important extension of the current burrowing type paradigm, which was primarily developed based on behavioral differences among crayfish species (Hobbs 1942), in that it provides the first empirical test of differences in environmental factors determining distributions of different ecomorphs. The results also provide an opportunity to develop and test hypotheses about potential physiological adaptations that may have evolved in species with different burrowing behavior. For example, behavioral thermoregulation has been observed in crayfish within burrows when temperatures approached their thermal maxima (Payette and McGaw 2003). To avoid overheating, crayfish submerge themselves in water at the bottom of the burrow and then move back into air, regulating their body temperatures through evaporative cooling (Payette and McGaw 2003). Hence, access to adequate water supply likely is more critical in the persistence of species than temperature per se.

Additionally, I found no evidence that crayfish distributional ranges will be directly impacted by climate change for any emission scenario used, as their geographic centers did not significantly shift and distributional areas did not contract in size. In fact, distributional areas tended to expand under some climate change scenarios and time frames used in this study. As crayfish are ecological engineers (Creed and Reed 2004), and have the ability to burrow and create microhabitats underground, which have a higher humidity and lower temperatures that are more constant (Lovich and Daniels 2000), it is likely that crayfish are able to persist underground when surface conditions are not suitable. Furthermore, since crayfish can burrow and create suitable microhabitats, their realized niche may in fact be close to their fundamental niche and further expansion of their distribution is not possible due to some other factor (Peterson et al. 2011), and crayfish may not be representative examples of aquatic fauna. For example, fish are less capable to altering their environments and may be more susceptible to climate change. Indeed, fish populations have declined due to climate change (Beatty et al. 2014, Muallil et al. 2014).

Finally, my results suggested that habitat destruction or alterations likely play major roles in species distributions relative to climate change. As Taylor et al. (2007) and Collen et al. (2014)

noted, habitat alterations and destruction are large contributors to crayfish declines worldwide, and my research suggests that efforts should be focused on conserving habitats and broader scale landscape variables, which in turn will help protect crayfish populations and other species occupying the same habitats.

In Chapter 4, I examined 30 morphological characteristics across 27 species of crayfish that occur in Oklahoma to test for general patterns of sexual dimorphism and potential convergent evolution in species belonging to the same burrowing type, while accounting for the taxonomic affiliation for different species. My results showed that there are morphological traits that consistent vary across sexes. For example, females tend to have longer and wider abdomens with longer pleopods and shorter less bulky chelae than males. Longer and wider abdomens theoretically allow for higher carry capacity of eggs and juveniles, which could be possible if the crayfish access to the required amounts of nutrients and capabilities to produce more eggs. Since female crayfish select males based on body size and chelae size (larger bodies and chelae are preferred; Gherardi 2002), it is likely that females that have consumed high quality food sources and have the ability to produce more eggs will be even pickier about their mate selection.

Furthermore, my results also show significant difference in morphology among burrowing types indicating that there is evidence for evolutionary convergence in morphological traits based on burrowing behavior For example, primary burrowing crayfish follow previous patterns with shorter, flatter, and narrower abdomens with bulkier/heavier chelae (relative to secondary and tertiary burrowers), which are both used for burrowing. Morphological variation among burrowing types follows a gradient with secondary burrowers exhibiting intermediate morphological traits between primary and tertiary burrowers. According to the framework developed by (Schluter 2000, Schluter 2001), adaptation - geographical or ecological - and the associated selection pressures are likely playing an important role in the diversification of crayfish. The diversification along burrowing type axes may be a common theme in crayfish diversification, similar to the diversification along the bento-pelagic axis found in many fishes (e.g., many traits diversifying in a predictable manner; Schluter 1996, Rundle et al. 2000, Schluter 2001, Albertson et al. 2003). As my results suggest a gradient of morphological characteristics among burrowing types, I did not examine if the variation was due to geographic or ecological isolation. Clearly, future work will need to focus on the impacts and roles of geographic (allopatry) and ecological (sympatry) in the vast diversity of North American crayfish.

The burrowing behavior paradigm based on behavioral differences among species appears to be a useful categorization of ecological variation among crayfish. My work indicates that the way crayfish behave has not only implications for their distributions, but also affected evolutionary trajectories, with species of similar ecologies evolving similar traits. To further refine this, future studies should broaden taxon sampling, include a wider variety of phenotypic traits (i.e., physiology), and focus on functional (mechanistic) questions to understand the proximate basis of correlational patterns. As further more in depth studies are conducted on crayfish morphology and other phenotypic traits, the categorization of broad ecological patterns will become more robust and the ability to categorize a species based on phenotypic traits will assist in conservation, management, and preservation of the vast biodiversity on earth. Additionally, understanding why the slight differences within and among species will give insight in how these species adapted to their changing environments and the evolutionary trajectories each species has undergone to persist and maintain their existence.

Finally, the notion that crayfish are omnivores with little or no dietary preferences leads to an ecological conundrum: what mechanisms facilitate coexistence of sympatric species? According to the competitive exclusion principle (Hardin 1960), species consuming the same food items will ultimately compete with one another and one species will lose, and likely becoming extirpated from the system. Multiple species of crayfish inhabit and coexist within the same systems, but mechanism(s) facilitating this coexistence are unknown. In Chapter 2, I highlighted regions within Oklahoma that have the highest diversity of crayfish occupying the same habitats. In Chapter 5, I focused on some of the most diverse regions to investigate the trophic ecology and test for potential trophic niche differentiation using stable isotopes ($\delta^{13}C$, $\delta^{15}N$) and stomach content analyses. My results suggested that sympatric crayfish do partition their food resources, as some species have different stable isotope signatures across multiple sites. As not all sympatric species exhibited partition of their food resources, further investigation is needed. For example, do the species only exhibit partitioning of food resources due to microhabitat competition and use, or is there another factor causing the partitioning in some species but not others? Ultimately, crayfish are omnivores as we found multiple food items from various trophic levels, but also partition their food resources when congeners are present. Understanding how crayfish coexist and partition resources gives insight for further more focused studies regarding the exact mechanisms that allow for the coexistence of aquatic species, especially omnivores. Species within an ecosystem interact with a variety of biotic and abiotic variables causing them to select certain habitats, food sources, and alter their behavior accordingly, and my results suggest only one potential mechanism for this coexistence.

Overall, my dissertation provides a foundation for the study of crayfish within Oklahoma and surrounding states and provides a basis of better understanding the evolutionary and ecological mechanisms that have lead to and helped maintain crayfish diversity in North America. My research provides many opportunities to build and further investigate crayfish with more focused questions on the physiological (i.e., temperature and desiccation) tolerances of species, microhabitat analyses of sympatric species, and functional impacts of crayfish on their respective ecosystems.

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Figure 1. Diagram showing the different burrow structures made by primary (top), secondary (bottom left), and tertiary (bottom right, within waterway) burrowing crayfish. This figure is modified from Hobbs (1942).

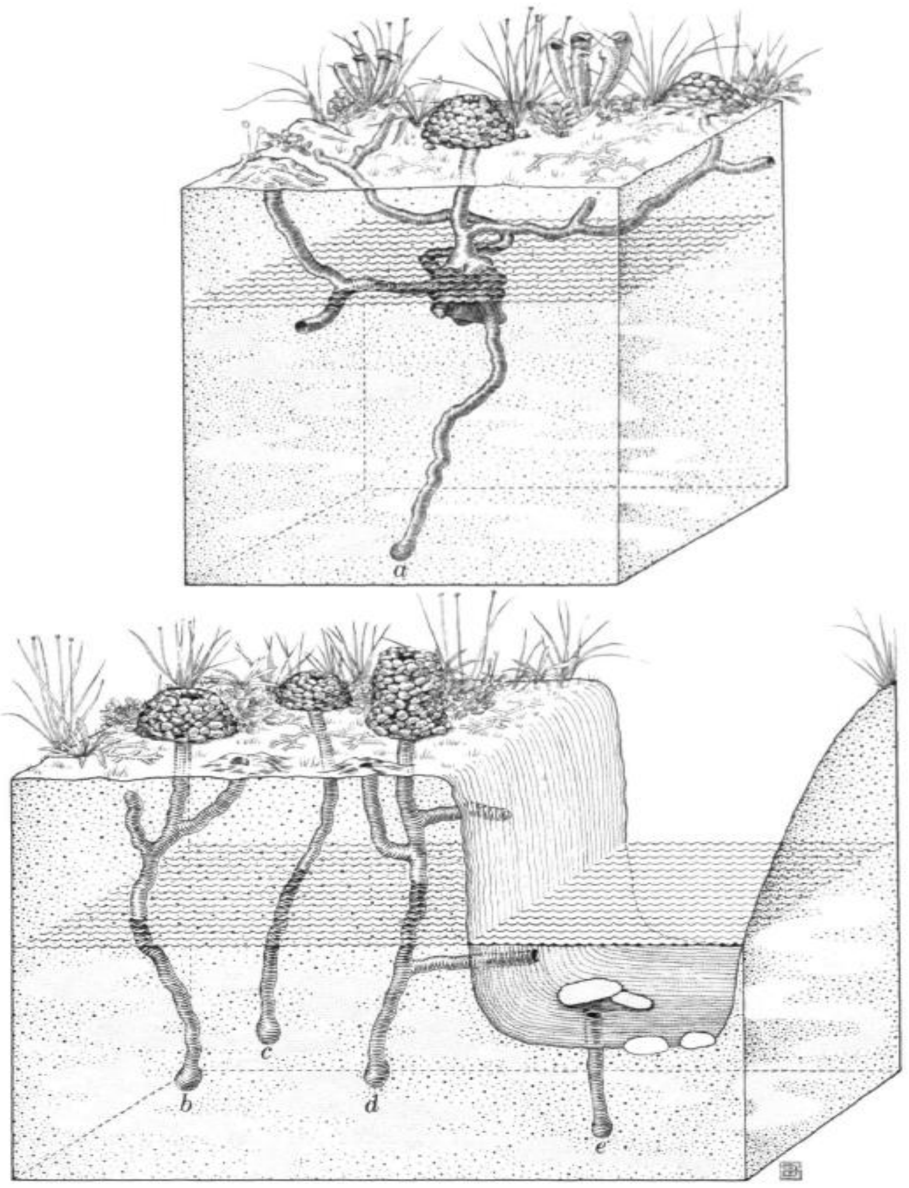

Figure 2. Pictures of crayfish burrow chimney created during the excavation of a burrow (top) and multiple crayfish chimneys (bottom).

CHAPTER II

CRAYFISHES (DECAPODA : CAMBARIDAE) OF OKLAHOMA: IDENTIFICATION, DISTRIBUTIONS, AND NATURAL HISTORY[1]

Reid L. Morehouse and Michael Tobler

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Abstract

We furnish an updated crayfish species list for the state of Oklahoma (United States of America), including an updated and illustrated dichotomous key. In addition, we include species accounts that summarize general characteristics, life coloration, similar species, distribution and habitat, life history, and syntopic species. Current and potential distributions were analyzed using ecological niche models to provide a critical resource for the identification of areas with conservation priorities and potential susceptibility to invasive species. Currently, Oklahoma harbors 30 species of crayfish, two of which were recently discovered. Eastern Oklahoma has the highest species diversity, as this area represents the western distribution extent for several species. The work herein provides baseline data for future work on crayfish biology and conservation in Oklahoma and surrounding states.

Keywords: Cambaridae, Crayfish, Crustacean, Dichotomous Key, Ecological Niche Modeling

Introduction

Crayfish are freshwater crustaceans of the families Astacidae, Cambaridae, and Parastacidae, and are native to every continent except for Antarctica and Africa (Hobbs, 1988). They inhabit a wide variety of aquatic habitats including streams, rivers, lakes, reservoirs, swamps, roadside ditches, wet pastures, and fields (Bouchard, 1978). In many habitats, crayfish play important roles in ecosystem functioning and can comprise the majority of invertebrate biomass (Momot et al., 1978; Rabeni et al., 1995). They are typically considered omnivores, exploiting a diversity of food sources from particulate organic matter to aquatic vertebrates and fish, and occupy an intermediate trophic position between other invertebrate consumers and fish (Schofield et al., 2001; Taylor & Soucek, 2010; Whitledge & Rabeni, 1997). Furthermore, crayfish have a substantial economic impact in the southern United States, particularly in Louisiana, where nearly $45 million worth of crayfish have been exported annually since the early 1980's (Walls, 2009).

Over 75% of the known crayfish species diversity (roughly 406 species and subspecies) occur in North America (Taylor, 2002). Two families of crayfish inhabit North America, Astacidae with 4 species is restricted to the Pacific Northwest (Larson & Olden, 2011), and Cambaridae distributed east of the Rocky Mountains, with two-thirds of its species endemic to the southeastern United States (Taylor et al., 2007). Cambarids are classified into two subfamilies, Cambarellinae including a single genus (*Cambarellus*) and Cambarinae, which contains ten genera. Three of the ten Cambarinae genera (*Cambarus*, *Orconectes*, and *Procambarus*) encompass 85% of all crayfish species and subspecies known in North America; *Procambarus* alone includes 163 described species and represents the most species-rich genus worldwide (Taylor, 2002; Taylor et al., 2007). The species level diversity of crayfishes is relatively well documented, but new species are continuously being described (e.g., Schuster, 2008; Taylor & Soucek, 2010; Taylor et al., 2006). In addition, a host of studies over the past decades have started to elucidate the phylogenetic relationships among North American taxa (e.g., Crandall, 2006; Fetzner & Crandall, 2002).

Nonetheless, relatively little information is available about the ecology and life history of many species, even though there is a growing interest in crayfish biology, particularly because of their increasing need for conservation. A recent review indicated that nearly 50% of all crayfish north of Mexico are imperiled (Taylor et al., 2007). Crayfish are particularly threatened because of loss or degradation of suitable habitats and the introduction of nonindigenous species, which is often exacerbated by narrow distributional ranges and high levels of endemism (Larson & Olden, 2011; Taylor et al., 2007; Welsh et al., 2010). While habitat loss and degradation have caused many detrimental impacts to crayfish, the introduction of nonindigenous species is likely the biggest threat (Gherardi, 2006; Holdich et al., 2009; Lodge et al., 2012; Lodge et al., 2000; Morehouse & Tobler, 2013). For example, nonindigenous crayfish introductions have caused drastic changes to ecosystems both through competitive exclusion of native congeners and physical habitat alterations (Morehouse & Tobler, 2013; Olden et al., 2009; Olden et al., 2006). In addition, nonindigenous crayfish species have been documented to negatively impact primary production and affect macroinvertebrate community structure in some systems (Lodge et al., 2012; Lodge et al., 1994; McCarthy et al., 2006).

On the ground conservation efforts for crayfish are often hindered by the lack of basic knowledge about resident crayfish species and their ecology: (1) Crayfish can be difficult to identify, particularly for non-specialists. While species are typically delineated based on multiple morphological characters (Hobbs, 1989), the structures of the gonopods, which are copulatory appendages in reproductive males, are often the only defining characteristic that allow for a positive identification and differentiation particularly among closely related species (Bouchard, 1978). (2) For many regions and species, there is a fundamental lack of knowledge about species distributions and patterns of crayfish biodiversity. To help close these information gaps, this paper focuses on reviewing the crayfish diversity in the state of Oklahoma.

Oklahoma and its crayfishes

Oklahoma is located in the south central region of the United States, and is an ecologically diverse state including a dozen distinct level III ecoregions (Woods et al., 2005). The state varies greatly in landscape cover and topography, ranging from arid desert-like conditions in the west to foothill and mountainous conditions in the Ozark and Ouachita Mountains to the east. Deciduous and pine forests cover most of the eastern side of the state and transition into mixed grass prairies in an east to west direction. Southern pine forests and swamps occur to a limited extent in the far southeast. Generally, the diversity of flora and fauna increases from west to east and is correlated with climate (particularly precipitation), soil, and geology (Woods et al., 2005).

The ecology and conservation of crayfish in Oklahoma has received increasing attention over the past few decades. Oklahoma is located just west of the center for the highest crayfish diversity in North America. With 30 species in six genera, Oklahoma has an intermediate diversity relative to other states (Jones & Bergey, 2005; Robison & McAllister, 2006; Taylor et al., 2004). Crayfish diversity in Oklahoma follows a west to east gradient, with the majority of species occurring in the Ozark and the Ouachita Mountains along the eastern state border. There are three endemic species, two of which are endangered cave specialists (Graening & Fenolio, 2005; Fenolio, et al., 2006). In the current paper, we review the crayfish fauna of Oklahoma and address the following objectives: (1) Expanding recent work by Jones and Bergey (2005), who recognized 28 species in the state, we revise the species list to include two additional species, *Procambarus liberorum* (Robison & McAllister, 2006) and *Cambarus ludovicianus* (Morehouse & Tobler, In Press), and particularly focus on providing a comprehensive overview of the state of knowledge for each species. (2) To facilitate identification of species, we present a revised and illustrated key to the crayfishes of Oklahoma. The current key for the crayfishes of Oklahoma (Reimer, 1969) is outdated and only includes 22 of the 30 currently recognized species. (3) To analyze distributional patterns, we generated species distribution models using locality data compiled from museum records, publications, and recent field collections. (4) To facilitate conservation efforts, we identified crayfish biodiversity hotspots within the state.

Materials and Methods

Dichotomous key

Male crayfish exhibit two different morphological forms depending on their reproductive state: form I (reproductive) and form II (non-reproductive). Positive identification of cambarids relies heavily on form I males; hence, morphological and taxonomic studies have largely focused on variation in these copulatory organs (gonopods). We used previously published crayfish keys from other states (Page, 1985; Pflieger, 1996; Taylor & Schuster, 2004), original species descriptions, and examination of specimens to build a dichotomous key for the crayfish of Oklahoma. The key was quality controlled by using museum specimens with known identities by two independent testers from Oklahoma State University, as well as a taxonomic professional from University of Illinois. Note that consistent with the majority of work on crayfish taxonomy, the dichotomous key presented here was primarily established based on form I males for identification; using form II males, females, or juveniles consequently may result in misidentification. To aid crayfish identification, we included a figure of the ventral side of a crayfish highlighting critical traits (Figure 1). To examine the pereiopods or gonopods the crayfish should be placed on its back (ventral side facing up) with the head facing away. A glossary is included as an appendix to facilitate crayfish identification for non-experts.

Species profiles

Species profiles, including information on general characteristics, life coloration, similar species, distribution and habitat, life history, syntopic species, conservation status, and additional resources, were based on extensive reviews of the current literature. Particularly, the works of Page (1985), Pflieger (1996), Taylor and Schuster (2004), and Walls (2009) provided the basis for the information assembled here and additional references are provided for each species separately. In addition, we examined specimens collected during our own sampling efforts and from museum collections (University of Oklahoma Sam Noble Museum of Natural History, Illinois Natural History Survey, and United States Natural History Museum). Descriptions of life colorations were based on the examination of living specimens or color photographs for species we were unable to collect in the field.

Over the past years, different research groups have independently assessed the conservation status of crayfish. In our review, we included conservation assessments that have been conducted both on a global (American Fisheries Society, AFS; The Nature Conservancy Heritage Ranks; International Union for Conservation of Nature, IUCN) and a regional (Oklahoma Department of Wildlife Conservation, ODWC) scale (Table 1). These assessments have relied on a variety of methodologies and considered factors such as current population size and distributional area, historic population trends, and known threats. Most notably the different research groups have used distinct classification systems and we provide a brief overview of their approaches and classification.

The AFS Endangered Species Committee (Subcommittee for Crayfishes; Taylor et al., 2007) reviewed the best available literature about distributional and status information for species over their entire range, irrespective of political boundaries. Conservation designations follow the criteria set forth by Williams et al. (1993) and include: Endangered (E): A species in danger of extinction throughout all or a significant portion of its range; Threatened (T): A species likely to become endangered throughout all or a significant portion of its range; Vulnerable (V): A species that may become endangered or threatened by relatively minor disturbances to its habitat and deserves careful monitoring of its abundance and distribution; Currently Stable (CS): A species whose distribution is widespread and stable and is not in need of immediate conservation management actions. We also included the species ranking of the Nature Conservancy/NatureServe and the Network of Natural Heritage Programs (Master, 1991). Their approach ranks taxa from 1 to 5 (1 being the most imperiled) based on a variety of factors such as abundance, distribution, population trends, and eminent threats (see www.natureserve.org/explorer/ranking.htm). Categories follow those of Master (1991) and are defined as follows: G1: Critically imperiled; G2: Imperiled; G3: Vulnerable to extirpation or extinction; G: Apparently secure; and G5: Demonstrably widespread, abundant, and secure. The IUCN classification system (http://www.iucnredlist.org/) is based on the assessment of multiple taxonomic specialists considering the native range of the species. Categories are defined as follows: Extinct (EX): No reasonable doubt that the last individual of a species has died; Extinct in the Wild (EW): Species is known only to survive in cultivation or in captivity; Critically Endangered (CR): Extremely high risk of extinction in the wild; Endangered (EN): Very high risk of extinction in the wild; Vulnerable (VU): High risk of endangerment in the wild; Near Threatened (NT): Likely to become endangered in the near future; Least Concern (LC): widespread and abundant; Data Deficient (DD): When there is inadequate information to make a direct or indirect assessment of a species' risk of extinction based on its distribution and/or population status. Lastly, the ODWC developed a conservation plan for all species that occur within the political boundaries of Oklahoma using a point system that is further explained within the Oklahoma's Comprehensive Wildlife Conservation Strategy (ODWC, 2005). This system has four categories; Tier 1: Very high conservation need; Tier 2: High conservation need; Tier 3: Moderate conservation need; Not Listed: No conservation need or not enough data to make a decision.

Occurrence data

Field sampling throughout the state of Oklahoma (113 localities) was conducted in the years 2005, 2011, and 2012 by the authors. Depending on habitat structure, seines of various sizes, hand nets, and backpack electrofishing were used to collect specimens. Terrestrial crayfish were located by the presence of chimneys and then excavated using shovels. Captured crayfish were fixed in a 10% buffered formalin solution, rinsed in water, and then stored in 70% ethanol, or directly fixed in 70% ethanol. All specimens are housed in the Zoology Department at Oklahoma

State University. Species locations (longitude and latitude) were recorded in decimal degrees using a global positioning system (GPS).

To complement the distribution and diversity data collected from our field surveys, we reviewed scientific literature, including state agency reports (Bergey et al., 2005; Robison & Crandall, 2005; Wagner et al., 2007), and queried collection databases (Global Biodiversity Information Facility, Smithsonian Institution Invertebrate Collection, Illinois Natural History Survey and the Oklahoma Natural Heritage Inventory) relating to crayfish occurrences within Oklahoma and an approximately 200 km buffer around the political boundaries of the state. The 200 km buffer was added to account for additional occurrences of species with a center of distribution outside of Oklahoma but reaching into the state, which allowed for a broader sampling of environmental conditions shaping distributional patterns. Locality records obtained from publications and collection databases were converted to decimal degrees from their respective coordinates. Records that only contained physical locality information were geo-referenced using the program GEOlocate v.3.22 (Rios & Bart, 2010) to obtain longitude and latitude. GEOlocate provides confidence levels (low, medium, high) that depend on the detail of the collection information and the error associated with geo-referencing. Only records with 'high' confidence levels were included in subsequent analyses. Species locations that only included township, range, and section were converted to decimal degrees based on the center of the respective section. These records were then plotted in ArcGIS v.10.0 and examined to see if they fell within the current known distribution for the species of interest. If the record fell outside of the known distribution it was removed from our dataset and not used for any analyses or modeling.

Distribution modeling

We used ecological niche modeling (ENM) based on 24 environmental variables to model the potential distribution of each species based on current known distributional records. Variables included are commonly used in ecological niche modeling for aquatic organisms (e.g., Chen et al., 2007; Costa & Schlupp, 2010; Dominguez-Dominguez et al., 2006; Larson & Olden, 2012; Larson et al., 2010; Morehouse & Tobler, 2013, In Press). Nineteen bioclimatic variables were obtained from the WorldClim database (Hijmans et al., 2005) at a 0.83 km^2 spatial resolution (http://www.worldclim.org/bioclim.htm), four hydrological variables were obtained from the United States Geological Survey HYDRO1k dataset at a 1 km^2 spatial resolution (http://eros.usgs.gov/#/Find_Data/Products_and_Data_Available/gtopo30/hydro/namerica), and one variable describing soil type from the Harmonized World Soil Database at a 1 km^2 spatial resolution (http://www.iiasa.ac.at/Research/LUC/External-World-soil-database/HTML/). All environmental variables were resampled at 1 km^2 resolution. Reducing the number of variables to those considered ecologically relevant and non-redundant (some environmental variables can be highly correlated) decreases the potential for model over-fitting (Warren & Seifert, 2011) and facilitates interpretation of results (Elith et al., 2011). Hence, we used the principal components tool in the ArcGIS v.10.0 Spatial Analyst extension to assemble a correlation matrix for the 24 variables across our spatial extent of analysis. We retained only a single variable for variables that were correlated at $r > 0.9$, preferentially choosing variables that measured extremes over those measuring averages (Shepard & Burbrink, 2008). Environmental extremes are more likely to set range limits of organisms due to physiological constraints (Kozak & Wiens, 2006). This procedure reduced the initial dataset to 19 variables (14 WorldClim, 4 Hydro1k, 1 Harmonized World Soils; Table 2).

To create maps of the actual and potential distributions of all crayfish species in Oklahoma, we used the maximum entropy ecological niche modeling method (Maxent; Phillips et al., 2006), which has been found to produce the most conservative prediction compared to other methods with regard to model over-fitting (Elith et al., 2006). Maxent estimates the probability distribution for a species' occurrence based on environmental constraints (Phillips et al., 2006). The environmental constraints are derived from environmental variables inputted into the model and a species' known occurrence points. Maxent requires only species presence data and continuous or categorical environmental variables layers for a given study area. We used Maxent software (version 3.3.3e; http://www.cs.princeton.edu/~schapire/maxent/), which produces a probability estimate of species presence that varies from 0 to 1. Validation is necessary to assess the predictive performance of each distribution model, and we used receiver operating characteristic (ROC) analysis (Peterson et al., 2008), which plots sensitivity (*y*-axis, lack of omission error) against 1-specificity (*x*-axis, commission error). Omission error is defined as known presences that are predicted absent and commission error as locations predicted suitable for which no presences are known. The area under the ROC curve (AUC), which is an indicator of model prediction accuracy, was calculated. The AUC ranges from 0.5 (random assignment of presences and absences) to a maximum value of 1.0 (perfect discrimination of presences and absences). The analysis was run for both the training dataset (80% of the data points randomly chosen) and the testing dataset (remaining 20% of the data points) to assess the average performance of the resulting models with a fixed threshold of 0.10 (10% omission error), which rejects the lowest 10% of possible predicted values. AUC values were ≥89% for all species, which indicates that the known test species locations were predicted as present and the models had an excellent fit based on the data provided. Maxent output map give two main pieces of information, solid white dots which represent known locations for the species and shading from white to black which represents the probability of that species being present at those locations based on the environmental variables used in the model (white = high probability of occurrence and black = very low probability). Note that these models do not account for the effects of any geographic barriers that may prevent species to reach regions with suitable environmental conditions.

Identification of biodiversity hotspots

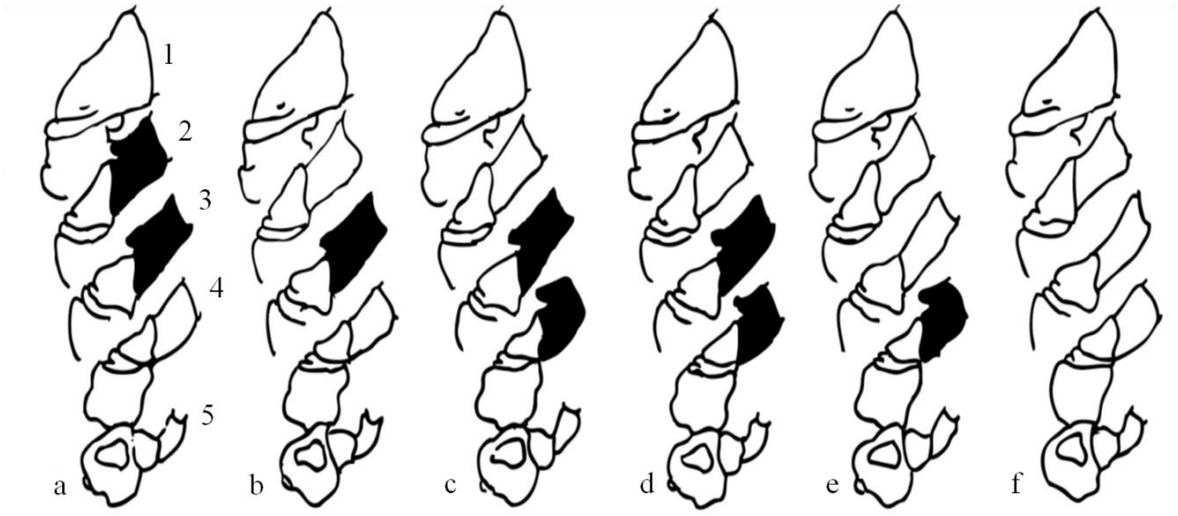
To identify geographic regions with high crayfish diversity, we combined individual species potential distribution models using the raster calculator tool in ArcGIS v.10.0 Spatial Analyst extension. The species potential distribution models are presented as raster data layers, and the raster calculator tool adds together the individual species probabilities for each grid cell to create a new raster layer, essentially depicting patterns of species richness in the study region (white = high diversity and black = low diversity).

Results

Dichotomous Key for Oklahoma Crayfish

1 Ischia of the second and third pairs of the pereiopods with hooks (a)..*Cambarellus puer* (page 40)

- Ischia of the second pair of pereiopods never bearing hooks (b-f)..(2)



2 Eyes inconspicuous without pigment or missing; body and appendages white; restricted to cave streams ....*Cambarus*, in part (7)

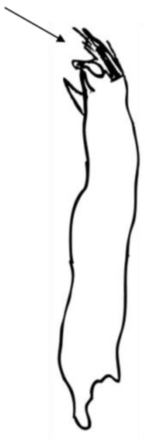
- Eyes well-developed, body, and appendages pigmented; not restricted to caves....................................(3)

Eye inconspicuous

Eye Conspicuous

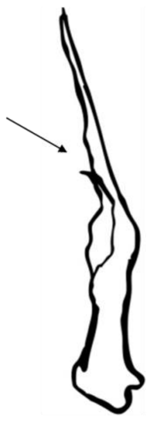
3 Gonopod terminating in more than 2 elements..*Procambarus* (10)

- Gonopod terminating in no more than 2 elements..(4)



More than 2 elements
(*Procambarus*)

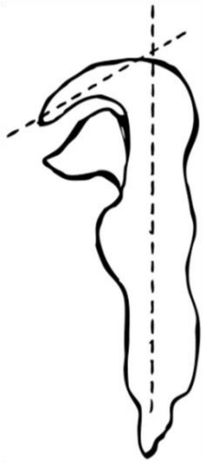
Two elements
(*Orconectes*)



Two elements
(*Faxonella*)

4 Gonopod with terminal elements bladelike and bent at 90° or more to shaft of appendage...................(5)

- Gonopod with terminal elements thin and curved near tip, or gently curved at less than 90° ....(6)



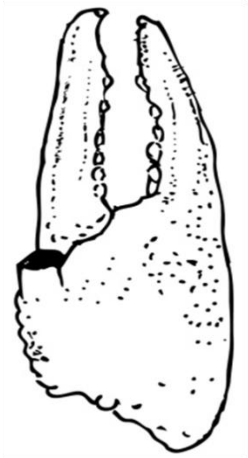
90° or greater

Less than 90°

5 Opposable margin of dactyl of chelae with abrupt excision in proximal half, marked distally by large tubercle (absent in regenerated chelae); suborbital angle absent .... *Fallicambarus fodiens* (page 48)

- Opposable margin of dactyl of chelae without abrupt excision in proximal half, no large tubercle; suborbital angle present .... *Cambarus*, in part (8)

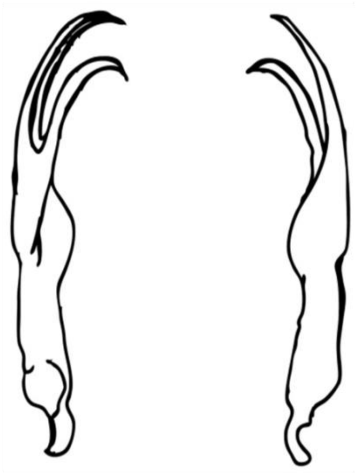
With abrupt excursion



Without abrupt excursion

6 Central projection of the gonopod less than 4 times as long as mesial process; central projections not overlapping in ventral view; both terminal elements representing at least one-fifth of total length of appendage.. *Orconectes* (17)

- Gonopod with central projection at least 4 times as long as mesial process; central projections of paired gonopods overlapping in ventral view; dactyl of chelae shorter than mesial margin of palm; tubercles on mesial surface of palm very small and inconspicuous .... *Faxonella* (9)



First pleopods never overlap (*Orconectes*)

First pleopods overlapping (*Faxonella*)

7 Central projection relatively slender and tapering towards the end ....*Cambarus subterraneus* (page 45)

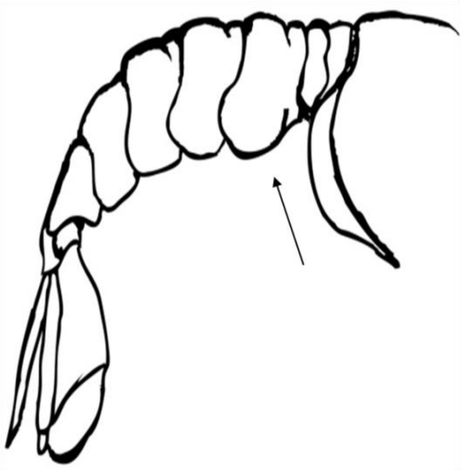
- Central projection short, heavy, not tapering, truncate apically ....*Cambarus tartarus* (page 46)

C. subterraneous

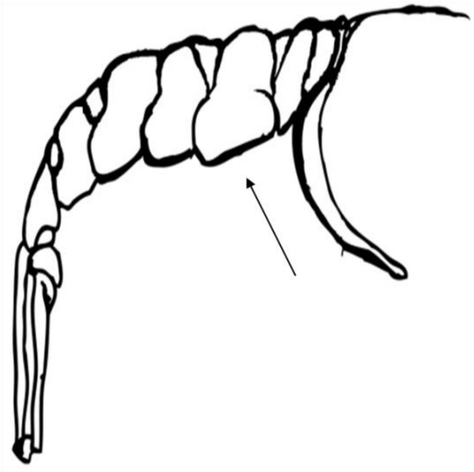
C. tartarus

8 Outer edge of first abdominal segment curved; carapace approximately equal in length to abdomen; olive green in color without stripes on abdomen .... *Cambarus diogenes* (page 42)

- Cephalic portion of carapace 1.4 times less the length of the areola; outer edge of first abdominal segment is straight; yellow to red stripes running back from either side of rostrum to join a single stripe over areola; abdomen has three parallel stripes running lengthwise ....*Cambarus ludovicianus* (page 44)



Curved outer edge (*C. diogenes*)



Straight outer edge (*C. ludovicianus*)

9 Central projection reaching coxae of the first pereiopod; mesial process longer and thinner. In females the annulus ventralis if firmly fused to the sternum, the sinus simpler in sculpture and has a prominent caudal lip...*Faxonella blairi* (page 50)

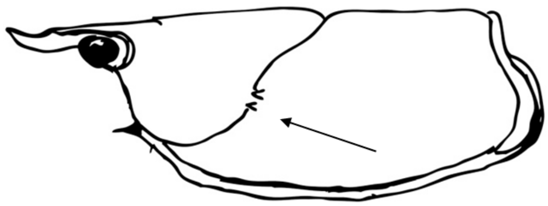
- Central projection not reaching the coxae of the first pereiopod; mesial process shorter and thicker. In females, the annulus ventralis is freely moveable, not fused to sternum, and with two prominent knobs on its anterior margin .... *Faxonella clypeata* (page 51)

F. blairi

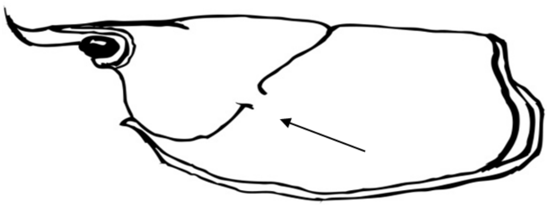
F. clypeata

10 Carapace contains two cervical spines on each side .... *Procambarus dupratzi* (page 75)

- Carapace contains one or no cervical spines on each side...(11)



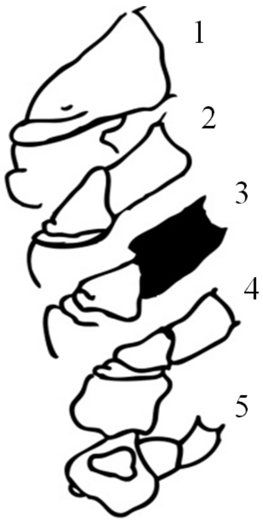
With two cervical spines

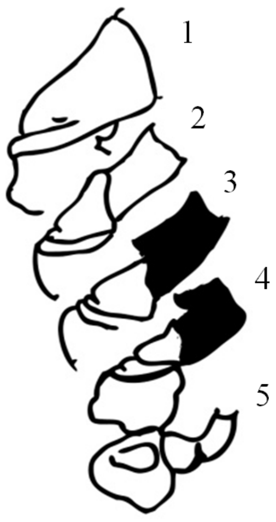


With no cervical spines

11 Hooks on ischia of third pereiopods only ....(14)

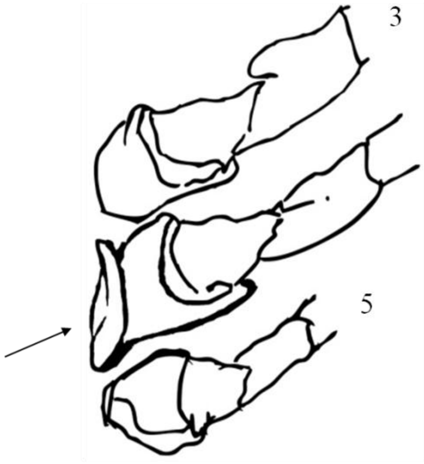
- Hooks on ischia of third and fourth pereiopods...(12)



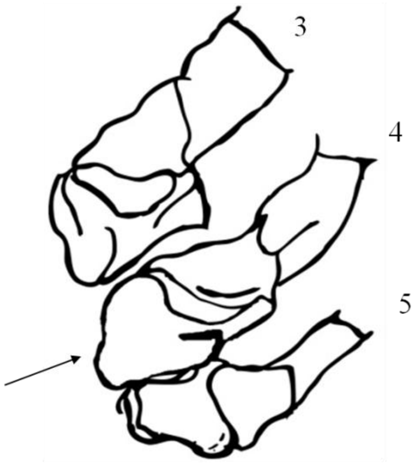


12 Carapace strongly compressed laterally; boss on coxae of fourth pereiopod greatly expanded ventrally, and directed in longitudinal axis of body..*Procambarus tenuis* (page 80)

- Carapace not strongly compressed laterally, boss on coxae of fourth pereiopod sometimes massive but never greatly expanded ventrally ....(13)



Boss expanded ventrally (*P. tenuis*)

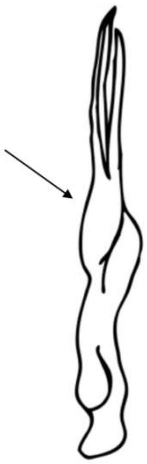


Boss not expanded ventrally

13 Shoulder on cephalic surface of gonopod; areola closed..........................*Procambarus clarkii* (page 72)

- No shoulder on cephalic process of gonopod; areola open ....*Procambarus acutus* (page 70)

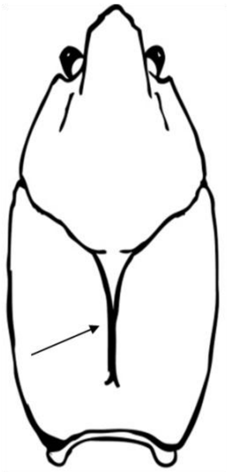
Shoulder



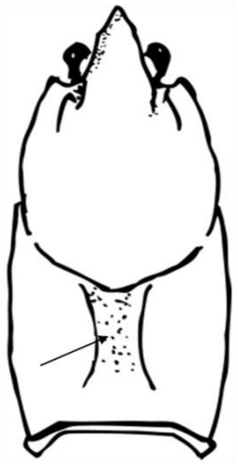
No shoulder

14 Areola closed ....(15)

- Areola open ....(16)



Areola closed

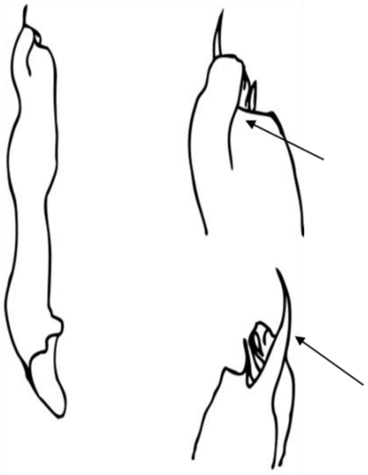


Areola open

15 Central projection longer than caudal process; shoulder at base of central projection less than 90°.. *Procambarus gracilis* (page 76)

- Central projection same length or shorter than caudal process; shoulder at base of central projection greater than or equal to 90°... *Procambarus liberorum* (page 77)

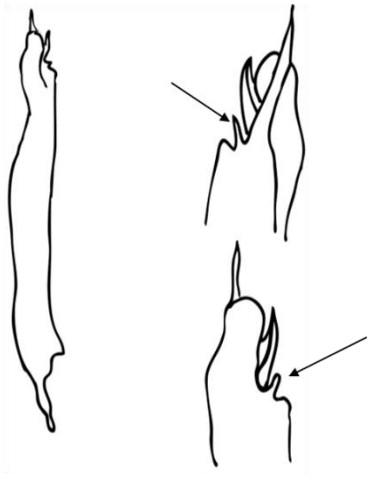
P. gracilis



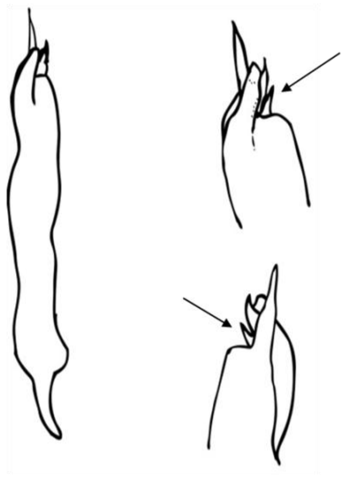
P. liberorum

16 Caudal process flat or broad in lateral view..*Procambarus curdi* (page 73)

- Caudal process narrow in lateral view... *Procambarus simulans* (page 79)



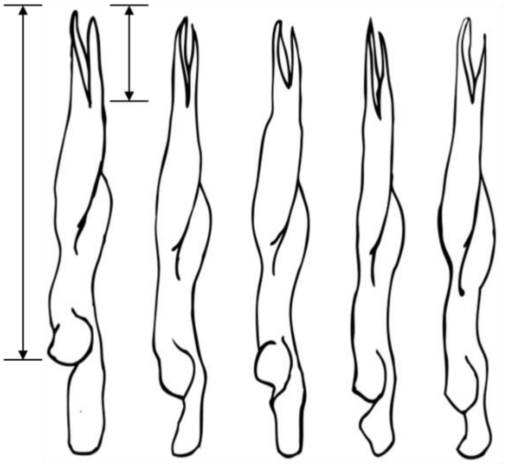
P. curdi



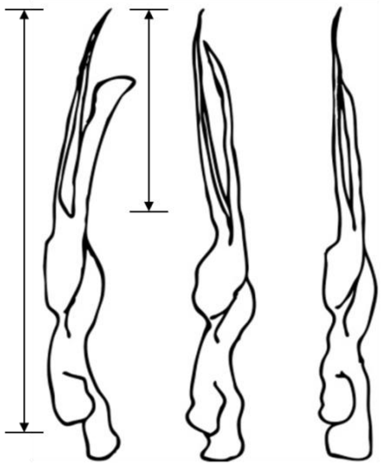
P. simulans

17 Central projection of gonopod constituting 1/4 or less of total length of appendage ....(18)

- Central projection of gonopod constituting more than 1/4 of total length of appendage ....(19)



Less than or equal to 1/4 of total length

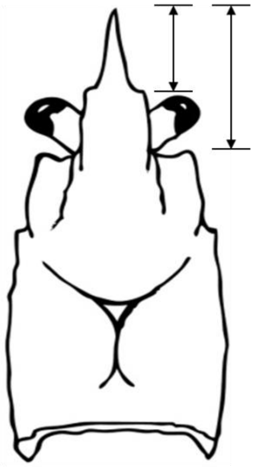


Greater than 1/4 of total length

18 Rostrum with acumen as long as, or longer than basal portion of rostrum...

....*Orconectes lancifer* (page 56)

- Rostrum with acumen not as long as basal portion of rostrum.....................*Orconectes difficilis* (page 55)



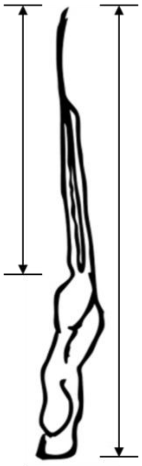
O. lancifer

O. difficilis

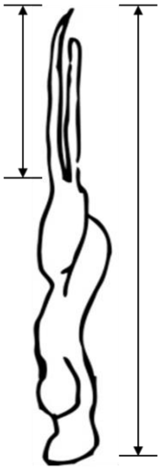
19 Central projection of gonopod constituting at least 1/2 total length of appendage....................................

.... *Orconectes leptogonopodus* (page 57)

- Central projection of gonopod constituting less than 1/2 total length of appendage..............................(20)



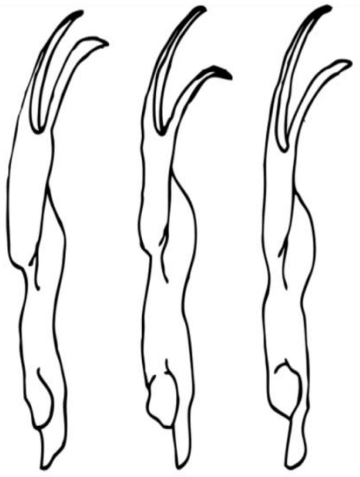
At least 1/2 of total length



Less than 1/2 of total length

20 Both terminal elements of gonopod curved caudally or caudodistally ....(21)

- Mesial process of gonopod never directed caudally or caudodistally ....(25)



Both terminal elements curved caudally

Mesial process never curved caudally

21 Areola closed (see figure in couplet 15) ....(22)

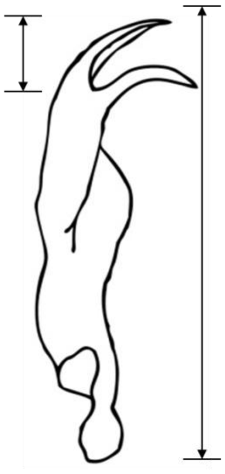
- Areola open (see figure in couplet 15) ....(23)

22 Central projection representing less than 1/5 of entire length of gonopod ....

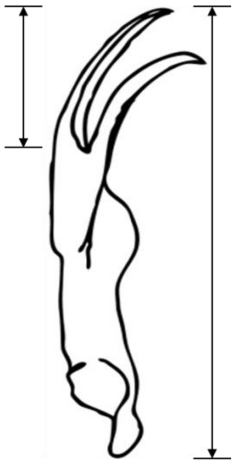
.... *Orconectes deanae* (page 54)

- Central projection representing 1/4 of entire length of gonopod...

....*Orconectes palmeri longimanus* (page 66)



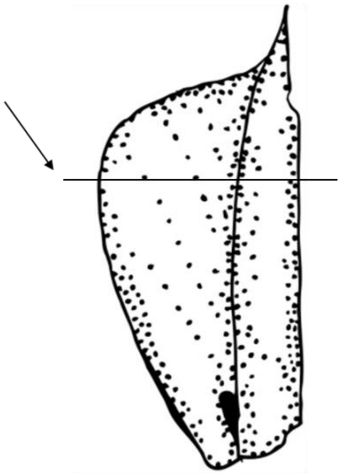
O. deanae

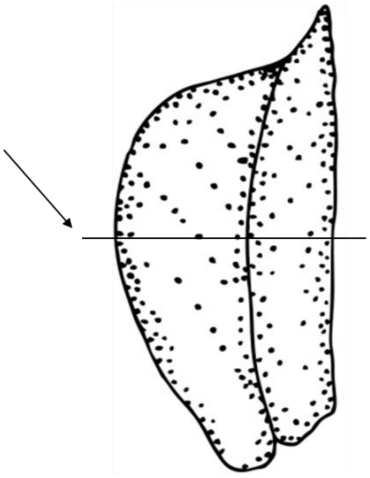


O. palmeri longimanus

23 Antennal scale widest anterior to midpoint..*Orconectes meeki brevis* (page 61)

- Antennal scale widest at or posterior to midpoint ....(24)


Widest anterior to midpoint


Widest proximal to midpoint

24 Cephalic edge of central projection of gonopod curved entire length ....

.... *Orconectes nais* (page 62)

- Cephalic edge of central projection of gonopod curved only at distal end, with a straight edge in basal half ....*Orconectes virilis* (page 69)

Note that the range of *Orconectes causeyi* extended into Oklahoma, but the species is nearly indistinguishable from *O. virilis* (Hobbs, 1989), see Discussion for additional information.

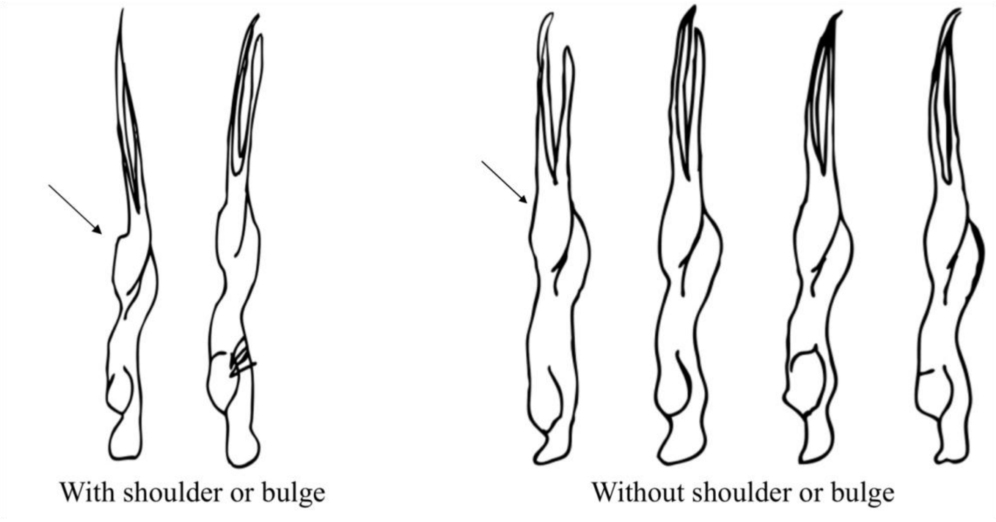

O. nais


O. virilis

25 Cephalic surface of gonopod with shoulder or distinct bulge..(26)

- Cephalic surface of gonopod without shoulder or distinct bulge ....

.... *Orconectes neglectus neglectus* (page 65)

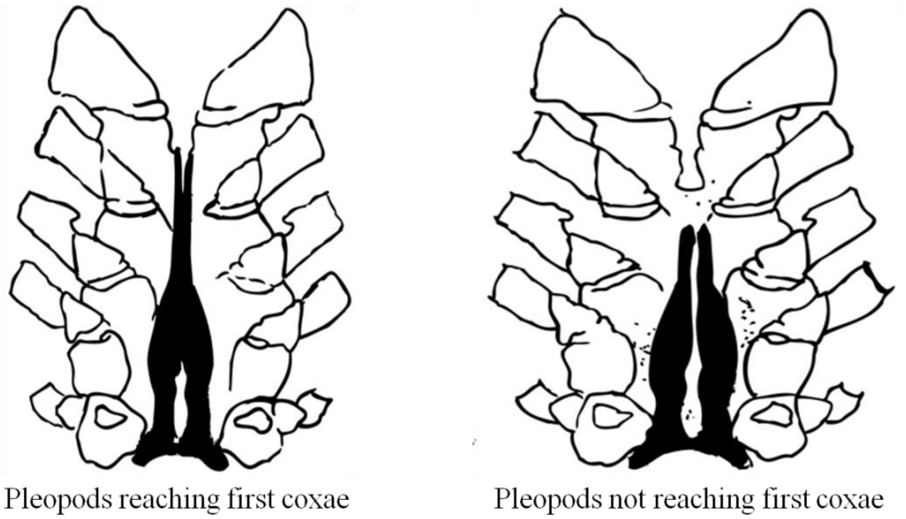


With shoulder or bulge

Without shoulder or bulge

26 Gonopods reaching coxae of first pereiopods when abdomen flexed..(27)

- Gonopods not reaching coxae of first pereiopods when abdomen flexed ....(28)

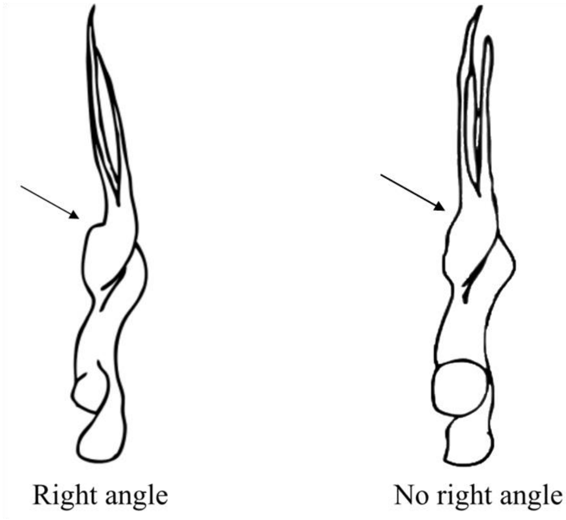


Pleopods reaching first coxae

Pleopods not reaching first coxae

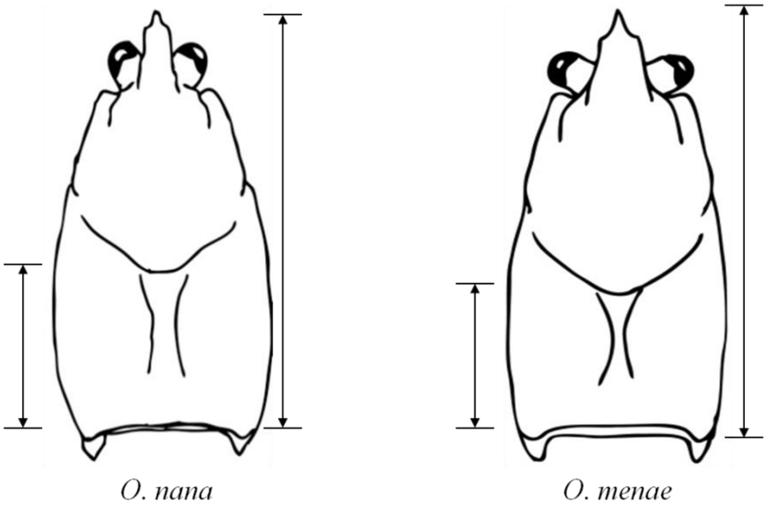
27 Distal margin of shoulder on cephalic surface of gonopod forming a right angle with base of central projection .... *Orconectes macrus* (page 58)

- Distal margin of shoulder on cephalic surface of gonopod not forming a right angle with base of central projection ....*Orconectes saxatilis* (page 67)



28 Areola length comprising more than 1/3 of total carapace length, rostrum narrow with narrow, deep, longitudinal excavation between greatly thickened margins......................*Orconectes nana* (page 64)

- Areola length comprising less than 1/3 of total carapace length, and more than 6 times longer than broad; rostrum wide, without greatly thickened margins.......................... *Orconectes menae* (page 60)



Species Accounts

***Cambarellus puer* Hobbs, 1945: Swamp Dwarf Crayfish**

GENERAL CHARATERISTICS: The body size of adults rarely exceeds 37 mm in total length. Females are typically slightly larger than males. The carapace is laterally compressed and moderately arched dorsoventrally with strong cervical spines and areola is open. The rostrum is flat and terminates in small spines at base of the acumen. The acumen is equal to or slightly longer than the width of the rostrum at the marginal spines. Chelae are small and slender with short fingers. The fingers and palm have rounded mesial and lateral margins with single setae covering dorsal surfaces, but lack longitudinal ridges and rows of tubercles. The dactyl is equal in length or shorter than the mesial margin of palm. In form I males, gonopods terminate in three caudodistally recurved elements of moderate and equal length. In females, the annulus ventralis is movable, subcircular, with a flattened or shallowly notched caudal edge, and has a strongly elevated central region (Taylor & Schuster, 2004).

LIFE COLORATION: The background color of the dorsal and lateral surfaces of the abdomen, carapace, and chelae range from orange-red to light brown and gray (Figure 27). The ventral surface is white to cream in color. The tips of the chelae lack orange coloration. *Cambarellus puer* populations exhibit a pigmentation polymorphism, where the carapace and abdomen either have two brown to black stripes or two rows of spots running their entirety. These alternative color patterns are controlled by a single mendelian gene, with the striped phenotype being dominant over the spotted one (Volpe & Penn, 1957). The polymorphism appears to be selectively neutral, and mating between the two color phenotypes is random (Pflieger, 1996).

SIMILAR SPECIES: *Cambarellus puer* is the only *Cambarellus* species known to inhabit Oklahoma and is unlikely to be confused with any other species.

DISTRIBUTION AND HABITAT: *Cambarellus puer* occurs from southern Illinois and Missouri southward along the Mississippi River to Louisiana and westward to southeastern Oklahoma and eastern Texas. Current records indicate a very limited distribution in Oklahoma. It is known from a single location: a swampy area with dense vegetation along the Little River in McCurtain County. Our ecological niche model indicates that the far southeastern corner of Oklahoma provides suitable environmental conditions for *C. puer*, along with areas extending approximately 120 km to the north (Figure 28). *Cambarellus puer* generally inhabits permanent water bodies such as swampy areas with dense stands of emergent and submerged vegetation, reservoir tail-waters, and lowland areas that are flooded. In other states, *Cambarellus puer* has been reported from habitats that have dried completely during summer months (Pflieger, 1996), likely by digging into the soil prior to drying as it is a tertiary burrower. This species has not been collected in Oklahoma since 1975. Our recent sampling efforts were also futile, therefore the population size and current distribution within the state requires further investigation.

LIFE HISTORY: Given that *Cambarellus puer* has only been documented from one location in Oklahoma, very little is known about the species' life history within the state. The majority of the information known about *C. puer* has been collected in Louisiana (Black, 1966), Illinois (Page, 1985), and Missouri (Pflieger, 1996). Ovigerous females have been collected from February to May, with egg diameters range from 1.0 to 1.1 mm (Black, 1966; Page, 1985). Black (1966) reported two periods of reproductive activity in Louisiana, one in late winter to early spring and another in mid-summer. Males require 13 to 14 molts to achieve sexual maturity, and most males will not breed during their first year of life (Pflieger, 1996). *Cambarellus puer* lives approximately 15 to 18 months after hatching (Black, 1966).

SYNTOPIC SPECIES: *Fallicambarus fodiens*, *Faxonella blairi*, and *Procambarus clarkii*.

CONSERVATION STATUS: AFS: Currently Stable; Heritage Rank: Widespread (G5); IUCN: Least Concern; ODWC: Not Listed.

ADDITIONAL RESOURCES: Black (1963).

***Cambarus diogenes* Girard, 1852: Devil Crawfish**

GENERAL CHARACTERISTICS: A stout crayfish with broad chelae that rarely exceeds 127 mm in total length. The carapace is approximately equal in length to the abdomen and somewhat laterally compressed. The head is narrower than the thorax and the areola is closed. The rostrum is broad and deeply excavated with a short acumen that lacks spines or tubercles. The lateral edge of the second abdominal segment is arched. Chelae are large and heavy with the dactyl just longer than the palm length. The dactyl has a broad notch at the base, which is most prominent in form I males. In form I males, central projection of the gonopod is corneous, recurved approximately 90° to the shaft, short, and bladelike. In females, the cephalic margin of the annulus ventralis is broadly rounded, while the caudal margin is triangular and has a deep horizontal fossa (Taylor & Schuster, 2004).

LIFE COLORATION: Nearly uniform olive-drab to tan and brown in color (Figure 29). The tips of chelae, rostrum, uropods, and telson are all lined with a deep orange to red coloration. Occasionally, specimens from the prairie region will have a golden stripe along the midline of the abdomen. The ventral side is cream to white in color.

SIMILAR SPECIES: In Oklahoma, *Cambarus diogenes* closely resembles *Cambarus ludovicianus*. It can be differentiated from *C. ludovicianus* by the shape of the abdomen. In lateral view, the abdomen of *C. diogenes* is thicker than in *C. ludovicianus* and the lateral edge of the second abdominal segment is arched in *C. diogenes* but straight in *C. ludovicianus*. *Cambarus ludovicianus* also has three lateral stripes running along the sides and top of the abdomen.

DISTRIBUTION AND HABITAT: *Cambarus diogenes* is widely distributed throughout the eastern United States, south of the Great Lakes and east of the Rocky Mountains (Hobbs, 1989). In Oklahoma, this species is known from a few locations in McCurtain and Choctaw Counties in the southeast (Creaser & Ortenburger, 1933; Hobbs, 1989; Reimer, 1969). *Cambarus diogenes* may also be found further west and north according to our ecological niche model (Figure 30). *Cambarus diogenes* is commonly collected from excavating burrows in or along creek banks, wet depressional areas, and roadside ditches. In Oklahoma, both collection locations were creeks, which this species typically visits during the spring months to release offspring into standing water. Due to the burrowing behavior (primary burrower) of *C. diogenes* and a lack of targeted sampling efforts, its distribution may be broader than currently known.

LIFE HISTORY: Form I males have been collected March through October in most states (Grow, 1981, 1982; Grow & Merchant, 1980; Page, 1985; Pflieger, 1996; Turner, 1926; Walls, 2009). Ovigerous females have been collected in March and April, and females with young in May

(Hobbs & Marchand, 1943; Penn & Marlow, 1959; Taylor & Schuster, 2004). In Missouri, Pflieger (1996) reported that mating takes place in the fall months. Females appear to lay and incubate their eggs while in the burrow, but release offspring into open water in spring (Pflieger, 1996). We have collected form II males and females in the spring.

SYNTOPIC SPECIES: *Fallicambarus fodiens* and *Procambarus simulans*.

CONSERVATION STATUS: AFS: Currently Stable; Heritage Rank: Widespread (G5); IUCN: Least Concern; ODWC: Not Listed.

ADDITIONAL RESOURCES: Grow (1981, 1982); Grow & Merchant (1980).

Cambarus ludovicianus **Faxon, 1884: Painted Devil Crayfish**

GENERAL CHARACTERISTICS: Adults rarely exceed 94 mm in total length. The carapace is approximately equal in length to the abdomen, bullet shaped in dorsal view, and laterally compressed. The head is narrower than the thorax and the areola is closed. The rostrum is broad and deeply excavated with a short acumen that lacks spines or tubercles. The lateral edge of the second abdominal segment is straight. Chelae are large and heavy, with the dactyl about twice as long as the palm length. The dactyl has a broad notch at the base, which is most prominent in form I males. In form I males, the central projection of the gonopod is corneous, recurved approximately 90° to shaft, short, and bladelike. In females, the annulus ventralis is subrhombodial in outline, and the cephalic and caudal margins are broadly rounded. A deep circular central area and oval fossa are also present in the annulus ventralis (Taylor & Schuster, 2004).

LIFE COLORATION: The base color of the chelae, carapace, and abdomen can range from olive-drab to a deep blue (Figure 31). The rostrum, cervical groove, and areola are outlined in red to burgundy. The abdomen has three evenly spaced light tan to red longitudinal bands running the entire length. Telson and uropods are outlined in red. The ventral side is a light tan to white.

SIMILAR SPECIES: In Oklahoma, *C. ludovicianus* closely resembles *C. diogenes* (see *C. diogenes* section for differences).

DISTRIBUTION AND HABITAT: Hobbs (1989) listed the range of *C. ludovicianus* as the lower Mississippi River drainage in Tennessee, Arkansas, Mississippi, Louisiana, and eastern Texas. *Cambarus ludovicianus* has also been reported from one location in western Kentucky (Taylor & Schuster, 2004). In Oklahoma, this species is only known from 3 locations in McCurtain County and 1 location in LeFlore County (Morehouse & Tobler, In Press). Our ecological niche model suggests that the species may be found further west in adjacent counties along Red River and further north into the Ouachita Mountains (Figure 32). *Cambarus ludovicianus* is a primary burrower. The sites where we collected this species from burrows were wooded bank areas along creeks. According to Penn and Marlow (1959), *C. ludovicianus* habitat closely resembles that of *C. diogenes*.

LIFE HISTORY: Ovigerous females have not been collected from Oklahoma. We have collected form I males, adult females, and juveniles in March, April, May, and November. Form I males have been collected in Louisiana from February through November, and ovigerous females were collected in December and January (Penn & Marlow, 1959).

SYNTOPIC SPECIES: *Orconectes palmeri longimanus*, *Procambarus acutus*, and *Procambarus dupratzi*.

CONSERVATION STATUS: AFS: Currently Stable; Heritage Rank: Widespread (G5); IUCN: Least Concern; ODWC: Not Listed.

ADDITIONAL RESOURCES: Marlow (1960); Reimer & Clark (1974).

***Cambarus subterraneus* Hobbs, 1993 : Delaware County Cave Crayfish**

GENERAL CHARACTERISTICS: A white (albinistic) crayfish with small, unpigmented eyes, and long slender chelae. Adults rarely exceed 50 mm in total length. The carapace lacks cervical spines. The rostrum is broadest at its base and exhibits small marginal spines. The body surface and pereiopods are covered in conspicuous stiff setae, which likely serve as sensory organs in the dark cave environment. In form I males, the gonopods terminate in two terminal processes recurved at angles greater than 90°, and the central projection is moderately long and slender. In females, the annulus ventralis is subsymmetrical in outline, and the caudal part is slightly movable. The cephalic half of the annulus ventralis is traversed by a deep submedian longitudinal trough (Hobbs, 1993).

LIFE COLORATION: Off-white to pinkish-white, especially in the abdominal region (Figure 33). Newly molted individuals are nearly all white. Smaller individuals can appear somewhat translucent.

SIMILAR SPECIES: *Cambarus subterraneus* closely resembles *C. tartarus*, the only other cave crayfish in Oklahoma. It can be differentiated from *C. tartarus* by the central projection of the gonopod, where *Cambarus subterraneus*' central projection is slender and tapers towards the end, while *C. tartarus*' central projection is heavy and non-tapering. Furthermore, *C. subterraneus* is found in only three caves, all of which are disjunct from the caves with *C. tartarus*.

DISTRIBUTION AND HABITAT: *Cambarus subterraneus* is a tertiary burrower and has been recorded in three caves (Twin, Star, and Jail) in Delaware County, Oklahoma (Figure 34). These caves have limestone bottoms covered with fine silt.

LIFE HISTORY: Form I males have been collected from May through October in the three different caves (Hobbs, 1993). Females with young have not been observed, but one ovigerous female was found in the late 1980's (Puckette, 1986).

SYNTOPIC SPECIES: No syntopic crayfish species are known at this time.

CONSERVATION STATUS: AFS: Endangered; Heritage Rank: Critically Imperiled (G1); IUCN: Critically Endangered; ODWC: Tier 1.

ADDITIONAL RESOURCES: Jones & Bergey (2005); Taylor et al. (2004).

Cambarus tartarus **Hobbs and Cooper, 1972: Oklahoma Cave Crayfish**

GENERAL CHARACTERISTICS: A white (albinistic) crayfish with small, unpigmented eyes, and long slender chelae. Adults rarely exceed 50 mm in total length. The carapace is lacking cervical spines and is subcylindrical. The rostrum is the broadest at the base and has small marginal spines. The body and pereiopods are covered in conspicuous stiff setae. In form I males, gonopods terminate in two terminal processes, both recurved at angles greater than 90°. The central projection is short, heavy, and does not taper. In females, the annulus ventralis is symmetrical with the caudal portion somewhat movable (Hobbs & Cooper, 1972).

LIFE COLORATION: Off-white to pinkish-white, especially in the abdominal region (Figure 35). Newly molted individuals are nearly all white. Smaller individuals appear somewhat translucent.

SIMILAR SPECIES: *Cambarus tartarus* closely resembles the only other cave crayfish in Oklahoma, which is *C. subterraneus* (see *C. subterraneus* section for differences).

DISTRIBUTION AND HABITAT: *Cambarus tartarus* is a tertiary burrower and is currently known from two caves (January-Stansbury and Long's) in Delaware County, Oklahoma (Figure 36). Both of these caves are situated along Spavinaw Creek. These caves are formed in limestone, and the bottom is covered with fine silt.

LIFE HISTORY: Populations have been monitored periodically by the United States Fish and Wildlife to ensure a viable population still exists and form I and II males and females have been documented from both caves (Fenolio et al., 2006).

SYNTOPIC SPECIES: *Orconectes neglectus neglectus* has been documented in January-Stansbury cave especially during the winter months. However, it appears that *O. neglectus neglectus* is restricted to the front part of the cave, where the substrate predominantly consists of gravel, while *C. tartarus* occurs in deeper parts of the cave over silt covered ground.

CONSERVATION STATUS: AFS: Endangered; Heritage Rank: Critically Imperiled (G1); IUCN: Critically Endangered; ODWC: Tier 1.

ADDITIONAL RESOURCES: Hobbs et al. (2006); Jones & Bergey (2005); Taylor et al. (2004).

***Fallicambarus fodiens* (Cottle, 1863): Digger Crayfish**

GENERAL CHARACTERISTICS: A heavy-bodied crayfish with broad chelae that rarely exceeds 80 mm in total length. The rostrum is broad and moderately excavated with no rostral spines. The acumen is very short with thinner margins than found on the rostrum. The areola is closed. Chelae are nearly oval or egg-shaped in outline, dorsoventrally flattened at the base of the fingers, and with a distinct basal notch on dactyl and dense patch of setae at base of propodus. There is a gap at the area of the notch when fingers are closed. In form I males, gonopods have two terminal processes that are at right angles to the main gonopod axis, and the primary process is strongly curved and bladelike. In females, the annulus ventralis is subcircular in outline and slightly asymmetrical with a deep medial trough through cephalic half (Taylor & Schuster, 2004).

LIFE COLORATION: Chelae, carapace, and abdomen are reddish-tan to light and dark brown in color (Figure 37). The ventral side may be lighter from light brown to pale yellow. The abdomen sometimes exhibits darker brown longitudinal stripes on each side of midline.

SIMILAR SPECIES: *Fallicambarus fodiens* most closely resembles *Cambarus diogenes* and *C. ludovicianus*. All of these species have a closed areola and a notch in the base of the dactyl. However, this notch is deeper and lacks tubercles along its distal margin in *F. fodiens*. *Fallicambarus fodiens* can also be separated from the two *Cambarus* species by the lack of a suborbital angle, a trait that is even visible in smaller individuals (Taylor & Schuster, 2004).

DISTRIBUTION AND HABITAT: *Fallicambarus fodiens* has a large but disjunct distribution (Hobbs, 1989; Hobbs & Robison, 1989; Jezerinac et al., 1995). The species occurs in the southern Great Lakes in Ontario and Michigan, south in the lower Ohio and central Mississippi River valleys, and along the Gulf Coast from east Texas to Florida. It can also be found along the Atlantic Coast from Maryland to South Carolina. Jezerinac and Stocker (1987) reported a third disjunct population along the Ohio River in west-central West Virginia. In Oklahoma, *F. fodiens* is known from 3 localities in LeFlore and McCurtain Counties, and 1 location in the north central portion of the state. According to the ecological niche model, suitable environmental conditions may also be found west of the 3 known southeast southeastern locations and north into the Ouachita and Boston Mountain ranges (Figure 38). *Fallicambarus fodiens* is a primary burrower in ephemeral wetlands, wooded flood plains, and low-lying fields (Jezerinac & Stocker, 1987; Page, 1985; Pflieger, 1996; Taylor & Schuster, 2004). Because this species is a primary burrower, it is often difficult to collect and easy to overlook. Hence, *F. fodiens*' distribution in Oklahoma may be broader than currently known.

LIFE HISTORY: *Fallicambarus fodiens* constructs one of the least complex burrows of any species in its genus (Hobbs & Robison, 1989). Burrows often consist of a single, nearly vertical shaft, and depth varies depending on the distance to the water table. Frequently, there are other side passages leading away from the main shaft to the surface or a nearby water source. Surface openings are identified by a mound or chimney of mud, which is usually capped during drier periods. During high humidity, especially after warm rains, the crayfish may sit at the entrance of their burrow or move around the entrance in search of food, mates, or a new location for a burrow. Their food consists of plant fragments, especially grass seeds, and animal material, including insect fragments, crayfish parts, and juvenile salamanders (Bovbjerg, 1952). Creaser (1931) reported copulations occurring in the fall and early spring. Other studies have corroborated this finding with the collection of form I males, ovigerous females, and females with young from February through May and August through November, depending on the latitude (Bovbjerg, 1952; Creaser, 1931; Jezerinac et al., 1995; Page, 1985; Pflieger, 1996; Taylor & Schuster, 2004). Furthermore, Ainscough et al. (2013) have stated that F. fodiens is a species complex so as more research is conducted certain life history attributes may change.

SYNTOPIC SPECIES: *Cambarellus puer*, *Cambarus diogenes*, and *Procambarus gracilis*.

CONSERVATION STATUS: AFS: Currently Stable; Heritage Rank: Widespread (G5); IUCN: Least Concern; ODWC: Not Listed.

ADDITIONAL RESOURCES: Ainscough et al. (2013); Bovbjerg (1952); Guiasu (2007); Guiasu & Dunham (2002); Jezerinac & Stocker (1987); Norrocky (1991); Taylor et al. (2010).

Faxonella blairi **Hayes and Reimer, 1977: Blair's Fencing Crayfish**

GENERAL CHARACTERISTICS: A small bodied crayfish with a bullet shaped carapace tapering towards the head that rarely exceeds 50 mm in total length. The rostrum is broad and without lateral spines or tubercles. The areola is open. Chelae are narrow and cylindrical with short abruptly tapering fingers that are shorter than palm length. In form I males, gonopods terminate in two terminal processes and the central projection of the gonopod is long, conspicuous, and reaches the base of the first pereiopods. Mesial process is long and thin. In ventral view, the gonopods cross each other. In females, the annulus ventralis is fused to the sternum with two prominent knobs on its anterior margin (Hayes & Reimer, 1977).

LIFE COLORATION: The background color is reddish-tan to olive-tan, with two black lines or dashes extending longitudinally along the dorsal surface of carapace and abdomen (Figure 39). The ventral side is tan to white.

SIMILAR SPECIES: In Oklahoma, *F. blairi* closely resembles *F. clypeata*. *Faxonella clypeata* differs in form I males by the central projection of gonopods reaching the base of the first pereiopods and having longer and thinner mesial processes. In females, it differs from *F. clypeata* by the annulus ventralis being firmly embedded in the sternum.

DISTRIBUTION AND HABITAT: *Faxonella blairi* is a tertiary burrower and occurs in the Gulf Coastal Plain of southeastern Oklahoma, Arkansas, northeastern Texas, and northwestern Louisiana. In Oklahoma, *F. blairi* has only been collected at three locations in McCurtain County, including a swamp located near the Little River and roadside ditches. Our niche model suggests that suitable environmental conditions for *F. blairi* may also exist north of the Ouachita Mountains in low-lying areas and west along the Red River (Figure 40).

LIFE HISTORY: *Faxonella blairi* presumably has similar life history characteristics as *F. clypeata* (see below) as these species are closely related.

SYNTOPIC SPECIES: *Cambarellus puer* and *Procambarus clarkii*.

CONSERVATION STATUS: AFS: Currently Stable; Heritage Rank: Vulnerable (G3); IUCN: Least Concern; ODWC: Tier 2.

ADDITIONAL RESOURCES: Hobbs (1990).

***Faxonella clypeata* (Hay, 1899): Ditch Fencing Crayfish**

GENERAL CHARACTERISTICS: A small bodied crayfish with a bullet shaped carapace tapering towards the head that rarely exceeds 50 mm in total length. The rostrum is broad and without lateral spines or tubercles and the areola is open. Chelae are narrow and cylindrical with short abruptly tapering fingers that are shorter than the palm's length. In form I males, gonopods end in two terminal processes and the central projection is long and conspicuous, but does not reach the base of the first pereiopods. The mesial process is short and thick. In ventral view, the gonopods cross each other. In females, the annulus ventralis is freely movable, not fused to sternum, and has two prominent knobs on its anterior margin (Hay, 1899).

LIFE COLORATION: The background color is reddish-tan to olive-tan with, two black lines or dashes extending longitudinally along the dorsal surface of carapace and abdomen (Figure 41). The ventral side is tan to white.

SIMILAR SPECIES: In Oklahoma, *F. clypeata* closely resembles *F. blairi* (see *F. blairi* section for differences).

DISTRIBUTION AND HABITAT: *Faxonella clypeata* is a tertiary burrower and occurs along the lower Mississippi Valley west of the Mississippi River proper from southeastern Missouri, the Gulf Coastal Plains of southeastern Oklahoma, eastern Texas, and Louisiana, eastward to Florida, and northward into Georgia and South Carolina. In Oklahoma, *F. clypeata* has been collected from three locations, one each in Choctaw, LeFlore, and McCurtain Counties. Hence, it appears that *F. clypeata* has a broader distribution in Oklahoma than *F. blairi*. *Faxonella clypeata* was found to inhabit swamps and standing pools of water in roadside ditches. Our ecological niche model indicates that other potential areas with suitable environmental conditions exist in southeastern Oklahoma and west along major river systems (Figure 42).

LIFE HISTORY: The main study that has examined the life history of *F. clypeata* was conducted in southern Louisiana (Smith, 1953). In that study, form I males were found in September. Ovigerous females were collected in late September and October, while females with young were collected in December. Pflieger (1996) collected juveniles in March and April in Missouri. Hence, it is likely that populations in southeastern Oklahoma reproduce in the fall as found in Missouri and Louisiana. Life span of *F. clypeata* ranges between 18 and 24 months (Pflieger, 1996).

SYNTOPIC SPECIES: In Oklahoma, no syntopic crayfish species are currently known.

CONSERVATION STATUS: AFS: Currently Stable; Heritage Rank: Widespread (G5); IUCN: Least Concern; ODWC: Not Listed.

ADDITIONAL RESOURCES: Hobbs (1989); Mobberly & Owens (1966); Mobberly & Pfrimmer (1967).

***Orconectes causeyi* Jester, 1967: Western Plains Crayfish**

GENERAL CHARACTERISTICS: Adults rarely exceed 100 mm in total length. The carapace is stocky, subovate, depressed, and the areola is open. The abdomen is slightly shorter than the carapace. The rostrum is long, excavate, and margins converge with weak lateral spines. Chelae are large with tubercles along mesial margin of palm and dactyl. In form I males, gonopods reach the base of second pereiopods and terminate in two processes. The central projection of gonopods is corneous, long, and slightly recurved caudally, while the mesial processes are non-corneous, slender, and shorter than the central projection. In females, the annulus ventralis is immovable and spindle-shaped (Jester, 1967).

LIFE COLORATION: The background color is reddish-brown to olive brown (Figure 43). The abdomen has two rows of black blotches running longitudinally. Chelae have a bluish-green tint, with yellow to off-white tubercles along the inner margin of the palm and fingers. Fingers are tipped with orange. The ventral side is white.

SIMILAR SPECIES: In Oklahoma, *O. causeyi* closely resembles *O. nais* and *O. virilis*. *Orconectes virilis* is virtually indistinguishable from *O. causeyi* (Hobbs, 1989). *Orconectes nais* differs from *O. causeyi* by exhibiting a light tan stripe along the side of the carapace in live specimens. The gonopods differ in the degree of curvature of the tips, although some individuals are difficult to discern based on this trait (Hobbs, 1989).

DISTRIBUTION AND HABITAT: *Orconectes causeyi* occurs in western Missouri, eastern Kansas, Oklahoma's Arkansas River drainage, and into northeastern New Mexico. This species has also been translocated into the Rio Grande River drainage and drainages north into Colorado (Jester, 1967). In Oklahoma, *O. causeyi* species has been collected in the upper section of the South Canadian River and surrounding reservoirs. We were unable to confirm reports of this species further east in Oklahoma, and likely they represent misidentifications of *O. nais* or *O. virilis*. Our ecological niche model shows that the northeastern and northwestern portions of the state have suitable environmental conditions (Figure 44). Due to potential confusion with *O. virilis* and *O. nais* further examination of the species and range are highly warranted.

LIFE HISTORY: *Orconectes causeyi* is a tertiary burrower and is likely a species from cool headwater systems of the South Canadian River and from there has colonized the cool, deep waters of surrounding reservoirs (Jester, 1967). Form I males have been collected from August through October, while form II males and females have been collected year round, and no ovigerous females or females with young have been reported. Juveniles were collected in New Mexico in July (Jester, 1967).

SYNTOPIC SPECIES: *Orconectes deanae*.

CONSERVATION STATUS: AFS: Currently Stable; Heritage Rank: Widespread (G5); IUCN: Least Concern; ODWC: Not Listed.

ADDITIONAL RESOURCES: Dean (1969).

Orconectes deanae **Reimer and Jester, 1975: Conchas Crayfish**

GENERAL CHARACTERISTICS: Adults rarely exceed 85 mm in total length. The rostrum has distinct spines, a slight central depression, and the areola is closed. Chelae are long and slender, and the dactyl is nearly twice as long as the palm. In form I males, gonopods terminate in two strongly curved processes. The central projection is bent at a 45° angle to the shaft, and the mesial process bent at a 90° angle to shaft. In females, the annulus ventralis is sub-elliptical and is wider than long (Reimer & Jester, 1975).

LIFE COLORATION: The background color is light brown to dark brown (Figure 45). The abdomen is slightly darker than the carapace. Dark speckling on dorsal side of chelae is present. Ventral side is off-white.

SIMILAR SPECIES: In Oklahoma, *O. deanae* closely resembles *O. palmeri longimanus*. It differs from *O. palmeri longimanus* in the curvature of the gonopods of form I males. In *O. deanae*, the mesial processes are curved at approximately a 90° angle to the shaft, while it is never curved to that extent in *O. palmeri longimanus*. Furthermore, the central projection of gonopods in *O. deanae* represents no more than 1/5 of the total appendage length, while it represents at least 1/4 of the total length in *O. palmeri longimanus* (Figure in couplet 22).

DISTRIBUTION AND HABITAT: *Orconectes deanae* was originally described from Conchas Reservoir in New Mexico. Conchas Reservoir is an impoundment in the northern reaches of the Canadian River. In Oklahoma, *O. deanae* is known form the North Canadian River drainage and the Arkansas River near its confluence with the North Canadian River. Our ecological niche model also indicated that the western portion of the Red River drainage provides suitable environmental conditions (Figure 46). *Orconectes deanae* is mostly found in lentic habitats along the North Canadian River. It occupies debris piles in turbid, muddy waters.

LIFE HISTORY: Details about the life history of *O. deanae* remain unclear. Most specimens have been collected from man-made ponds and reservoirs and is a tertiary burrower. Form I males and females have been collected in January and juveniles in July (Reimer & Jester, 1975). We have collected females and form II males in October.

SYNTOPIC SPECIES: *Orconectes causeyi*, *Orconectes nais*.

CONSERVATION STATUS: AFS: Currently Stable; Heritage Rank: Apparently Secure (G4); IUCN: Least Concern; ODWC: Not Listed.

ADDITIONAL RESOURCES: Johnson (2010).

Orconectes difficilis **(Faxon, 1898): Painted Crayfish**

GENERAL CHARACTERISTICS: Adults rarely exceed 80 mm in total length. The carapace is robust, depressed, and the areola is closed. The rostrum has prominent lateral spines and a pointed acumen that is shorter than the basal portion. Chelae are triangular and flattened, often as long as the carapace in form I males. In form I males, gonopods are short, stout with central and mesial processes that are short and blunt. In females, the annulus ventralis is diamond shaped (Faxon, 1898).

LIFE COLORATION: The background color is olive brown to grayish tan. There is black speckling on the chelae and occasional speckling on the carapace and abdomen (Figure 47). Fingers may have strong tints of blue to green, especially in form I males, and often have cream to yellow tips. Ventral side is cream to white.

SIMILAR SPECIES: In Oklahoma, *O. difficilis* closely resembles *O. deanae* and *O. palmeri longimanus*. It can be differentiated from *O. palmeri longimanus* by the shape of the gonopods in form I males. In *O. difficilis*, the central projection and mesial process are short and less than 1/4 of the total length, while *O. palmeri longimanus*' central projection and mesial process are long, slender, and more than 1/4 of the total gonopod length. *Orconectes difficilis* differs from *O. deanae* by the curvature in the mesial process (90° angle to the shaft in *O. deanae*).

DISTRIBUTION AND HABITAT: *Orconectes difficilis* is a tertiary burrower and occurs in streams of southeastern Oklahoma, southwestern Arkansas, northeastern Texas, and northwestern

Louisiana. In Oklahoma, *O. difficilis* has been found in rocky, clear streams of Pittsburgh, Latimer, and McCurtain Counties. Our ecological niche model indicates that the southeastern quarter of the state provides suitable environmental conditions for *O. difficilis* (Figure 48).

LIFE HISTORY: Information regarding the life history of *O. difficilis* comes from a study conducted by Walls (1985), where he reported form I males from June through February, with the majority collected in September and October, and suggests most reproductive activity occurs in September and October. We have collected form II males and females in October in southeast Oklahoma.

SYNTOPIC SPECIES: *Orconectes palmeri longimanus*.

CONSERVATION STATUS: AFS: Currently Stable; Heritage Rank: Vulnerable (G3); IUCN: Least Concern; ODWC: Not Listed.

ADDITIONAL RESOURCES: Johnson (2010); Walls (1985).

Orconectes lancifer **(Hagen, 1870): Shrimp Crayfish**

GENERAL CHARACTERISTICS: Adults rarely exceed 76 mm in total length. The carapace has strong cervical spines, is nearly equal in length relative to the abdomen, and the areola is closed. The rostrum has a deep trough-like depression, and the margins are nearly straight terminating in spines or tubercles at the base of an extremely long acumen. Chelae are slender with short fingers, dactyl shorter than the length of the palm, and they are lacking longitudinal ridges and tubercles. In form I males, gonopods terminate into two very short processes. The mesial process is non-corneous and equal in length or slightly longer than central projection. In females, the annulus ventralis lacks a well-developed fossa (Taylor & Schuster, 2004).

LIFE COLORATION: The background color is reddish-brown to gray, with specks of light to dark brown creating a mottled appearance (Figure 49). The ventral side is pale-yellow to white.

SIMILAR SPECIES: The long acumen and gonopods in form I males having two short truncated terminal processes are characteristics that no other crayfish in Oklahoma possesses.

DISTRIBUTION AND HABITAT: *Orconectes lancifer* occurs from southwestern Illinois and southeastern Missouri, southward along the Mississippi River to southeastern Oklahoma, eastern Texas, and Louisiana. In Oklahoma, *O. lancifer* is only known from two localities in McCurtain County, an oxbow lake of the Red River and a pond at Red Slough National Wildlife Refuge. The pond in at Red Slough was drained several years ago, and since draining this species has not been detected. Additionally, in 2005 we visited the oxbow lake but did not detect *O. lancifer* there either. Our ecological niche model shows that the southeastern most corner of Oklahoma provides suitable environmental conditions for the species (Figure 50). Generally, *Orconectes lancifer* can be found in swamps, oxbow lakes, and floodplains with mud or silt substrates. It can also inhabit large slow moving rivers. This species can survive drying conditions by finding refuge under wood debris and thick vegetation patches as it is a tertiary burrower (Pflieger, 1996; Taylor & Schuster, 2004).

LIFE HISTORY: As only two locations are known for *O. lancifer* (D. Arbour, personal communication), no life history information is available from Oklahoma. In Louisiana and Illinois (Page, 1985; Walls, 2009), form I males have been collected from August to November, which corresponds to the peak of breeding activities (Black, 1972). Form II males and females have been collected year round, but dominated collections from April to July. In Louisiana, females have been reported to carry the eggs throughout the winter, while young can be found in late spring into early summer (Walls, 2009). In Illinois, ovigerous females have been collected in September and October (Page, 1985).

SYNTOPIC SPECIES: In Oklahoma, no syntopic crayfish species are known at this time.

CONSERVATION STATUS: AFS: Currently Stable; Heritage Rank: Widespread (G5); IUCN: Least Concern; ODWC: Not Listed.

ADDITIONAL RESOURCES: Hobbs (1989); Taylor et al. (2004).

Orconectes leptogonopodus **Hobbs, 1948: Little River Creek Crayfish**

GENERAL CHARACTERISTICS: Adults rarely exceed 80 mm in total length and the areola is open. The rostrum has a slight depression and lateral spines and margins that are slightly thickened. Chelae are somewhat broad and have a thick or inflated palm region. In form I males, gonopods are slender with the central process consisting of at least 1/2 of the total length (Hobbs, 1948).

LIFE COLORATION: The background color is uniform gray to brown. Hints of red throughout the abdomen, usually along the edges are present (Figure 51). The telson occasionally has some red coloration near the base. The ventral side is cream to white.

SIMILAR SPECIES: In Oklahoma, *O. leptogonopodus* closely resembles *O. menae*, from which it can be distinguished based on the length of the gonopods, as the central process is at least 1/2 of the total length of the gonopods in form I males.

DISTRIBUTION AND HABITAT: *Orconectes leptogonopodus* occurs in the Little River drainage in southeastern Oklahoma and southwestern Arkansas. Our ecological niche model confirms the high endemism of this species, as only the Little River drainage is indicated to have suitable environmental conditions (Figure 52). This species is found in small rocky streams with clear water in fast flowing water and is a tertiary burrower (Williams, 1954).

LIFE HISTORY: Form I and II males and females have been collected from September through November. As with other closely related species, it is likely that spawning occurs during the fall and early winter months.

SYNTOPIC SPECIES: *Orconectes menae*, *Orconectes palmeri longimanus*, and *Procambarus tenuis*.

CONSERVATION STATUS: AFS: Currently Stable; Heritage Rank: Apparently Secure (G4); IUCN: Least Concern; ODWC: Not Listed.

ADDITIONAL RESOURCES: Dyer et al. (2013).

***Orconectes macrus* Williams, 1952: Neosho Midget Crayfish**

GENERAL CHARACTERISTICS: Adults rarely exceed 50 mm in total length. The carapace is nearly equal in length to the abdomen. The rostrum is narrow with a well-developed trough-like depression. Chelae are short, broad, and look oversized relative to body size. In form I males, gonopods have two long, slender, and slightly curved processes that reach the base of the first pair of pereiopods. In females, the annulus ventralis has a deep fossa (Pflieger, 1996).

LIFE COLORATION: The background color is uniform olive-tan to brown without any colorful markings. There is typically a dark brown to black saddle on the conjunction of the carapace and abdomen (Figure 53). The ventral side is light yellow to white.

SIMILAR SPECIES: In Oklahoma, *O. macrus* closely resembles *O. meeki brevis* and *O. nana*. *O. macrus* does not have black speckling on its chelae like *O. meeki brevis*. It differs from *O. nana* in the length of the gonopods in form I males, which reach the base of the first pair of pereiopods as opposed to the second pair of pereiopods in *O. nana*. Furthermore, the two species have an allopatric distribution, with *O. nana* occurring in the upper Illinois River drainage, while *O. macrus* occurs in the Neosho River, Spavinaw Creek, and Spring Creek drainages.

DISTRIBUTION AND HABITAT: *Orconectes macrus* occurs in the Neosho River Drainage including southwestern Missouri, southeastern Kansas, northwestern Arkansas, and northeastern Oklahoma. In Oklahoma, *O. macrus* is found predominantly in small tributaries of the Neosho River and Spavinaw Creek. Our ecological niche model shows that *O. macrus* appears to be confined to the tributaries of the Neosho River and Spavinaw Creek, although there are areas scattered throughout the southern portions of the Neosho River drainage that have suitable environmental conditions (Figure 54). The species inhabits clear, permanently flowing Ozark streams over gravel substrate in fast shallow water and is a tertiary burrower. It usually digs under large rocks or constructs short tunnels under smaller pieces of gravel.

LIFE HISTORY: Pflieger (1996) documented form I males from September through March, suggesting a fall and winter breeding season as observed in other stream crayfish in the Ozark region. Ovigerous females were collected in late March and early April. We collected one ovigerous female in April and form I and II males and non-ovigerous females throughout the year. The ovigerous female only had five relatively large eggs attached to her abdomen. It is suggested that *O. macrus* reaches sexual maturity within the first year of life (Pflieger, 1996). We conducted stomach content analyses and found that the majority of the individuals contained macroinvertebrates, which could be due their small body size and ability to get into the substrate.

SYNTOPIC SPECIES: *Orconectes meeki brevis* and *Orconectes neglectus neglectus*.

CONSERVATION STATUS: AFS: Currently Stable; Heritage Rank: Apparently Secure (G4); IUCN: Least Concern; ODWC: Not Listed.

ADDITIONAL RESOURCES: Crandall (1998); Dillman et al. (2010); Taylor & Knouft (2006).

Orconectes menae **Creasar, 1933: Mena Crayfish**

GENERAL CHARACTERISTICS: Adults rarely exceed 80 mm in total length and the areola is open. The rostrum is wide with convex margins and blunt lateral spines. Chelae are deeply punctate dorsally and ventrally, and fingers have deep longitudinal grooves. In form I males, gonopods terminate in two long processes, with the central projection corneous and bent caudally at the tip. In females, the annulus ventralis is nearly spherical with tubercles on either side of sinus, and the fossa is median and deep (Creaser, 1933).

LIFE COLORATION: The background color is tan to brown and uniform. The carapace and abdomen are slightly mottled (Figure 55). Chelae are usually tipped in orange.

SIMILAR SPECIES: In Oklahoma , *O. menae* closely resembles *O. leptogonopodus* (see *O. leptogonopodus* for differences).

DISTRIBUTION AND HABITAT: *Orconectes menae* is a tertiary burrower and found in tributaries of the Ouachita River in Polk and Montgomery Counties in Arkansas and tributaries of the Red River in LeFlore and McCurtain Counties in Oklahoma. Our ecological niche model shows that the distribution and suitable environmental conditions of *O. menae* is confined to the Ouachita Mountain region (Figure 56).

LIFE HISTORY: Form I males have been found from March through July, while form II males have been collected from April through July (Creaser & Ortenburger, 1933; Reimer, 1969). Ovigerous females have been collected from April and May (Robison et al., 2009), but no females with young have been reported to our knowledge. As we have collected form I and II males and females from October through April, the reproductive season seems to be very broad.

SYNTOPIC SPECIES: *Orconectes leptogonopodus, Orconectes palmeri longimanus*, and *Procambarus tenuis*.

CONSERVATION STATUS: AFS: Threatened; Heritage Rank: Vulnerable (G3); IUCN: Least Concern; ODWC: Tier 1.

ADDITIONAL RESOURCES: Dyer et al. (2013).

Orconectes meeki brevis **Williams, 152: Meek's Short Pointed Crayfish**

GENERAL CHARACTERISTICS: Adults rarely exceed 60 mm in total length. The carapace is subovate, slightly depressed, and the areola is open. The rostrum is divergent at the base and is slightly ridged dorsally, while the acumen is blunt and lacking lateral spines. In form I males, gonopods terminate in two slender processes both curved caudally at 90° to the shaft. In females, the annulus ventralis is firmly fused to sternum (Williams, 1952).

LIFE COLORATION: The background color is reddish brown to brown. Darker markings around the cervical groove and the posterior end of the carapace are present (Figure 57). Chelae have scattered dark spots. There is a pronounced dark spot at the base of the dactyl. Fingers are usually tipped with orange. The ventral side is cream to white.

SIMILAR SPECIES: In Oklahoma, *O. meeki brevis* closely resembles *O. macrus* and *O. nana*. It can be differentiated from the two by the black speckling on the chelae and the antennal scale being widest anterior to the midpoint.

DISTRIBUTION AND HABITAT: *Orconectes meeki brevis* is restricted to the upper Illinois River and Spavinaw Creek drainage basins in northwestern Arkansas and northeastern Oklahoma.

Along with the above drainages, our ecological niche model indicates that areas further downstream may provide suitable environmental conditions for this species (Figure 58); however, no specimens could be found in these areas during our sampling efforts. *Orconectes meeki brevis* is a tertiary burrower and typically occurs in habitats with cobble substrate and clear, cool water. In addition, we have also collected *O. meeki brevis* in areas having accumulated leaf litter and root snags.

LIFE HISTORY: We have collected form I and II males and females from September through June. We have not collected any ovigerous females or females with young. Like other crayfish in the Ozark region, *O. meeki brevis* likely breeds in the fall and early winter..

SYNTOPIC SPECIES: *Orconectes macrus*, *Orconectes nana*, and *Orconectes neglectus*.

CONSERVATION STATUS: AFS: Threatened; Heritage Rank: Imperiled (G2); IUCN: Least Concern; ODWC: Not Listed.

ADDITIONAL RESOURCES: Williams (1954).

Orconectes nais **(Faxon, 1885): Water Nymph Crayfish**

GENERAL CHARACTERISTICS: Adults rarely exceed 130 mm in total length. The carapace is smooth, lightly punctate dorsally, granulate laterally, and the areola is open. The abdomen is nearly the same length as the carapace. The rostrum is long, centrally depressed, and has lateral margins converging into small but distinct spines. Chelae are broad, flattened, and long. The fingers are long with tubercles along the mesial margins of palm and dactyl. Tubercles also line the inner margin on the non-movable finger, and long setae are present at the base of the fingers. In form I males, gonopods terminate in two slender processes, and the mesial process curves the entire length of the gonopod. In females, the annulus ventralis is triangular with a median longitudinal fissure (Faxon, 1885).

LIFE COLORATION: The background color is greenish brown to brown with cream stripes running along the bottom halves of the carapace. The abdomen has two rows of black blotches running longitudinally (Figure 59). Chelae have a bluish-green tint, with yellow to off-white tubercles along the inner margin of the palm and fingers. Fingers usually tipped with orange. Ventral side is white in color.

SIMILAR SPECIES: In Oklahoma, *O. nais* closely resembles *O. virilis* and *O. causeyi*. *Orconectes virilis* differs from *O. nais* in the shape of the gonopods of the form I males. In *O. nais*, the mesial process curves the entire length, while it only curves at the tip in *O. virilis*. See *O. causeyi* for differences between these two species.

DISTRIBUTION AND HABITAT: *Orconectes nais* occurs in the Great Plains of Kansas, Oklahoma, and Texas. It likely also occurs in the southwestern corner of Missouri and northwestern corner of Arkansas, but has not been reported to date. In Oklahoma, *O. nais* is found state wide, usually in larger rivers and streams with sand or silt as substrate. Additionally, we have excavated *O. nais* from burrows in roadside ditches that previously held standing water as it is a tertiary burrower. Our ecological niche model confirms the current distribution of *O. nais*, as much of the state is considered as having suitable environmental conditions (Figure 60).

LIFE HISTORY: The majority of specimens of *O. nais* have been collected from April through October. Ovigerous females have been collected from October and April, and females ready to spawn were also collected in April, suggesting reproduction may occur multiple times a year (Armitage et al., 1972).

SYNTOPIC SPECIES: *Orconectes deanae, Orconectes neglectus neglectus, Orconectes virilis*, and *Procambarus acutus*.

CONSERVATION STATUS: AFS: Currently Stable; Heritage Rank: Widespread (G5); IUCN: Least Concern; ODWC: Not Listed.

ADDITIONAL RESOURCES: Armitage & Topping (1962); Armitage & Wall (1982); Evans-White et al. (2001); Evans-White et al. (2003); Johnson (2010); Mathews et al. (2008); Pippitt (1977).

Orconectes nana **Williams, 1952: Midget Crayfish**

GENERAL CHARACTERISTICS: Adults rarely exceeds 50 mm in total length. The carapace is nearly equal in length to the abdomen. The rostrum is narrow with a well-developed trough-like depression. Chelae are short but broad and look oversized relative to body size. In form I males, gonopods have two long, slender, and slightly curved processes that reach the base of the second pair of pereiopods. In females, the annulus ventralis has a deep fossa (Williams, 1952).

LIFE COLORATION: The background color is uniform olive-tan to brown without any colorful markings. The cheeks exhibit a yellowish spot with a reddish edge. There is a dark brown to black saddle at the conjunction of the carapace and abdomen (Figure 61). The ventral side is light yellow to white.

SIMILAR SPECIES: In Oklahoma, *O. nana* closely resembles *O. macrus* and *O. meeki brevis*. See *O. macrus* and *O. meeki brevis* sections for differences.

DISTRIBUTION AND HABITAT: *Orconectes nana* occurs in the upper Illinois River in eastern Oklahoma and northwestern Arkansas. Our ecological niche model indicates that *O. nana* is likely confined to this region, as larger rivers do not provide suitable environmental conditions and habitat (Figure 62). *O. nana* inhabits clear, permanently flowing Ozark streams with gravel substrate in fast shallow water. It usually digs under large rocks or digs short tunnels under smaller gravel and is a tertiary burrower.

LIFE HISTORY: Little is known about the life history of *O. nana*, but due the close relationship it is likely similar to *O. macrus*. We have collected form I males in September and October as well as form II males and females throughout the year. We collected one ovigerous female in October that carried 5 large eggs.

SNYTOPIC SPECIES: *Orconectes meeki brevis* and *Orconectes neglectus neglectus*.

CONSERVATION STATUS: AFS: Vulnerable; Heritage Rank: Imperiled (G3); IUCN: Least Concern; ODWC: Tier 1.

ADDITIONAL RESOURCES: Crandall (1998); Dillman et al. (2010); Taylor & Knouft (2006).

Orconectes neglectus neglectus **(Faxon, 1885): Ringed Crayfish**

GENERAL CHARACTERISTICS: Adults rarely exceed 100 mm in total length. The carapace is egg-shaped, nearly equal in length to the abdomen, and the areola is open. The rostrum has a trough-like depression and thick lateral margins, which abruptly narrow into a well-defined acumen. Chelae are broad and heavy, especially in form I males where there is a wide gap between the fingers when they are closed. In form I males, gonopods terminate in two slender processes and curve towards each other such that their tips nearly touch. In females, the annulus ventralis has a slit-like fossa that reaches under the anterior margin (Pflieger, 1996).

LIFE COLORATION: The background color is olive-green to brown with two dark saddles, one above the cervical groove and the other on the posterior margin of the carapace (Figure 63). The lateral edges of the abdomen are lined with a dark stripe. Chelae are tipped orange followed by a distinct black ring. The ventral side is mainly white in color.

SIMILAR SPECIES: *Orconectes neglectus neglectus* does not resemble any other crayfish in Oklahoma, as the chelae with orange tips followed by a distinct black ring is characteristic of this species and visible at all stages of development.

DISTRIBUTION AND HABITAT: *Orconectes neglectus neglectus* occurs in southwestern Missouri, northwestern Arkansas, northeastern Oklahoma, and isolated populations in central Kansas, southwestern Nebraska, northeastern Colorado, and south-central Oklahoma (Pflieger, 1996). In Oklahoma, *O. neglectus neglectus* is native to the Neosho River drainage in the northeast region, but has reportedly been translocated (likely by fisherman) to the Blue River located in south-central Oklahoma (Taylor et al., 2004). However, this translocation is currently debated as the Blue River harbors a variety of faunal elements (particularly fishes) otherwise found in the northeastern region of the state, despite its geographic isolation (Mayden, 1985; Mayden & Matthews, 1989). Molecular genetic studies will be requisite to determine the population status in the Blue River. Our ecological niche model indicates suitable environmental conditions are located within the native and proposed introduced areas (Figure 64). *Orconectes* *neglectus neglectus* can be found in clear, rocky, and permanently flowing streams and is a tertiary burrower. *Orconectes neglectus neglectus* also occurs in root wads, undercut stream backs, and riffles along with other shallow areas that are free of silt and other fine sediments.

LIFE HISTORY: In the native range of *O. neglectus neglectus*, breeding occurs from September through April. Ovigerous females have been collected from April through June, with the majority being collected in April. Females with young have been collected in May. In natural habitats, life span ranges 2 to 3 years (Pflieger, 1996).

SYNTOPIC SPECIES: *Cambarus tartarus, Orconectes macrus, Orconectes meeki brevis, Orconectes nais,* and *Orconectes nana*.

CONSERVATION STATUS: AFS: Currently Stable; Heritage Rank: Widespread (G5); IUCN: Least Concern; ODWC: Not Listed.

ADDITIONAL RESOURCES: Evans-White et al. (2001); Gore & Bryant (1990); Imhoff et al. (2012); Larson & Magoulick (2008, 2009); Larson et al. (2009); Magoulick & DiStefano (2007); Pearl et al. (2013).

***Orconectes palmeri longimanus* (Faxon, 1898): Western Painted Crayfish**

GENERAL CHARACTERISTICS: Adults rarely exceed 80 mm in total length. The rostrum has a trough-like depression and well-developed lateral margins and spines. The areola is closed. In form I males, gonopods terminate in two long and slender processes that are curved caudally and the mesial process ends in a spoon-shaped tip. In females, the annulus ventralis is deep with a slit-like fossa at its anterior half. The posterior margins of the annulus ventralis are thick and inflated (Taylor & Schuster, 2004).

LIFE COLORATION: The background color is olive brown to grayish tan. Black speckling on the chelae and occasional speckling on the carapace and abdomen is present (Figure 65). Fingers may have strong tints of blue to green, especially in form I males, and often have cream to yellow tips. The ventral side is cream to white.

SIMILAR SPECIES: In Oklahoma, *O. palmeri longimanus* closely resembles *O. difficilis* and *O. deanae* (see *O. difficilis* and *O. deanae* sections for differences).

DISTRIBUTION AND HABITAT: *Orconectes palmeri longimanus* occurs in Kansas, Oklahoma, Arkansas, Texas, and Louisiana, including a majority of the western tributaries of the Mississippi River from the Arkansas River to the Gulf of Mexico (Hobbs, 1989). In Oklahoma, we have only found this species in the east central and southeastern regions of the state, with the highest populations numbers in Latimer, Pushmataha, and Choctaw counties concurring with past surveys (Creaser & Ortenburger, 1933). Our ecological niche model also indicates suitable environmental conditions slightly to the west of the counties mentioned above (Figure 66). *Orconectes palmeri longimanus* mainly inhabits permanent streams with large rocks and boulders. This species will burrow to follow receding water levels as it is a tertiary burrower.

LIFE HISTORY: Form I males have been collected during the fall months, which follows similar patterns found in other crayfish in the region. This suggests that breeding likely takes place in late fall and winter and females release young late spring and early summer. Form II males and females have been collected throughout the year.

SYNTOPIC SPECIES: *Cambarus ludovicianus*, *Orconectes difficilis*, *Orconectes leptogonopodus*, *Orconectes menae*, *Orconectes saxatilis*, *Procambarus dupratzi*, and *Procambarus tenuis*.

CONSERVATION STATUS: AFS: Currently Stable; Heritage Rank: Widespread (G5); IUCN: Least Concern; ODWC: Not Listed.

ADDITIONAL RESOURCES: Johnson (2010); Jones & Bergey (2007).

Orconectes saxatilis **Bouchard and Bouchard, 1976: Kiamichi Crayfish**

GENERAL CHARACTERISTICS: Adults rarely exceed 60 mm in total length. The carapace has no cervical spines or tubercles and the areola is open. The rostrum has a central depression and marginal spines. Chelae have two subserrate rows of small tubercles along the mesial margin. In form I males, gonopods terminate in two processes which reach the base of the first pair of pereiopods when the abdomen is flexed. In females, the annulus ventralis is symmetrical with the cephalic half divided by a medial trough (Bouchard & Bouchard, 1976).

LIFE COLORATION: The background color is uniformly olive-brown to reddish brown. The posterior margin of the carapace has a prominent dark band (Figure 67). The tail fan has a faint red margin, and the ventral side is mainly white.

SIMILAR SPECIES: In its restricted range, *O. saxatilis* may be confused with similar sized individuals of *O. palmeri longimanus* and *O. tenuis*. It differs from these two species in the length of the gonopods of the form I males, which reach the base of the first pair of pereiopods when abdomen is flexed. Furthermore, *O. saxatilis* lacks cervical spines, which are present in the other two species.

DISTRIBUTION AND HABITAT: *Orconectes saxatilis* is only known from the upper 45 km of the Kiamichi River in Oklahoma. Our ecological niche model confirms the highly endemic nature of *O. saxatilis*' distribution. Suitable environmental conditions may be available just south of the Kiamichi River, but due to the mountainous terrain it is unlikely *O. saxatilis* can disperse to this area (Figure 68). When adequate stream flow is present, the species is mainly found in riffle areas containing cobble and gravel substrates (Jones & Bergey, 2007). As water recedes, *O. saxatilis* will move to the nearest pool habitat or dig shallow burrows under large rocks as it is a tertiary burrower (Bouchard & Bouchard, 1976).

LIFE HISTORY: Form I males and females with glair (a white substance excreted before eggs are laid) were collected in September and October suggesting that reproduction occurs in the fall (Jones & Bergey, 2007). Ovigerous females were collected in March. We have collected form II males and females throughout the year.

SYNTOPIC SPECIES: *Orconectes palmeri longimanus* and *Procambarus tenuis*.

CONSERVATION STATUS: AFS: Endangered; Heritage Rank: Critically Imperiled (G1); IUCN: Least Vulnerable; ODWC: Tier 1.

ADDITIONAL RESOURCES: Taylor et al. (2007).

Orconectes virilis **Hagen, 1870: Virile Crayfish**

GENERAL CHARACTERISTICS: Adults rarely exceed 130 mm in total length. The carapace is slightly longer than the abdomen and the areola is open. The rostrum is moderately broad with a trough-like depression, and lateral margins are thick and set off by spines from the acumen. Chelae have prominent tubercles along the inner margins. In form I males, gonopods terminate in two long slender processes and the central projection is longer and gently curved, while the mesial process is shorter and curved in same direction as central projection with a distinct space between the two. In females, the annulus ventralis is rounded on the posterior margin, without any triangular posterior extensions (Pflieger, 1996).

LIFE COLORATION: The background color is reddish-brown to olive brown. The abdomen has two rows of black blotches running longitudinally (Figure 69). Chelae have a bluish-green tint with yellow to off-white tubercles along the inner margin of the palm and fingers. Fingers are usually tipped with orange. The ventral side is white in color.

SIMILAR SPECIES: In Oklahoma, *O. virilis* closely resembles *O. nais* and *O. causeyi* (see *O. causeyi* and *O. nais* sections for differences).

DISTRIBUTION AND HABITAT: *Orconectes virilis* has a broad distribution and occurs from the southern tip of the Hudson Bay, southward from New England to western Montana and through the Missouri, Mississippi, and Ohio River basins to northern Arkansas and Oklahoma. In Oklahoma, *O. virilis* is found in the Cimarron and Arkansas River drainages in the northern two thirds of the state. Our ecological niche model indicates that the north-central and northeastern portions of the state provide suitable environmental conditions for *Orconectes virilis* (Figure 70). In general, *O. virilis* is most often collected in open water or around logs, rocks, and other debris. It is a tertiary burrower, but rarely burrows into the sediment or surrounding landscape. As fall leads into winter, *O. virilis* has been noted to move to deeper pools and become relatively inactive

(Aiken, 1968). This pattern has also been noted in Missouri (Pflieger, 1996) and in Oklahoma (personal observation).

LIFE HISTORY: *Orconectes virilis* is the most northern ranging crayfish species reaching into Oklahoma. Throughout its range, breeding occurs over an extended period of time from July to late November and early December (Taylor & Schuster, 2004). Eggs are laid in late spring, and females with young have been collected in mid-May and into June. In Oklahoma, we have collected ovigerous females in March and April. Form I and II males have been collected in the fall and spring.

SYNTOPIC SPECIES: *Orconectes nais* and *Procambarus acutus*.

CONSERVATION STATUS: AFS: Currently Stable; Heritage Rank: Widespread (G5); IUCN: Least Concern; ODWC: Not Listed.

ADDITIONAL RESOURCES: Bovbjerg (1953); Dorn & Wojdak (2004); Keller & Hazlett (2010); Martinez (2012); Perry et al. (2000).

Procambarus acutus **(Girard, 1852): White River Crawfish**

GENERAL CHARACTERISTICS: Adults rarely exceed 140 mm in total length. The carapace is laterally compressed with small tubercles along the sides giving it a granular texture, and the areola is open. The rostrum is moderately excavated and the acumen is short and separated from the rostrum by spines or tubercles. Chelae are slender and densely covered with tubercles. In form I males, gonopods have four short processes, three of which are strongly curved laterally to the midline. The gonopods do not have a prominent shoulder. In females, the fossa of the annulus ventralis is located to the right of body midline and partially covered by the largest of three tubercles present (Taylor & Schuster, 2004).

LIFE COLORATION: The background color can range from a deep burgundy red to a light brown. The abdomen exhibits a broad, black, wedge shaped stripe running longitudinally (Figure

71). Tubercles along the body and the chelae are light tan in color. The ventral side is light tan to white.

SIMILAR SPECIES: In Oklahoma, *P. acutus* closely resembles *P. clarkii*. These species can be distinguished by the shape of gonopods in form I males, as *P. clarkii* has a shoulder on the cephalic surface and *P. acutus* lacks a shoulder. Additionally, the areola in *P. clarkii* is closed and open in *P. acutus*.

DISTRIBUTION AND HABITAT: *Procambarus acutus* has a large, disjunct distribution including large portions of eastern United States from Maine to Georgia, along the Gulf Coast from Florida to Mexico, northward through the Mississippi Valley and along the southern Great Lakes from Minnesota to Ohio (Hobbs, 1989). In Oklahoma, *P. acutus* is found statewide. Our ecological niche model confirms the known distribution of *P. acutus* throughout the state, indicating that the entire state except for the panhandle provides suitable environmental conditions (Figure 72). *Procambarus acutus* is very adaptable and can be found in creeks, marshes, swamps, wetlands, wet depressional areas, and roadside ditches. This species will burrow to escape drying conditions and is a secondary burrower.

LIFE HISTORY: Form I and II males and ovigerous females or females with young have been found year round (Pflieger, 1996; Taylor & Schuster, 2004; Turner, 1926). In Oklahoma, we have collected form I males and females with young on warm days in February. The number of young attached the female ranged from 26 to 72. Form II males and females are present throughout the year. Based on the known collections, it is likely that *P. acutus* reproduces mainly in the fall and winter.

SYNTOPIC SPECIES: *Cambarus ludovicianus*, *Orconectes nais*, *Orconectes virilis*, *Procambarus clarkii*, *Procambarus gracilis*, and *Procambarus simulans*.

CONSERVATION STATUS: AFS: Currently Stable; Heritage Rank: Widespread (G5); IUCN: Least Concern; ODWC: Not Listed.

ADDITIONAL RESOURCES: Eversole & Mazlum (2002); Mazlum (2005, 2007); Mazlum et al. (2007); Mazlum & Eversole (2005); Simon et al. (2005).

Procambarus clarkii **(Girard, 1852): Red Swamp Crawfish**

GENERAL CHARACTERISTICS: Adults rarely exceed 160 mm in total length. The carapace is laterally compressed with small tubercles running along its sides and the areola is closed. The rostrum has a trough-like depression with thick lateral margins and spines extending from the acumen. Chelae are slender and are covered in tubercles, with the largest occurring along the inside margins of the palms. In form I males, gonopods have four short, bladelike terminal processes that strongly curve laterally to the midline. Gonopods also have a shoulder on the cephalic surface. In females, the annulus ventralis lacks a definite fossa, but has two anterior tubercles (Taylor & Schuster, 2004).

LIFE COLORATION: This species is variable in color (Walls, 2009; personal observation), but in Oklahoma, the background color usually is deep red to burgundy. The abdomen exhibits a broad, black, wedge shaped stripe running longitudinally (Figure 73). Tubercles on the chelae are light tan to cream. The ventral side ranges from dark cream to light cream depending on habitat.

SIMILAR SPECIES: In Oklahoma, *P. clarkii* closely resembles *P. acutus* (see *P. acutus* for species differences).

DISTRIBUTION AND HABITAT: *Procambarus clarkii* is widely distributed and naturally occurs along the Gulf Coastal Plain from northeastern Mexico east to the Florida panhandle, and northward along the Mississippi River to southeastern Missouri and southwestern Illinois (Page, 1985; Pflieger, 1996; Taylor & Schuster, 2004; Walls, 2009). *Procambarus clarkii* is an important aquaculture species (Walls, 2009) and has been introduced and has established populations throughout much of the United States due to the aquarium trade, fishermen, and human food consumption (Taylor et al., 2007). In Oklahoma, *P. clarkii* occurs naturally in the extreme southeastern corner where the Gulf Coastal Plain reaches into the state. *Procambarus* *clarkii* inhabits a wide variety of habitats, including swamps, flooded ditches, creeks, and will burrow to follow receding water tables as it is a secondary burrower. Substrate in creeks included sandy silt with woody debris and rooted vegetation. Our ecological niche model suggests that the southern half of Oklahoma (along the Red River) provides suitable environmental conditions for *P*. *clarkii* (Figure 74).

LIFE HISTORY: Reproduction occurs from July to October throughout most of its range (Pflieger, 1996). Form I males have been collected from May through January, while females with eggs or young have been collected in September (Penn, 1943; Pflieger, 1996). *Procambarus clarkii* is able to reproduce two times a year (Huner, 2002). In Oklahoma, form I males were found in June and October, while form II males and females are found year round. No ovigerous females or females with young were found during our collecting efforts.

SYNTOPIC SPECIES: *Cambarellus puer*, *Faxonella blairi*, and *Procambarus acutus*.

CONSERVATION STATUS: AFS: Currently Stable; Heritage Rank: Widespread (G5); IUCN: Least Concern; ODWC: Not Listed.

ADDITIONAL RESOURCES: Barbaresi et al. (2004); Chucholl (2011, 2013); Deng et al. (1993); Pearl et al. (2013); Simon et al. (2005).

Procambarus curdi **Reimer, 1975: Red River Burrowing Crayfish**

GENERAL CHARACTERISTICS: Adults rarely exceed 100 mm in total length. The carapace is ovate with reduced or no cervical spines and the areola is open. The rostrum is lacking lateral spines and has a short acumen with a trough-like depression. Chelae are subcylindrical, long, and the mesial surface of palm has tubercles. In form I males, gonopods reach the base of the third pereiopods and terminate in four terminal processes. Central projection is corneous, subtriangular, and flattened lateromesially. In females, annulus ventralis is subovate, and the cephalic half has a broad V-shaped trough (Reimer, 1975).

LIFE COLORATION: Background color olive-green to light bluish gray. Highlights of red are present on the tail, cervical groove, and on chelae (Figure 75). Chelae usually are a lighter gray or with a blue tint. Two rows of darker blotches run longitudinally on the dorsal side of abdomen. Ventral side is whitish.

SIMILAR SPECIES: In Oklahoma, *P*. *curdi* closely resembles *P*. *simulans*. *Procambarus curdi* can be differentiated from *P*. *simulans* by the caudal process of the gonopod, which is flattened lateromesially rather than cephalocaudally as in *P*. *simulans* (Reimer, 1975).

DISTRIBUTION AND HABITAT: *Procambarus curdi* occurs in the Red River drainage of southeastern Oklahoma and southwestern Arkansas, as well as the Brazos River drainage in Texas (Johnson & Johnson, 2008). *Procambarus curdi* generally occurs in semi-permanent water bodies such as ditches, backwater pools, and intermittent streams. It can also be found in open water during the juvenile release period. *Procambarus curdi* will burrow when water sources start to recede. In Oklahoma, *P*. *curdi* is found in the southeastern counties along the Red River. Our ecological niche model indicates that *P*. *curdi* is mainly confined to the Red River drainage, although one area just north of the Ouachita Mountains may provide suitable environmental condition conditions (Figure 76).

LIFE HISTORY: *Procambarus curdi* appears to be a secondary burrower as the majority of collections known were from burrows located on the bank of streams or rivers (Reimer, 1975). Males (form I and II) and females have been collected year round from burrows. To our knowledge no ovigerous females or females with young have been collected in Oklahoma. *Procambarus curdi* is more active and leaves burrows on warm humid nights usually after rain events.

SYNTOPIC SPECIES: *Procambarus simulans*.

CONSERVATION STATUS: AFS: Currently Stable; Heritage Rank: Widespread (G5); IUCN: Least Concern; ODWC: Not Listed.

ADDITIONAL RESOURCES: Hobbs (1990).

Procambarus dupratzi **Penn, 1953: Southwestern Creek Crayfish**

GENEARL CHARACTERISTICS: Adults rarely exceed 100 mm in total length. As a member of the subgenus *Pennides*, *P*. *dupratzi* is the only known crayfish in Oklahoma to have two cervical spines. The rostrum is rather long with prominent lateral spines. Chelae are narrow and cylindrical. Fingers are approximately the same length as the palm. In form I males, the mesial process is slender and directed approximately 90° to shaft. The caudal knob is poorly developed and pentastyle is absent (Walls, 2009). In females, the annulus ventralis has median sinus and is partially covered by tubercles on anterior end (Penn, 1953).

LIFE COLORATION: The background color olive drab to brown. There is a darker brown band at the posterior edge of the carapace that extends forward along the lower edge of the carapace. Black stripes run longitudinally along the outer edges of the abdomen (Figure 77). Fingers are usually orange at the tips. The ventral side is light brown to white.

SIMILAR SPECIES: No other species resembles *P*. *dupratzi*, as this species is the only *Procambarus* species in Oklahoma to have two cervical spines.

DISTRIBUTION AND HABITAT: *Procambarus dupratzi* has a disjunct distribution and occurs in southeastern Oklahoma and southwestern Arkansas as well as southeast Texas and southwestern Louisiana. In Oklahoma, *P*. *dupratzi* was collected in three tributaries of the Little River in McCurtain County (Jones & Bergey, 2005). Our ecological niche model indicated that suitable environmental conditions may also exist further north into the Ouachita and Boston Mountains (Figure 78). *Procambarus dupratzi* typically inhabits relatively cool streams with clear and sometimes tannin stained water and is a tertiary burrower. We have collected in microhabitats with emergent aquatic vegetation, leaf litter, and other debris which has been found in other surveys (Walls, 2009).

LIFE HISTORY: In Louisiana, form I males have been found year round (Walls, 2009). In Oklahoma, this species was collected in January, May, October, and November. To our knowledge, no form I males, ovigerous females or females with young have been collected in

Oklahoma, as this species was only discovered recently during survey work conducted within the state (Jones & Bergey, 2005).

SYNTOPIC SPECIES: *Cambarus ludovicianus* and *Orconectes palmeri longimanus*.

CONSERVATION STATUS: AFS: Currently Stable; Heritage Rank: Widespread (G5); IUCN: Least Concern; ODWC: Not Listed.

ADDITIONAL RESOURCES: Hobbs (1989, 1990); Walls & Black (2008).

***Procambarus gracilis* (Bundy, 1876): Prairie Crayfish**

GENERAL CHARACTERISTICS: Adults rarely exceed 85 mm in total length. The carapace is dome shaped, longer than the abdomen, and the areola is closed. Chelae are broad, powerful, and have a notch near the base of the dactyl, and lack tubercles except along inside margins of the dactyl and the palm. In form I males, gonopods have four short processes, with the longest process being slender, slightly curved, and tapering into a sharp tip. In females, the annulus ventralis is round in outline and has a deep fossa on either side of the midline (Pflieger, 1996).

LIFE COLORATION: The background color is reddish brown to grayish brown and nearly uniform. Chelae are similar in color but with a bluish green tint (Figure 79). The ventral side is light tan to white.

SIMILAR SPECIES: In Oklahoma, *P. gracilis* closely resembles other primary burrowers such as *Cambarus diogenes*, *C. ludovicianus*, *Fallicambarus fodiens*, and *Procambarus liberorum*. *Procambarus gracilis* can be easily differentiated from the first three species, due to its four short processes on the male gonopod as opposed to two long, curved, bladelike processes. It differs from *P. liberorum* by the caudal process being thinner and more narrow. In females of all listed species, the annulus ventralis of *P. gracilis* is unique, as it does not have a groove in its anterior margin.

DISTRIBUTION AND HABITAT: *Procambarus gracilis* occurs from southeastern Wisconsin and northwestern Indiana through Iowa, Illinois, northern Missouri, and into eastern Kansas, Oklahoma, and northern Texas. In Oklahoma, it is found throughout the prairie region in the north central and northeastern portions, down through the eastern side into the southeast corner of the state. Our ecological niche model confirms that the northeastern quarter of the state provides suitable environmental conditions in addition to the known distribution (Figure 80). As a primary burrower, *P*. *gracilis* inhabits native grasslands and areas that were formerly native grasslands, as well roadside ditches. Notably, this species can often be found long distances away from permanent water sources.

LIFE HISTORY: *Procambarus gracilis* remains in its burrow for extended periods of time, usually emerging only during warm humid nights (Bundy, 1876). It has been noted that this species is most active right before sunset until an hour or so after sunset (Hayes, 1975). Reproduction may occur over an extended period of time as juveniles recently dispersed from the females have been found from late October through June (Page, 1985). In Missouri, form I males have been collected in traps set at the entrances of burrows in June (Pflieger, 1996). We have collected form II males and females in June from roadside ditches in the north central part of the state. *Procambarus gracilis* has an approximate life span of three to four years (Page, 1985).

SYNTOPIC SPECIES: *Cambarus diogenes*, *Fallicambarus fodiens*, *Procambarus acutus*, and *Procambarus liberorum*.

CONSERVATION STATUS: AFS: Currently Stable; Heritage Rank: Widespread (G5); IUCN: Least Concern; ODWC: Not Listed.

ADDITIONAL RESOURCES: Hobbs & Rewolinski (1985); Hobbs & Robison (1988); Secker (2013).

Procambarus liberorum **Fitzpatrick, 1978: Osage Burrowing Crayfish**

GENERAL CHARACTERISTICS: Adults rarely exceed 90 mm in total length. The carapace has no cervical spines or tubercles, and the areola is closed. The rostrum has gently curving margins, lacks marginal spines, and the acumen is barely present. Chelae are blunt, heavy, and tubercles line the mesial margins of the palm and dactyl. In form I males, gonopods extend to the base of the third pereiopods, terminate in four processes, and have a strong right-angled shoulder at base of central projection. The central projection terminates distally and is directed slightly caudolaterally. In females, the annulus ventralis is deeply excavated in the cephalomedian half and has surrounding margins with spines or tubercles (Fitzpatrick, 1978).

LIFE COLORATION: The background color is uniform and reddish brown (Figure 81). Ventral side is cream to white. There are no distinct coloration characteristics for this species.

SIMILAR SPECIES: In Oklahoma, *P. liberorum* closely resembles *P. gracilis*. It differs from *P. gracilis* by having gonopods having a wider caudal process, a base of the mesial process being straight, and by the cephalic process being directed less cephalically (Fitzpatrick, 1978).

DISTRIBUTION AND HABITAT: *Procambarus liberorum* is a primary burrowing species that occurs near the eastern border of Oklahoma and throughout much of Arkansas (Robison & McAllister, 2006). According to our ecological niche model, regions with suitable environmental conditions are located within the Neosho River drainage, the western foothills of the Boston and Ouachita Mountains, and along the Red River in McCurtain and Choctaw counties (Figure 82). As a primary burrower, *P. liberorum* inhabits grasslands and areas that were formerly covered with native grasses, roadside ditches in these areas, and mountainous regions within the Boston and Ouachita Mountains (Robison & McAllister, 2006). It can often be found long distances from a permanent water source. Occasionally, this species can be found near creeks or wetland areas.

LIFE HISTORY: *Procambarus liberorum* spends the majority of time within its burrow. Form I and II males as well as mature females have been collected by excavating burrowers in April and July (Robison & McAllister, 2006). It is likely that *P. liberorum* has a similar life history as *P. gracilis*.

SYNTOPIC SPECIES: *Procambarus gracilis*.

CONSERVATION STATUS: AFS: Currently Stable; Heritage Rank: Apparently Secure (G4); IUCN: Least Concern; ODWC: Not Listed.

ADDITIONAL RESOURCES: Crandall et al. (2009); McAllister et al. (2011).

Procambarus simulans **(Faxon, 1884): Southern Plains Crayfish**

GENERAL CHARACTERISTICS: Adults rarely exceed 100 mm in total length. The carapace is ovate and narrows towards the rostrum, is granulate laterally, and the areola is open. The rostrum is broad and deeply excavated with strong margins and no lateral spines. Chelae are long and slender. The surface of the chelae is dentate, with tubercles lining the mesial margins of palm and dactyl. In form I males, gonopods are thick and straight with four short processes. Central projection is straight, and caudal process is narrow. In females, the annulus ventralis has two tubercles on the anterior end (Faxon, 1884).

LIFE COLORATION: The background color is olive-green to light bluish gray (Figure 83). Occasionally, highlights of red are present on the tail, cervical groove, and on chelae. Chelae are usually lighter gray or with a blue tint. Two rows of darker blotches are running longitudinally on the dorsal side of abdomen. The ventral side is cream colored.

SIMILAR SPECIES: In Oklahoma, *P*. *simulans* closely resembles *P*. *curdi* (see *P*. *curdi* for differences).

DISTRIBUTION AND HABITAT: *Procambarus simulans* has a broad distribution and occurs in Colorado, New Mexico, Kansas, Oklahoma, Texas, Arkansas, and Louisiana (Hobbs 1989). In Oklahoma, this species is found statewide in a variety of habitats. The species can be found anywhere from roadside ditches, wetlands and swamps, to ponds and streams. *Procambarus simulans* is a secondary burrower and will burrow into the ground to follow receding water levels. Our ecological niche model confirms the wide distribution of *P*. *simulans* as the entire state – except for the western half of the panhandle – provides suitable environmental conditions (Figure 84).

LIFE HISTORY: Form I and II males and females have been collected year round in Oklahoma. Females with young were collected in February from a shallow wetland area in north central

Oklahoma. The number of young attached to the females ranged from 89 to 156. We have not collected any ovigerous females. As females were collected with young in February, this suggests that the majority of breeding takes place in the fall and winter months.

SYNTOPIC SPECIES: *Cambarus diogenes*, *Procambarus acutus*, and *Procambarus curdi*.

CONSERVATION STATUS: AFS: Currently Stable; Heritage Rank: Widespread (G5); IUCN: Least Concern; ODWC: Not Listed.

ADDITIONAL RESOURCES: Williams (1954); Williams & Leonard (1952); Young (1971).

***Procambarus tenuis* Hobbs, 1950: Ouachita Mountain Crayfish**

GENERAL CHARACTERISTICS: Adults rarely exceed 125 mm in total length. The carapace is strongly compressed, and the areola is very narrow and nearly closed. The boss on the coxae of the fourth pereiopod is greatly expanded ventrally. The rostrum does not have lateral spines. Chelae are stout and oval in shape, and palms have a row of 7 to 9 tubercles lining their mesial surface. In form I males, gonopods terminate in three processes and the central projection is corneous and the most prominent of the processes, while the mesial process is thin, triangular, and directed caudally at nearly a 90° angle with the axis of shaft (Hobbs, 1948).

LIFE COLORATION: The background color is usually light tan to reddish brown with dark dots over the whole body (Figure 85). Ventral side is pale yellow to whitish.

SIMILAR SPECIES: In the native range of *P. tenuis*, there are no other *Procambarus* species that could be confused with *P. tenuis*.

DISTRIBUTION AND HABITAT: *Procambarus tenuis* occurs in the Arkansas, Ouachita, and Red River basins of western Arkansas and southeastern Oklahoma. In Oklahoma, *P. tenuis* has been found in three counties (LeFlore, Pushmataha, Pittsburg). Our ecological niche model indicates that suitable environmental conditions may be available in Haskell, Latimer, Atoka, and McCurtain counties (Figure 86). *Procambarus tenuis* has been found burrowing adjacent to and within clear cool springs and streams, and found under rocks in permanent flowing streams exhibiting qualities of both a secondary and tertiary burrower (Hobbs, 1989; Jones & Bergey, 2007).

LIFE HISTORY: *Procambarus tenuis* is rare within its native range. We have collected form II males, females, and juveniles in March and April. Form II males and females have also been collected year round (J. Dyer, personal communication).

SYNTOPIC SPECIES: *Orconectes leptogonopodus, Orconectes menae, Orconectes palmeri longimanus*, and *Orconectes saxatilis*.

CONSERVATION STATUS: AFS: Vulnerable; Heritage Rank: Imperiled (G3); IUCN: Data Deficient; ODWC: Tier 1.

ADDITIONAL RESOURCES: Jones & Bergey (2007).

Discussion

The native crayfish fauna of Oklahoma consists of 30 species in 6 genera all within the family Cambaridae. The most species rich genus is *Orconectes* with 14 species, followed by *Procambarus* (8), *Cambarus* (4), *Faxonella* (2), as well as *Cambarellus* and *Fallicambarus* each with 1 species. Oklahoma currently has three endemic species: *Cambarus tartarus*, *Cambarus subterraneus* (both of which are restricted to cave habitats in the Ozark Plateau), and *Orconectes saxatilis*, which occurs in the Kiamichi River. Oklahoma has an intermediate crayfish diversity relative to the rest of the United States. States located in the southeastern region can reach species richness values above 60, while states to the west have species richness value in the single digits or no known native crayfish (Taylor et al., 2007).

Patterns of biodiversity and conservation priorities in Oklahoma

Our analyses indicate that high species diversity is particularly found along the eastern side of Oklahoma (Figure 89), and of the 30 known species, more than half can be found in the northeastern and southeastern corner of the state. The northeastern portion of the state (Ozark

Plateau) provides habitat for the two endangered cave crayfishes and the imperiled stream dwelling midget crayfishes (*O. macrus* and *O. nana*). The restricted nature of these species' distributions calls for immediate protection from anthropogenic impacts within this region. Similarly, the South Central Plains and Ouachita Mountains ecoregions in southeastern Oklahoma are biogeographically distinct compared to the rest of the state. They are partially covered by hilly pine forests dissected by rivers and streams with cobble substrates as well as lowland areas consisting of cypress bogs and swamps. In accordance with the high habitat diversity, these ecoregions sustain a diversity of crayfish with different ecological attributes (including stream-dwellers and terrestrial species). Notably, the highly endemic *Orconectes saxatilis* can be found here. It has been recorded only from the upper 45 km of the Kiamichi River (Jones & Bergey, 2007), which has recently suffered tremendously from severe drought conditions causing minimal to zero stream flow. The impacts of low stream flow on the population of *O. saxatilis* remains to be investigated. In addition, the Ouachita Mountains region also harbors *O. leptogonopodus*, *O. menae*, and *O. tenuis*, which all have a limited distribution in Oklahoma and adjacent areas in Arkansas. While the conservation statuses of all species remain to be studied in detail, a recent analysis suggested that climate change would likely truncate their narrow distribution even further (Dyer et al., 2013). Other species with relatively narrow distributions in eastern Oklahoma also occur in Missouri, Arkansas, Louisiana, and eastern Texas, such that their occurrence in Oklahoma merely represents the westernmost distribution edge. Given the present data on crayfish and other aquatic organisms (such as freshwater mussels and fish; Allen et al. 2013), the northeastern and southeastern portions of the state should clearly receive priority for local conservation efforts.

Overall, the conservation status of crayfish in Oklahoma follows the same trend noticeable in the rest of the United States in that an increasing number of known species are imperiled to some extent (Taylor, 2002). In Oklahoma, 3 species are endangered or critically imperiled, 4 are threatened, imperiled, or vulnerable, and 23 are currently stable depending on the

IUCN, AFS, and the Nature Conservancy ranking systems (see Table 1 for an overview). Considering the different methodologies and spatial scales (global vs. regional), the general conservation classifications of the IUCN, AFS, Nature Conservancy Heritage, and ODWC are remarkably consistent. Nonetheless, we would like to emphasize that on the ground evaluation of conservation statuses, as well as planning and implementation of conservation measures, have mostly been lacking. Such efforts will be critical to maintain Oklahoma's crayfish diversity, particularly considering the increasing pressures on habitats suitable for crayfish due to direct habitat alterations and changed land use practices, increased water withdrawal and decreasing stream flows, as well as increased nutrient loadings (Taylor et al., 2007). Successful conservation of Oklahoma's crayfishes will first and foremost require sound evaluation of their biology, actual distribution, and population trends. This is true not only for some of the stream-dwelling crayfish with narrow distributions, but also for terrestrial species that have been understudied because of their reclusive nature.

Currently, there are no known nonindigenous crayfish species in Oklahoma. However, *O. neglectus neglectus* has putatively been introduced from the Ozark Plateau region in the northeastern corner to the Blue River in southern Oklahoma (Taylor et al., 2004), but this may warrant additional research as discussed in detail in the species account. Our maps derived from ecological niche models may be useful for further investigations into the invasive potential of individual species. If combined with a more thorough assessment of biogeographic barriers and biotic interactions, the maps will hopefully allow managers and biologists to better focus their efforts on high-risk areas and species. At this point, it is important to note that the sale of crayfish via bait shops can still serve a direct vector for invasive species introductions (DiStefano et al., 2009). Currently, there are no restrictions on bait shops regarding the sale of crayfish in Oklahoma, increasing the likelihood for future introductions. Surveying species available in the state's bait trade and assessing the environmental suitability of Oklahoman ecosystems for prevalent species would be a significant step towards taking preventive measures against future introductions.

Future directions

The current review also highlights that some major gaps in our knowledge about crayfish in Oklahoma and elsewhere: (1) As more surveys are completed the number of crayfish known to inhabit Oklahoma may continue to change. Several species that have been previously recorded in Oklahoma have not been collected in decades. For example, *Cambarellus puer* was recorded in the 1970's in a swampy area near the Little River in southeastern Oklahoma, but has not been found in recent surveys conducted in 2002 (Taylor et al., 2004), 2005, and 2012 (authors' observation). This pattern also holds true for *Faxonella blairi*, *F. clypeata*, and *Orconectes lancifer* (Taylor et al., 2004), whose distributions barely reach into Oklahoma. Local extirpations at distributional margins of these species may have effectively caused their disappearance from the state. More targeted surveys are warranted to elucidate the current status of these species in Oklahoma. Additionally, as more surveys are conducted and the taxonomy of species is revised, it is possible that new state records will be documented, as crayfish remain undersampled throughout the state (see Morehouse & Tobler, In Press; Robison & McAllister, 2006).

(2) The taxonomic status of some species in Oklahoma still remains unclear. This is particularly evident in *Orconectes causeyi*, which exhibits similar traits and is difficult to distinguish from *Orconectes virilis* and *Orconectes nais*. Hobbs (1989) already stated that *O. virilis* and *O. causeyi* are virtually indistinguishable from one another, even based on the gonopod morphology in form I males. In addition, Pflieger (1996) did not recognize *Orconectes nais* as part of the crayfish fauna of Missouri, even though some specimens are distinguishable from *Orconectes virilis* and others have intermediate gonopod curvature. Our distributional analyses indicate a clear overlap in the occurrence of the three species, and molecular analyses will be

requisite to determine the validity of the taxonomic statuses and test for potential signals of hybridization where ranges overlap.

(3) Lastly, our review highlights the dearth of knowledge we have about the ecology and life history of most crayfish species. The information reviewed here is largely based on studies of the same species from other states, and for many species even basic information about habitat use, reproduction, and resource use are simply not available. Few studies have been conducted on Oklahoma crayfish and most so far have focused on distributional patterns and habitat use of endemic crayfish in the southeastern corner of the state (Dyer et al., 2013; Jones & Bergey, 2007; Robison et al., 2009).

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Table 1. Conservation Status and ranks of Oklahoma crayfish based on the American Fisheries Society (AFS), Heritage global ranks, International Union for Conservation of Nature (IUCN), and Oklahoma Department of Wildlife Conservation (ODWC). Rankings are based on the global distribution of each species irrespective of political boundaries. E = Endangered, T = Threatened, V = Vulnerable, CS = Currently Stable, G1 = Critically Imperiled, G2 = Imperiled, G3 = Vulnerable, G4 = Apparently Secure, G5 = Widespread, LC = Least Concern, NT = Near Threatened, VU = Vulnerable, EN = Endangered, CR = Critically Endangered, EW = Extinction in the Wild, EX = Extinct, and DD = Data Deficient. NL = Not Listed, 1 = Very high conservation need, 2 = High conservation need, 3 = Moderate conservation need.

Species	**AFS**	**Heritage Rank**	**IUCN Rank**	**ODWC**
Cambarellus puer	CS	G5	LC	NL
Cambarus diogenes	CS	G5	LC	NL
Cambarus ludovicianus	CS	G5	LC	NL
Cambarus subterraneus	E	G1	CR	1
Cambarus tartarus	E	G1	CR	1
Fallicambarus fodiens	CS	G5	LC	NL
Faxonella blairi	CS	G3	LC	2
Faxonella clypeata	CS	G5	LC	NL
Orconectes causeyi	CS	G5	LC	NL
Orconectes deanae	CS	G4	LC	NL
Orconectes difficilis	CS	G3	LC	NL
Orconectes lancifer	CS	G5	LC	NL
Orconectes leptogonopodus	CS	G4	LC	NL
Orconectes macrus	CS	G4	LC	NL
Orconectes meeki brevis	T	G2	LC	NL
Orconectes menae	T	G3	LC	1
Orconectes nais	CS	G5	LC	NL
Orconectes nana	V	G3	LC	1
Orconectes neglectus	CS	G5	LC	NL
Orconectes palmeri longimanus	CS	G5	LC	NL
Orconectes saxatilis	E	G1	VU	1
Orconectes virilis	CS	G5	LC	NL
Procambarus acutus	CS	G5	LC	NL
Procambarus clarkii	CS	G5	LC	NL
Procambarus curdi	CS	G5	LC	NL
Procambarus dupratzi	CS	G5	LC	NL

Procambarus gracilis	CS	G5	LC	NL
Procambarus liberorum	CS	G4	LC	NL
Procambarus simulans	CS	G5	LC	NL
Procambarus tenuis	V	G3	DD	1

Table 2. Bioclimatic variables used for the ecological niche modeling from the WorldClim, Hydro1K, and Harmonized World Soils datasets.

WorldClim

BIO2 = Mean Diurnal Range (Mean of monthly (max temp - min temp))
BIO3 = Isothermality (BIO2/BIO7) (* 100)
BIO4 = Temperature Seasonality (standard deviation *100)
BIO5 = Max Temperature of Warmest Month
BIO6 = Min Temperature of Coldest Month
BIO7 = Temperature Annual Range (BIO5-BIO6)
BIO8 = Mean Temperature of Wettest Quarter
BIO9 = Mean Temperature of Driest Quarter
BIO10 = Mean Temperature of Warmest Quarter
BIO11 = Mean Temperature of Coldest Quarter
BIO12 = Annual Precipitation
BIO13 = Precipitation of Wettest Month
BIO14 = Precipitation of Driest Month
BIO18 = Precipitation of Warmest Quarter

Hydro1K

Aspect
Elevation
Slope
Topographic Index

Soil

World Harmonized Soils

Figure captions:

Figure 1. Ventral side of crayfish showing orientation and locations of pereiopods and gonopods for identification purposes.

Figures 2-28. Figures showing location of important characteristics within each couplet for the dichotomous key.

Figures 29-36. 29. *Cambarellus puer* 30. Potential distribution of *Cambarellus puer* 31. *Cambarus diogenes* 32. Potential distribution of *Cambarus diogenes* 33. *Cambarus ludovicianus* 34. Potential distribution of *Cambarus ludovicianus* 35. *Cambarus subterraneus* 36. Potential distribution of *Cambarus subterraneus* (distribution map was not made for this species due to it subterranean lifestyle; climatic variables outside the cave systems do not accurately represent the climate within the cave).

Figures 37-44. 37. *Cambarus tartarus* 38. Potential distribution of *Cambarus tartarus* (distribution map was not made for this species due to it subterranean lifestyle; climatic variables outside the cave systems do not accurately represent the climate within the cave) 39. *Fallicambarus fodiens* 40. Potential distribution of *Fallicambarus fodiens* 41. *Faxonella blairi* 42. Potential distribution of *Faxonella blairi* 43. *Faxonella clypeata* 44. Potential distribution of *Faxonella clypeata*.

Figures 45-52. 45. *Orconectes causeyi* 46. Potential distribution of *Orconectes causeyi* 47. *Orconectes deanae* 48. Potential distribution of *Orconectes deanae* 49. *Orconectes difficilis* 50. Potential distribution of *Orconectes difficilis* 51. *Orconectes lancifer* 52. Potential distribution of *Orconectes lancifer*.

Figures 53-60. 53. *Orconectes leptogonopodus* 54. Potential distribution of *Orconectes leptogonopodus* 55. *Orconectes macrus* 56. Potential distribution of *Orconectes macrus* 57.

Orconectes menae 58. Potential distribution of *Orconectes menae* 59. *Orconectes meeki brevis* 60. Potential distribution of *Orconectes meeki brevis*.

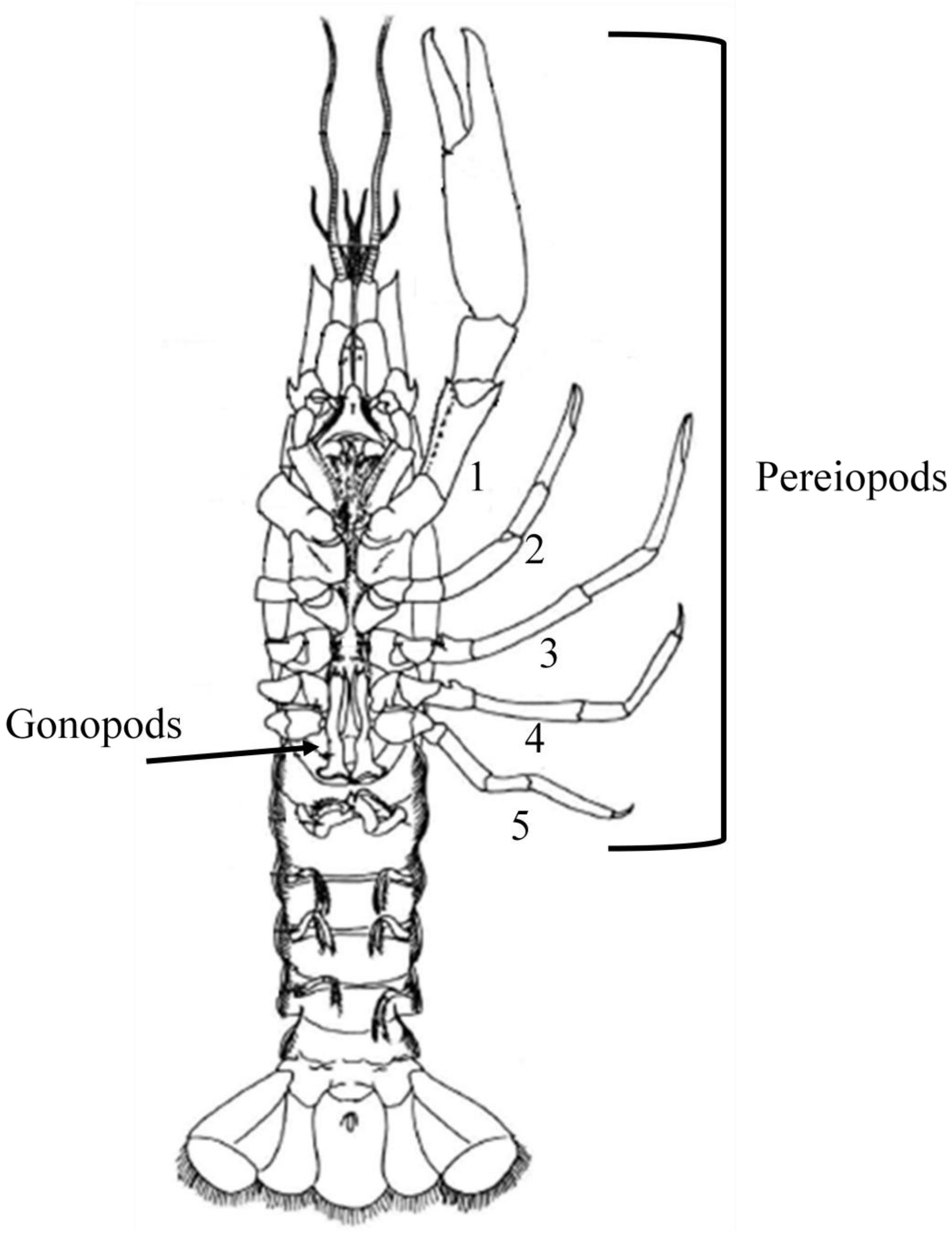
Figures 61-68. 61. *Orconectes nais* 62. Potential distribution of *Orconectes nais* 63. *Orconectes nana* 64. Potential distribution of *Orconectes nana* 65. *Orconectes neglectus neglectus* 66. Potential distribution of *Orconectes neglectus neglectus* 67. *Orconectes palmeri longimanus* 68. Potential distribution of *Orconectes palmeri longimanus*.

Figures 69-76. 69. *Orconectes saxatilis* 70. Potential distribution of *Orconectes saxatilis* 71. *Orconectes virilis* 72. Potential distribution of *Orconectes virilis* 73. *Procambarus acutus* 74. Potential distribution of *Procambarus acutus* 75. *Procambarus clarkii* 76. Potential distribution of *Procambarus clarkii*.

Figures 77-84. 77. *Procambarus curdi* 78. Potential distribution of *Procambarus curdi* 79. *Procambarus dupratzi* 80. Potential distribution of *Procambarus dupratzi* 81. *Procambarus gracilis* 82. Potential distribution of *Procambarus gracilis* 83. *Procambarus liberorum* 84. Potential distribution of *Procambarus liberorum*.

Figures 85-89. 85. *Procambarus simulans* 86. Potential distribution of *Procambarus simulans* 87. *Procambarus tenuis* 88. Potential distribution of *Procambarus tenuis* 89. Biodiversity hotspots within the study region. Map was obtained by combining all species' distribution maps using the raster calculator within ArcGIS. The calculator adds up each value within each pixel to generate a diversity map, where lighter colors represent areas where more species are predicted based on environmental variables.

Figure 1.



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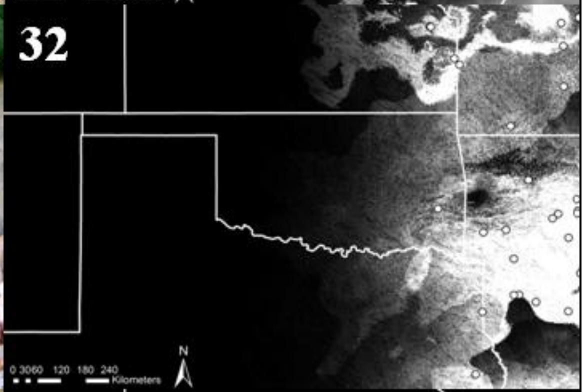

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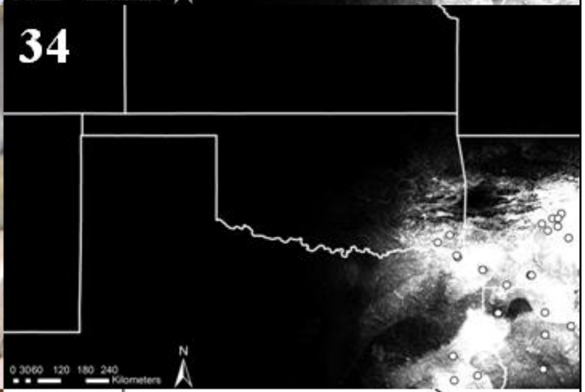

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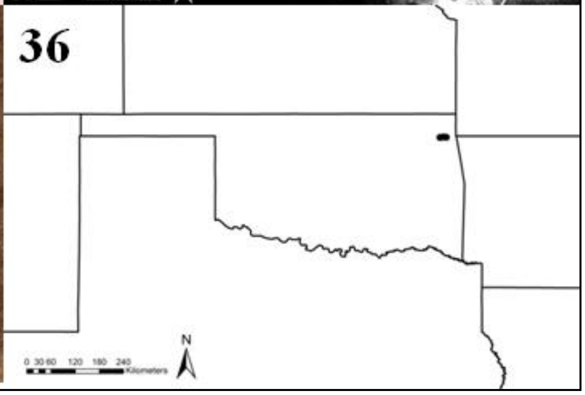

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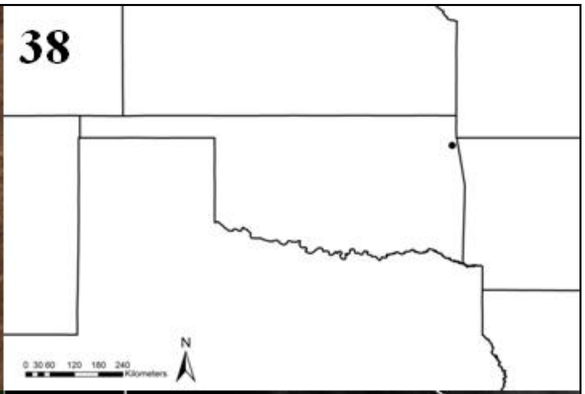

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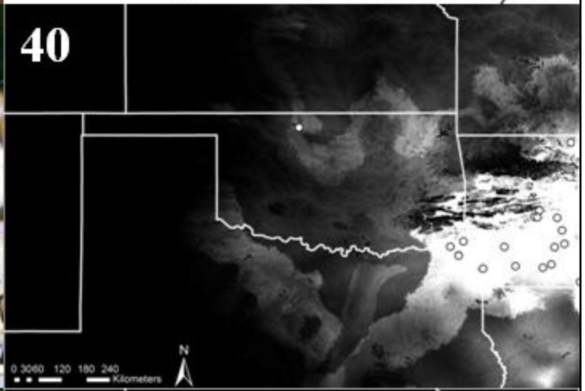

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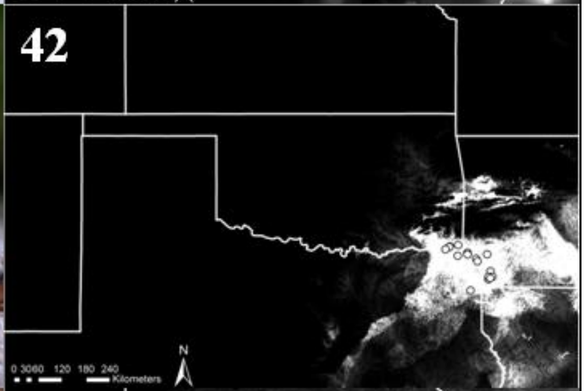

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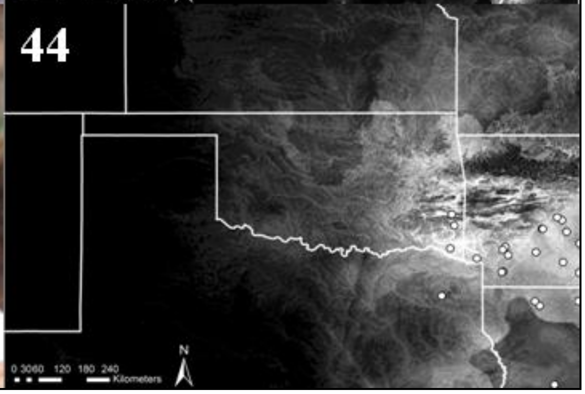

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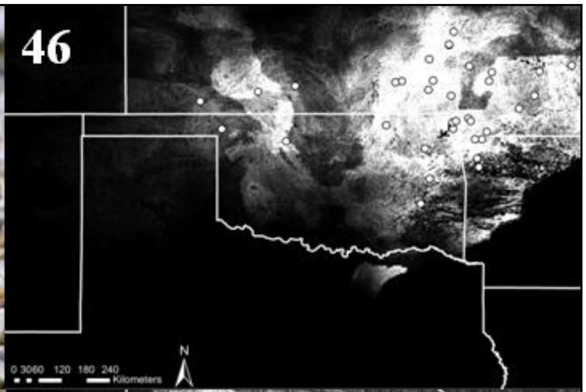

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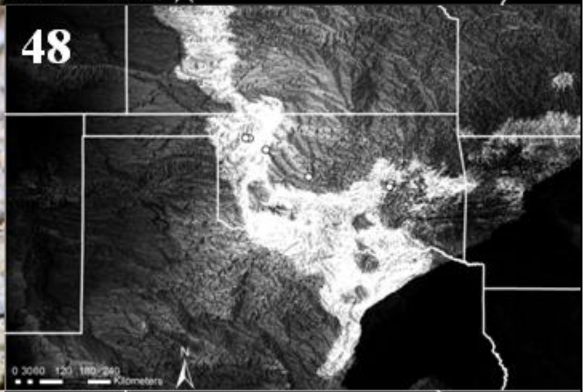

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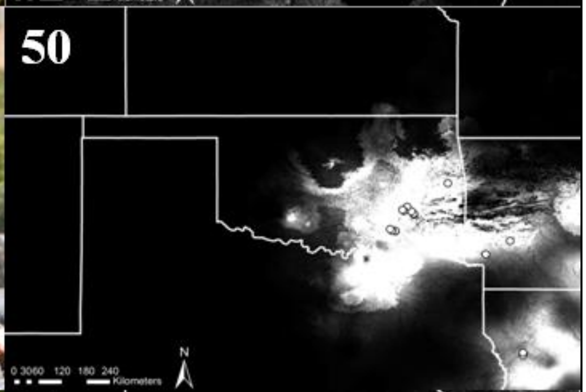

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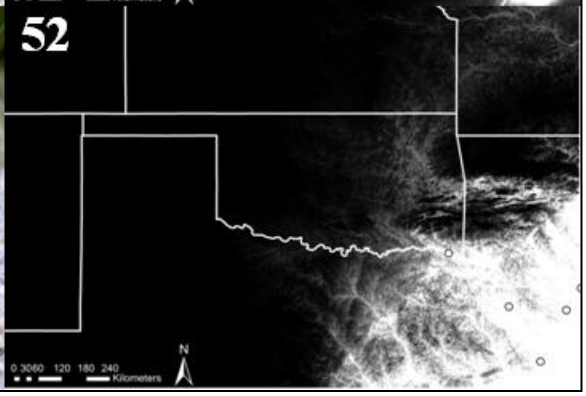

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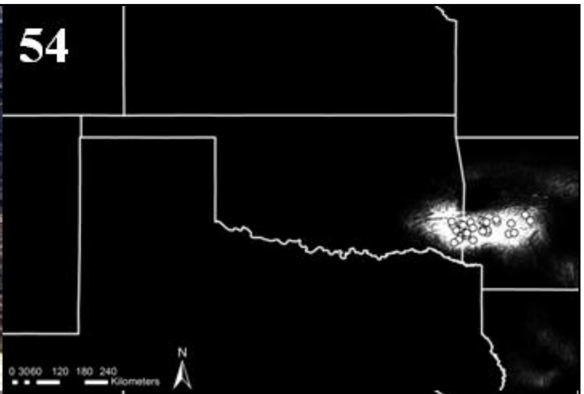

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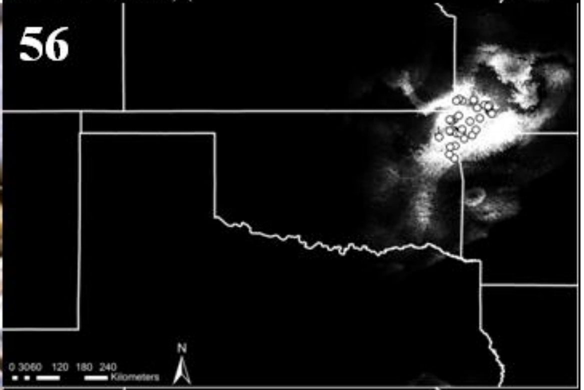

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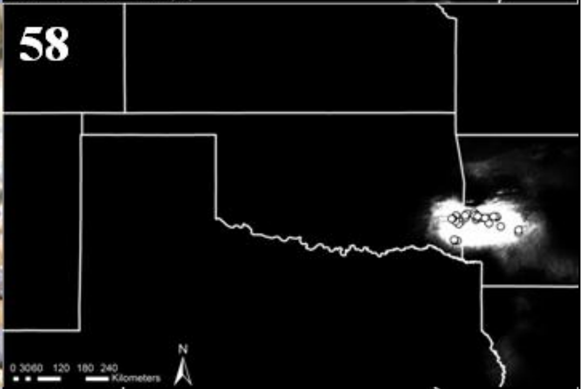

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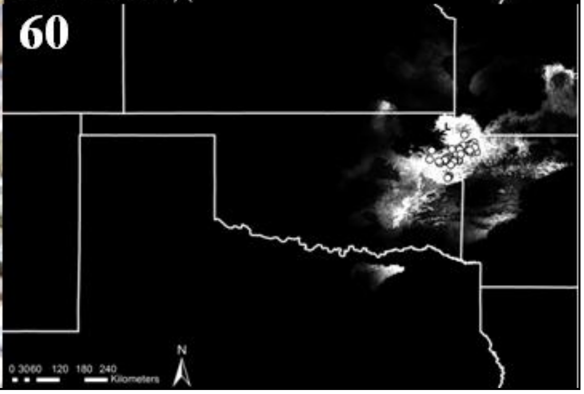

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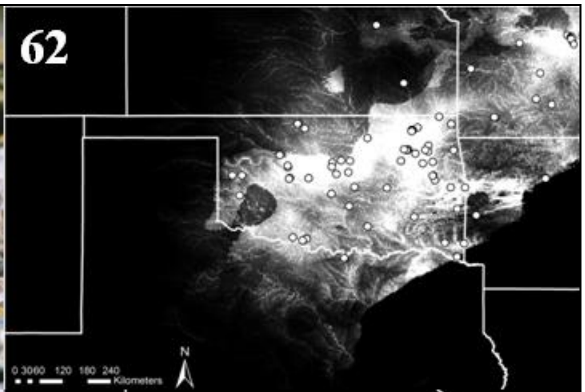

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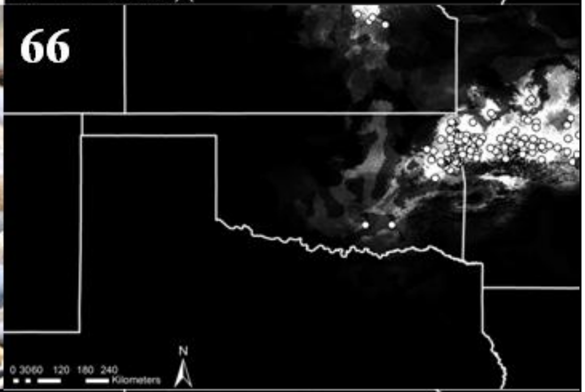

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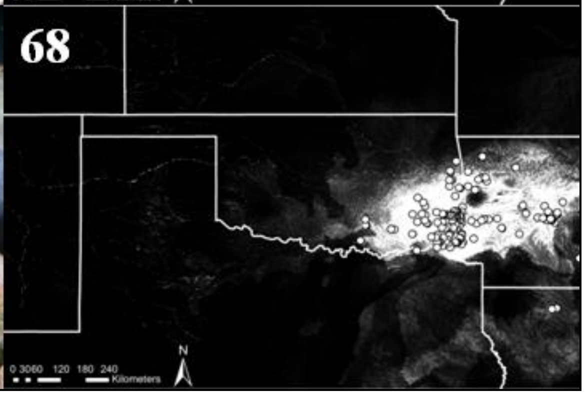


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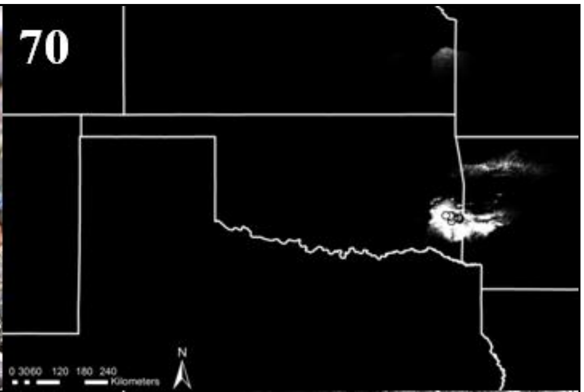
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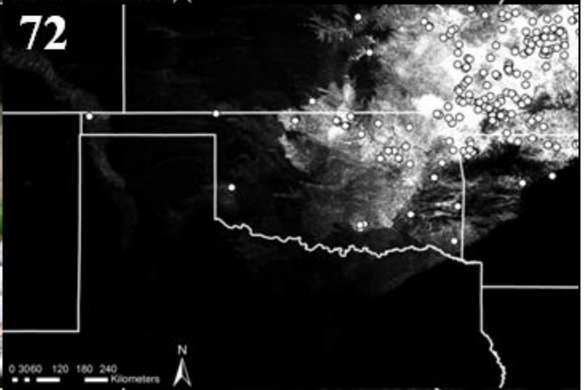
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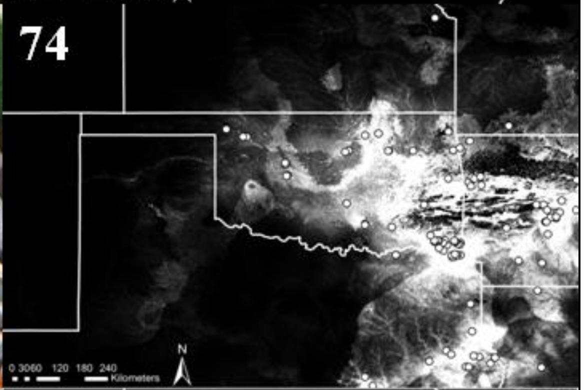
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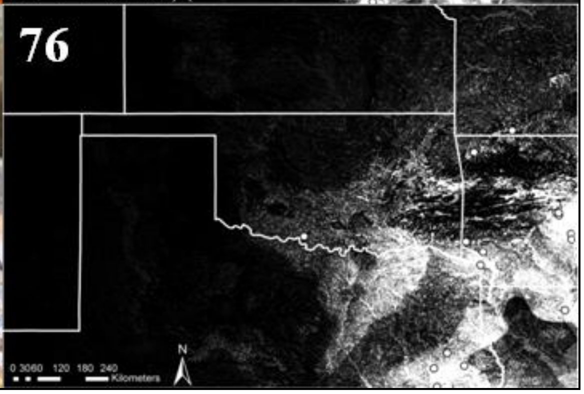
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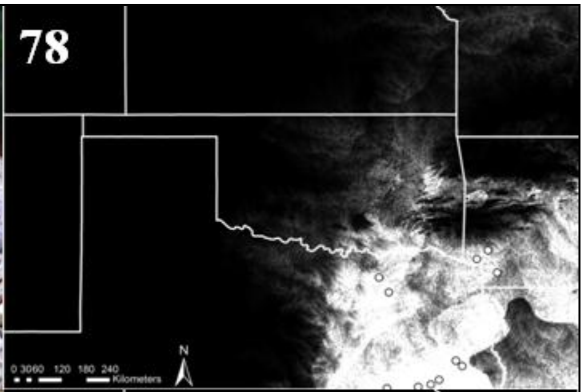
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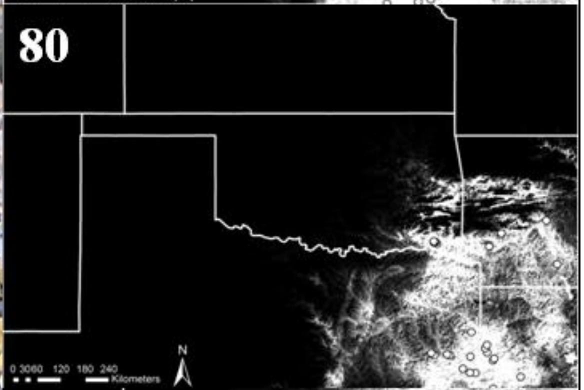
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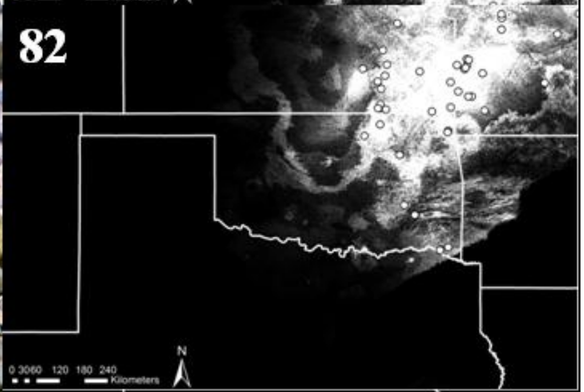
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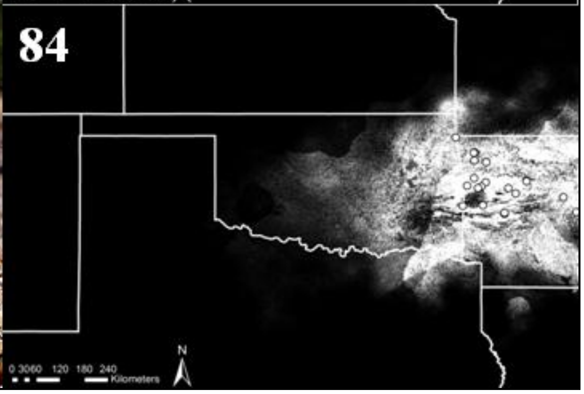
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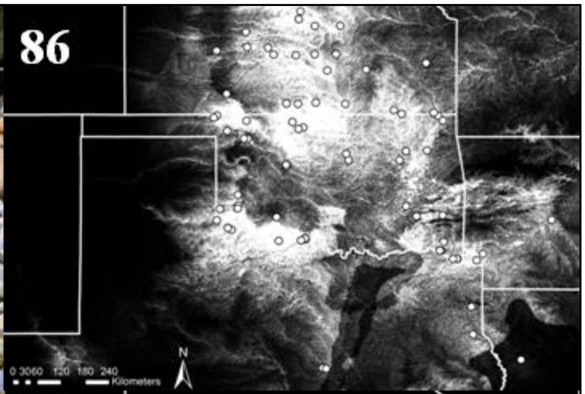

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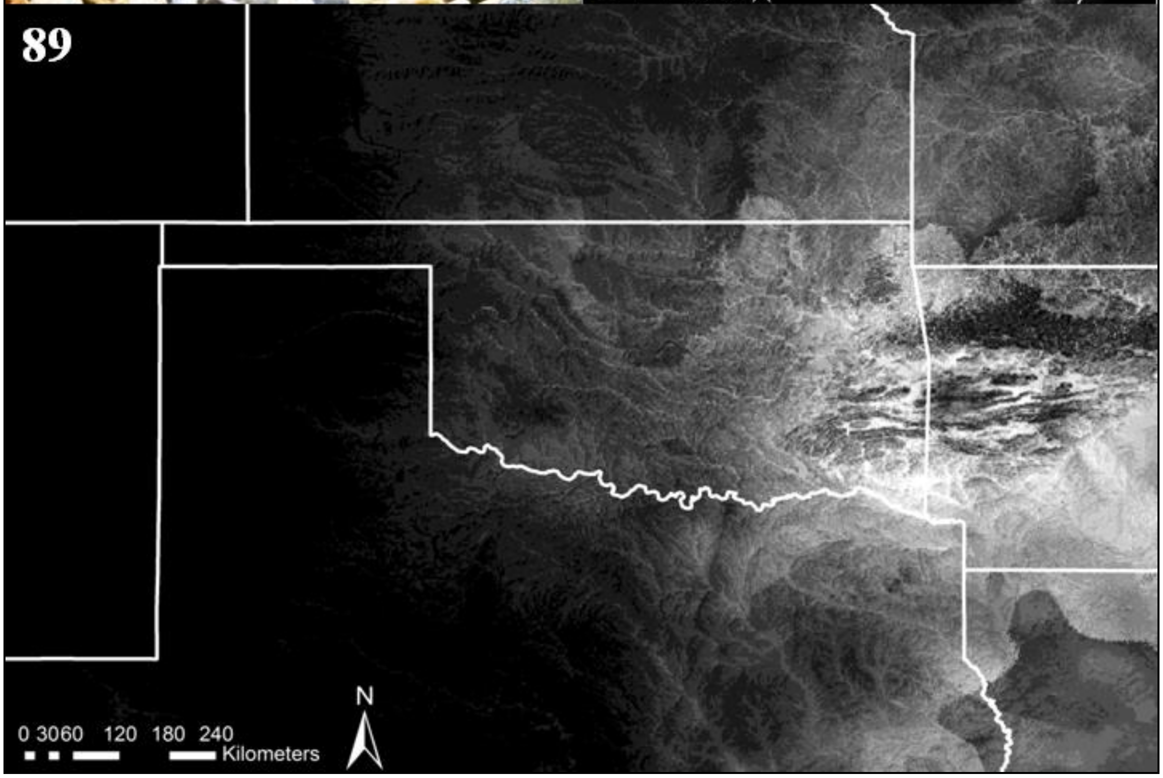

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Glossary

Acumen: The pointed extension of the rostrum.

Annulus ventralis: A raised pocket-like structure on the underside of a female crayfish used for sperm storage.

Antennal scale: Bladelike structure ending in a spine found at the base of each antennae.

Areola: Hourglass shape on the dorsal side of the carapace that is between the cervical groove and abdomen defined by a pair of shallow concave grooves.

Carapace: A hardened, unsegmented covering the anterior half of the body.

Caudal: Referring to the posterior end or further back than middle.

Caudal process: One of the terminal processes of the gonopod, usually found on species belonging to the genera *Cambarellus* and *Procambarus*.

Central process: One of the terminal processes of the gonopod and usually the longest.

Cervical groove: A shallow transverse groove separating the head from the rest of the carapace.

Chelae: Enlarged claw-like terminal end of the first walking leg. Also known as the pincher.

Coxae: First segment of the leg that attaches to the body of the crayfish.

Dactyl: Moveable finger of the chelae.

Distal: Referring to the areas away from the center or middle of appendage or body.

Dorsal: Referring to the "back side" of an organism or structure.

Fossa: A shallow depression on the ventral surface of the annulus ventralis in female crayfish.

Gonopod: Modified first pair of pleopods in male crayfish used to transfer sperm during copulation.

Ischium (Ischia): Third segment (counting from the base) of pereiopods.

Mesial: Referring to the middle or centerline of appendage or body.

Mesial process: One of the terminal processes of the gonopod, usually smaller than the central process.

Ovigerous: Stage during a female's reproductive cycle when they are carrying eggs attached to their abdomen.

Palm: Part of the chelae between the base of the dactyl to the base of the chelae.

Pentastyle: One of the terminal processes of the gonopod, mesial to the central process.

Pereiopod: Segmented walking leg of the crayfish. Crayfish have 5 pairs of pereiopods.

Pleopod: Segmented appendage found on the ventral side of the abdomen. They are also known as "swimmerets".

Rostrum: A triangular-shaped extension of the carapace located between the eyes.

Setae: Hair-like structures that may be present on the body and chelae of crayfish.

Sinus: Thin groove on the caudal half of the annulus ventralis.

Spine: A sharp extension frequently on the lateral surface of the carapace and rostrum.

Tubercle: A round knoblike structure commonly found on the chelae of some crayfish.

Ventral: Referring to the underside or bottom of an organism or structure.

CHAPTER III

IMPACTS OF CLIMATE CHANGE AND LAND COVER USE ON CRAYFISH DISTRIBUTIONS

Reid L. Morehouse

Abstract

1) Climate change has been occurring at exceptional rates in the past decades and has the potential to affect physical and biological aspects of the environments, thus impacting species both directly and indirectly. Recent studies examining crayfish distributions under different climate scenarios have provided contradicting results in terms of suitable habitat availability.

2) Here, we investigated how climate change would affect species distributions in crayfish with different ecologies (burrowing types). We employed ecological niche modeling to predict the current potential distribution of 28 crayfish species and their potential future distributions for the years 2030, 2050, and 2080 based on changes in bioclimatic variables for three climate-change scenarios. We also quantified current land cover at localities with confirmed crayfish occurrences to quantify the proportion of sites occurring in disturbed habitats and test whether there are differences among burrowing types.

3) Our results indicated that climate change has no significant negative effects on potential crayfish distributions (both for the area occupied and the location of the geographic centroid of distribution), and there was no difference in responses among burrowing types. Additionally, our results suggest that endemic species will increase their distributions disproportionately relative

to the wide spread species. However, our results also suggest land cover and use patterns have the potential to shape crayfish distributional patterns, particularly because many (and for some species most) historical sites with crayfish currently lie in disturbed areas.

4) Overall, our results show potential increases in crayfish species distributions under future climate change scenarios, but land cover and land use patterns likely play a larger role in shaping crayfish distributions, highlighting the importance of onsite conservation approaches to maintain populations of imperiled species.

Keywords: Climate Change, Crayfish, Decapoda, Ecological Niche Modeling, Land Cover

Introduction

Biodiversity plays important roles in maintaining ecosystem productivity, stability, sustainability, and other services that are critical for ecosystem function and human well-being (Grimm, Chapin, Bierwagen *et al.*, 2013, Grimm and Jacobs, 2013, Pereira, Navarro, and Martins, 2012, McNaughton, 1977, Pimm, 1984, Tilman, 1999). Loss of biodiversity has become a foremost concern in conservation biology, and major drivers include habitat destruction and degradation, eutrophication, pollution, over-exploitation, as well as the presence of invasive species (Cardinale, Duffy, Gonzalez *et al.*, 2012, Vittoz, Cherix, Gonseth *et al.*, 2013). Moreover, climate change has been hypothesized to be one of the most important factors affecting the suitability of environmental conditions for species persistence, potentially altering patterns of biodiversity at multiple spatial scales (IPCC, 2007, Li, Tian, Wang *et al.*, 2013, Araujo and Rahbek, 2006, Beaumont, Pitman, Poulsen *et al.*, 2007, Chen, Hill, Ohlemueller *et al.*, 2011).

Climate change has been occurring at exceptional rates in the past decades, largely due to the anthropogenically increased emission rates of CO_2 (IPCC, 2007). Global surface temperatures have increased by 0.50 - 0.75°C in the last two hundred years and – depending on CO_2 emission scenario – are predicted to increase by an additional 1.5 - 5.5°C by the year 2100 (IPCC, 2007).

Simultaneously, precipitation is estimated to increase by approximately 0.5 - 1.0% per decade in intermediate and high-latitude land areas, while more extreme precipitation events are predicted at lower latitudes in the northern hemisphere (IPCC, 2007). Accordingly, the predicted changes in temperature and precipitation patterns are expected to cause both unpredictable flooding and intense prolonged drought conditions throughout the United States (Backus, Lowry, and Warren, 2013, Strzepek, Yohe, Neumann *et al.*, 2010, Bates, Kundzewicz, Wu *et al.*, 2008), potentially causing unsuitable environmental conditions for the persistence of and affecting the distribution of many species (Easterling, Meehl, Parmesan *et al.*, 2000, Parmesan, 2001, Parmesan, 2006, Parmesan and Yohe, 2003, Walther, Post, Convey *et al.*, 2002).

Climate change has the potential to affect physical and biological aspects of the environments, thus affecting species both directly and indirectly (Vittoz *et al.*, 2013). In order to survive in changing environments and avoid extinction, species have to adapt through modifications of life cycles, changing behaviors, or shifting their habitat use and distributions (Bellard, Bertelsmeier, Leadley *et al.*, 2012, Mantyka-Pringle, Martin, and Rhodes, 2012, Parmesan and Yohe, 2003). A number of studies have already documented that species have changed the timing of life cycle events in response to variation in annual temperature (Rosenzweig, Karoly, Vicarelli *et al.*, 2008, Thackeray, Sparks, Frederiksen *et al.*, 2010), undergone shifts in their ranges toward higher latitudes and elevations (Parmesan and Yohe, 2003, Thomas, 2010), and reduced body sizes (Cheung, Sarmiento, Dunne *et al.*, 2012, Caruso, Sears, Adams *et al.*, 2014). Despite the ability of some species to cope with consequences of climate change, others are becoming extinct at alarming rates. For example, Thomas, Cameron, Green *et al.* (2004) estimated that by the year 2050, 15 - 37% of the world's species are destined to extinction as a direct result of climate change, and estimates increase to approximately 40% when only endemic species with narrow distributions are considered (Malcolm, Liu, Neilson *et al.*, 2006).

Freshwater organisms are particularly susceptible to environmental change, as they are more imperiled than their marine or terrestrial counterparts due to relatively small natural ranges constrained by watershed boundaries (Strayer and Dudgeon, 2010). Along with freshwater mussels, crayfish are one of the most imperiled taxa in North America, with approximately 50% of known species being of conservation concern (e.g., imperiled, threatened, or endangered status; Taylor, Schuster, Cooper *et al.*, 2007). Crayfish are ecologically diverse and inhabit a wide variety of habitats including streams, rivers, lakes, reservoirs, swamps, roadside ditches, wet pastures, and fields (Bouchard, 1978). They play important roles in ecosystem functioning, can comprise the majority of invertebrate biomass (Momot, Gowing, and Jones, 1978, Rabeni, Gossett, and McClendon, 1995, Parkyn, Collier, and Hicks, 2001), and are keystone species that act as ecosystem engineers (Schofield, Pringle, Meyer *et al.*, 2001, Taylor and Soucek, 2010, Whitledge and Rabeni, 1997). Currently, there are over 400 recognized species of crayfish in North America with the majority distributed east of the Rocky Mountains (Taylor *et al.*, 2007, Hobbs, 1989). They can be categorized into three broad ecological groups (burrowing types) based on their burrowing behavior (Hobbs, 1981): (1) Primary burrowers dig vertically into the ground to reach the water table below, allowing them to inhabit areas with semi-permanent water sources, such as road side ditches, ephemeral wetlands, and wet fields/prairies. They create complex and elaborate burrows reaching one to three meters deep with multiple tunnels, shafts, and surface openings. Primary burrowers spend the majority of their lives within the burrow, except to forage and mate, which usually occurs on wet and warm humid nights in the spring and fall. (2) Secondary burrowers tend to have less complex and elaborate burrows than primary burrowing crayfish, usually only constructing one vertical burrow down to the water table and another tunnel connecting the burrow directly to a permanent water source (e.g., ponds or streams). Secondary burrowers spend a large portion of their lives within the burrow, but frequently visit permanent water sources. (3) Tertiary burrowers inhabit permanent water sources such as ponds, lakes, rivers, and streams. They will retreat under logs and large rocks in simple, pocket-like burrows during drought conditions or when females are carrying eggs.

Crayfish are particularly threatened because of loss or degradation of suitable habitats and the introduction of nonindigenous species, which is often exacerbated by narrow distributional ranges and high levels of endemism (Larson and Olden, 2011, Taylor *et al.*, 2007, Welsh, Loughman, and Simon, 2010, Lodge, Taylor, Holdich *et al.*, 2000). In contrast, it remains relatively unknown whether and how climate change may impact crayfish biology and species distributions. A recent study suggested unfavorable future outcomes for native species in Europe where suitable climate conditions were predicted to decrease between 19% and 72%, and the majority of future suitable areas were geographically inaccessible (Capinha, Larson, Tricarico *et al.*, 2013). Additionally, Capinha, Anastacio, and Tenedorio (2012) showed similar results for invasive crayfish species in Europe, with an overall decline in environmental suitability under future climatic conditions. However, some of these models also identified high levels of predictive uncertainty for some species, as they did not accurately predict current species distributions. A study on endemic crayfish of the Ouachita Mountains, USA, predicted decreases in distributional ranges for three out of four species examined under a low-emission scenario and decreases in range for two out of four species under moderate-to-high emission scenarios (Dyer, Brewer, Worthington *et al.*, 2013). A common theme from all of these studies is that they all used relatively broad spatial resolutions, ranging from 4.5 km^2 to 50 km^2, and all of the crayfish studied were stream-dwelling (i.e., tertiary burrowers).

In this study we examined the potential future distributional ranges for 28 crayfish species of the family Cambaridae that occur in Oklahoma and adjacent states, USA, under three different emission scenarios at a 1 km^2 spatial resolution. These species encompass members of all burrowing types, multiple genera, and species with broad as well as highly endemic distributions. Detailed analyses of current distributions have already been conducted at a 1 km^2 spatial resolution (see Morehouse and Tobler, 2013). We were particularly interested in testing whether and how species of different burrowing types differed in future distributional trends in response to direct and indirect effects of climate change and in response to human habitat alteration. Specifically, we posed the following questions: (1) Do different climatic variables shape the distributions of the three burrowing types? We used ecological niche modeling to determine which climatic variables best predicted the occurrence of individual crayfish species. As different burrowing types vary in their ecologies and habitat requirements, we tested how bioclimatic variables varied in their importance in predicting current species distribution, which could have implications for climate change responses. We predicted that distribution models for primary and secondary burrowers are more associated with minimum precipitation (ephemeral habitats in which these species typically occur in rely on rain water for persistence), and that maximum temperatures would affect the occurrence of stream dwellers disproportionally, as some streams in our study area can be relatively cool, mountainous, and spring-fed. (2) How are the distributional ranges of the different burrowing types affected by climate change? We used ecological niche modeling in conjunction with projections of future climate conditions to assess several metrics quantifying changes in species distributions and contrast effects for different burrowing types. As temperature and precipitation regimes change, we predicted shifts in distributional ranges and contractions of suitable environmental conditions. (3) Are there differences in land cover use among burrowing types that can shed insight into future distributional trends and conservation priorities? Habitat destruction and degradation are known factors negatively impacting crayfish populations (Taylor *et al.*, 2007). Hence, we assessed current land cover at localities with confirmed crayfish occurrences to quantify what proportion of sites occur in disturbed habitats and test whether there are differences among burrowing types. We predicted that primary and secondary burrowers are disproportionally affected by anthropogenic impacts, because ephemeral wetlands are frequently transformed into agricultural land and open fields are used for economic development.

Methods

Occurrence data, current and future climatic layers, and ecological niche modeling

Current occurrence data for 28 crayfish species occurring in Oklahoma and surrounding states were taken from Morehouse and Tobler (2013; see Figure 1). All occurrence points included latitude and longitude of the sampling site based on information from field sampling by the authors, reviews of the primary literature, and mining of databases of major crayfish collections (see Morehouse and Tobler, 2013 for detailed methods regarding species occurrences). Occurrence points were considered, if they were located in the state of Oklahoma or within a 200 km perimeter around the state in each cardinal direction.

GIS-based climatic layers including minimum and maximum temperature and precipitation averages from 1950 - 2000 (hereafter "current") were obtained from the data portal of the Research Program on Climate Change, Agriculture and Food Security of the Consultative Group on International Agriculture Research (Jones, Thornton, and Heinke, 2009). To investigate the potential distributions of crayfish under different climate-change scenarios, we downloaded the predicted climate data for the time periods of 2021 - 2040 (hereafter 2030), 2041 - 2060 (hereafter 2050), and 2071 - 2090 (hereafter 2080) down-scaled from MICRO 3.2 General Circulation Model (GCM), which represents one of the GCMs used in the Fourth Assessment Report of the Intergovernmental Panel on Climate Change (IPCC) (Solomon, Qin, Manning *et al.*, 2007). We used the A1B, A2, and B1 emission scenarios included in the IPCC Special Report on Emission Scenarios. The A1B scenario represents current trends in which human energy use continues to increase (with a balance between fossil and non-fossil fuel sources), but CO_2 emissions are stabilized to some extent by technological advances and public awareness. An estimated CO_2 concentration of 850 ppm and temperature increase of 2.8 °C was used. The A2 scenario focuses on regional economic development and slower changes towards technological advances relative to other scenarios. It is characterized by an increase of CO_2 concentrations to 1250 ppm and of temperature by 3.4 °C in 2100. In the B1 scenario, human population growth declines around 2050 and the focus is on environmental protection and social equity. Cleaner technology is implemented, and CO_2 concentrations increase to 600 ppm and temperature rises by 1.8 °C, the lowest increases of any scenario (IPCC, 2007). Hence, the degree of predicted climate change varies between scenarios, with B1 < A1B < A2.

Current and future temperature and precipitation variables were used to calculate 19 "bioclimatic" variables for current, 2030, 2050, and 2080 periods representing quarterly and monthly climate seasonality and extremes (Hijmans, Cameron, Parra *et al.*, 2005). Bioclimatic variables were generated in ArcInfo using available AML code (http://www.worldclim.org/bioclim). All environmental variable layers had a 1 km^2 resolution and were masked to the extent of our study area. Reducing the number of variables to those considered ecologically relevant and non-redundant (some environmental variables can be highly correlated) decreases the potential for model over-fitting (Warren and Seifert, 2011), and facilitates interpretation of results (Elith, Phillips, Hastie *et al.*, 2011). Hence, we used the principal components tool in the ArcGIS v.10.0 Spatial Analyst extension to assemble a correlation matrix for the 19 variables across our spatial extent of analysis. We retained only a single variable for variables that were correlated at $r^2 > 0.9$, preferentially choosing variables that measured extremes over those measuring averages (Shepard and Burbrink, 2008). Environmental extremes are more likely to set range limits of organisms due to physiological constraints (Kozak and Wiens, 2006). After the principal components analysis, 14 bioclimatic variables remained for the use in the models.

To create current and potential future distributions of all crayfish species in Oklahoma, we used the maximum entropy ecological niche modeling method (Maxent; Phillips, Anderson, and Schapire, 2006), which has been found to produce the most conservative predictions compared to other methods with regard to model over-fitting (Elith, Graham, Anderson *et al.*, 2006). Maxent estimates the probability distribution for a species' occurrence based on environmental constraints (Phillips *et al.*, 2006). The environmental constraints are derived from environmental variables inputted into the model and a species' known occurrence points. Maxent requires only species presence data and continuous or categorical environmental variables layers for a given study area. We used Maxent software (version 3.3.3e; http://www.cs.princeton.edu/~schapire/maxent/), which produces a probability estimate of species presence that varies from 0 to 1. Since most of the species examined had large data sets, we used the random seed and test percentage option in Maxent to randomly split the occurrence points into training (80% of the data points) and testing (20% of the data points) data sets. We applied a "jackknife" procedure to all of the environmental layers to determine individual percentage of contribution to the model's overall accuracy gain for each species. For each species, we chose only the variables that contributed more than 5% to the model to refine our predictions in the final models. The models generated using the subset of environmental variables were projected onto the 2030, 2050, and 2080 environmental datasets for each of the three climate scenarios, resulting in nine predictions for each species (three time periods and three emission scenarios). Predicting species' distributions using projections of ecological niche models on future datasets can provide insights to possible changes in species distributions (Pearson and Dawson, 2003, Araujo, Pearson, Thuiller *et al.*, 2005), whether they are expansions or contractions (see Bradley, Wilcove, and Oppenheimer, 2010, Saupe, Papes, Selden *et al.*, 2011, Dyer *et al.*, 2013).

Validation is necessary to assess the predictive performance of each distribution model, and we used receiver operating characteristic (ROC) analysis (Peterson, Papes, and Soberon, 2008), which plots sensitivity (*y*-axis, lack of omission error) against 1-specificity (*x*-axis, commission error). Omission error is defined as known presences that are predicted absent and commission error as locations predicted suitable for which no presences are known. The area under the ROC curve (AUC), which is an indicator of model prediction accuracy, was calculated. The AUC ranges from 0.5 (random assignment of presences and absences) to a maximum value of 1.0 (perfect discrimination of presences and absences). The analysis was run for both the training dataset and the testing dataset to assess the average performance of the resulting models with a fixed threshold of 0.10 (10% omission error), which rejects the lowest 10% of possible predicted values. This method assigns pixels with a probability of presence value less than the lowest value corresponding to 10% of the training points a value of zero and pixels with a probability of presence above this value are given a value of one. The usefulness of this validation method has recently been scrutinized (Peterson *et al.*, 2008, Jimenez-Valverde, 2012), and a simplified but possibly clearer assessment is provided by the omission error alone (Lee, Papes, and Van Den Bussche, 2012). We ran the AUC analyses for all of our models, present and future.

Climatic variables shaping current distributions of different burrowing types

To determine if burrowing types differed in climatic variables shaping their distributions, we took the top six (three temperature and three precipitation) climatic variables that contributed the most to the distribution models for all species. We used the percent contribution of each climatic variable (arc-sine square-root transformed) as dependent variables in analyses of covariance (ANCOVA) to test for differences in climatic variable contribution between the burrowing types with the current distributional area (square pixels, log-transformed) as our covariate.

Distributional changes in response to climate change

We assessed potential distributional expansions or contractions as well as geographic shifts in distributions by using several metrics based on current and predicted distributions (see Figure 2 for a graphical illustration of all metrics). (1) To test for potential changes in distributional area, we quantified the total area predicted present for each species in square pixels using the "measuring geographic distributions" toolset in ArcGIS10 for all scenarios and across all four time periods examined. To test for changes in absolute and relative distributional area among burrowing types, we used a repeated measures analysis of covariance (RM-ANCOVA) with distributional area for each time period as dependent variables, time period, scenario, and burrowing type as fixed factors, and area occupied currently (square pixels, log-transformed) as a covariate. This analysis allowed us to test whether species' ranges increase or decrease in response to different climate change scenarios, whether patterns vary between burrowing types, and depending on present distributional area (i.e., highly endemic species are predicted to be affected more than widespread ones).

(2) To test for potential distributional shifts, we calculated the geographic centroid of each species' current and predicted future distributions along with the standard distance with the "measuring geographic distributions" toolset listed above. Standard distance is a measure of the degree to which the predicted presence pixels are concentrated or dispersed around the geographic centroid. For each scenario, we calculated the Euclidean distances between the centroids of the current and the predicted distributions at each year (absolute centroid movement) as well as the Euclidean distances between each time period (i.e., current - 2030, 2030 - 2050, 2050 – 2080; relative centroid movement). Euclidean distances were then divided by the standard distance to standardize centroid movement in relation to the dispersion of currently predicted occurrence points around the centroid. Distributional shifts can be considered significant when relative centroid movement greater than 1, indicating that the center of distribution has moved beyond one standard distance of the current distribution. To test for differences in absolute and relative centroid movement among groups, we used a RM-ANCOVA with centroid movement for each time period as dependent variables, time period, scenario, and burrowing type as fixed factors, and area occupied currently (square pixels, log-transformed) as a covariate.

Land cover at known crayfish locations

Land cover analysis was conducted using ArcGIS10 using the 2006 land cover data layer downloaded at a 1 km^2 spatial resolution from the National Land Cover Database (NLCD; Fry, Xian, Jin *et al.*, 2011). We used the "extract values to points" function, which assembles the land use type (e.g., developed, disturbed, wetlands, pasture/hay, mixed forest) for each actual location point of crayfish collected. We then calculated the percent of occurrence points that land cover types classified as developed or disturbed relative to the remaining categories. Following the classification scheme of the NLCD for 2006, “developed or disturbed" land covers included developed, barren land, and cultivated crop categories. As a result from combining all "developed" categories into one, our final classification scheme had three categories that fell under the "developed/disturbed" category and seven other categories, including open water, deciduous forest, evergreen forest, mixed forest, shrub, grassland, pasture/hay, and wetlands, that were considered “natural”. To test for differences in the percent of occurrence points located in developed or disturbed areas among burrowing types, we ran an ANCOVA on arc-sine square root transformed land cover percentages and area occupied currently (square pixels, log-transformed) as a covariate.

Results

Climatic variables shaping current distributions of different burrowing types

The top six climatic variables contributing the most to the distributional models of at least two out of the three burrowing types were precipitation of the driest month, mean temperature of the driest quarter, precipitation seasonality, mean temperature of the wettest quarter, temperature seasonality, and precipitation of the wettest month (Figure 3). The contribution of precipitation of the driest month to predicting current species range was significantly different between burrowing types ($F_{2,3} = 4.118$; $P = 0.028$). Precipitation during the driest month contributed 37%, 45%, and 19% for primary, secondary, and tertiary burrowers, respectively. None of the other climatic variables varied significantly among the burrowing types (Table 1). Percent contributions of all variables for all species are available in the Supplementary Table 1.

Distributional changes in response to climate change

Our baseline "current" (Supplementary Table 2) and "future" (Supplementary Table 3) models accurately predicted the current distributions of crayfish species based on test AUC values being above 0.75 (random prediction AUC = 0.50) for all species. The sole exception was *Orconectes deanae*, which had an AUC value of 0.63. Absolute distributional areas did not change significantly across time periods ($F_{1,74} = 0.352$, $P = 0.555$; Figure 4). In addition, changes in absolute distributional areas were not different among burrowing types, climate-change scenarios, and species with varying current distribution sizes ($F \leq 2.273$, $P \geq 0.110$). In contrast, there was a significant change in relative distributional area covered across time periods ($F_{1,74} = 10.704$, $P = 0.002$), but contrary to expectations areas tended to increase over time (Figure 4). This change in relative distributional area across time periods was dependent on the current distributional area of species ($F_{1,74} = 7.514$, $P = 0.008$), with species having a smaller current distributional ranges experiencing disproportional expansions in relative area occupied in the future. There were no statistical differences among burrowing types and emission scenarios in relative distributional areas ($F \leq 0.473$, $P \geq 0.625$).

All geographic centroid movements were substantially below 1 (range: 0.013 - 0.783), indicating that species distributional shifts were small relative to the standard distance. The absolute geographic centroid movement for species distribution was significantly dependent on the emission scenario ($F_{4,146} = 3.129$, $P = 0.017$), with centroid shifts being evident in the 2050 time period for the A1B scenario and in the 2030 and 2080 timer periods of the A2 and B1 scenarios (Figure 5). There were no significant differences among burrowing types and no effect of the current distributional area of species ($F \leq 1.480$, $P \geq 0.210$). Relative geographic centroid movement (between years) did not vary significantly across years, burrowing types, emission scenarios, and the areas of current distribution ($F \leq 2.550$, $P \geq 0.085$).

Land cover at known crayfish locations

Twenty-five percent of all crayfish species in this study had 50% of their occurrence points classified as developed/disturbed. Furthermore, 82% of all species had at least 25% of their occurrence points classified as developed/disturbed. We found no significant differences in developed/disturbed land cover among the burrowing types ($F_{2,27} = 1.978$; $P = 0.160$) or effects of endemism (area predicted present in the current models) ($F_{2,27} = 0.685$; $P = 0.416$). All primary and secondary burrowers had more than 25% of their occurrences classified as developed/disturbed (Table 2). In tertiary burrowers, 74% of all species were classified above 25% developed/disturbed, and 21% had more than 50% of their occurrence points in the developed/disturbed category.

Discussion

Given the predicted changes in temperature and precipitation patterns globally (IPCC, 2007), it is pivotal to understand potential impacts of climate change on already imperiled species and estimate whether and how species' ecologies could affect long term distributional outcomes. We investigated potential effects of climate change in 28 species of crayfish belonging to three burrowing types with different ecological requirements in the central United States. Our analyses indicated that distributions of the three burrowing types are shaped by different bioclimatic variables. However, predicted distributions of crayfish under different climate-change scenarios neither indicated significant reductions in distributional area, nor major distributional shifts. Instead, and contrary to our predictions, the results actually suggest a trend of range expansion that was disproportionally large for species with currently narrow distributional areas. Consequently, climate change – at least in context of the variables considered here – may play a comparatively small role in the conservation biology of the crayfish species in Oklahoma. However, analysis of land use patterns suggests that a significant proportion of known collection localities lie in disturbed environments, confirming previous research postulating that habitat destruction is a major driver in reducing crayfish occurrences and abundances (Taylor *et al.*, 2007).

Climatic variables shaping current distributions of different burrowing types

Although crayfish species used in this study exhibit varying levels of burrowing behavior and accordingly have very different ecological requirements (Morehouse and Tobler, 2013), there was overall a high degree of similarity in the bioclimatic variables that substantially contributed to the distribution models of species classified as different burrowing types. However, the relative proportion each variable contributed to the models varied significantly between burrowing types. Specifically, precipitation during the driest month was a more important predictor for primary and secondary burrowers than tertiary burrowers that typically inhabit permanent stream environments. Adequate amounts of precipitation in the driest month is likely requisite for the persistence of ephemeral wetlands inhabited by primary and secondary burrowers and for the maintenance of ground water at levels that can be reached during burrowing activities to avoid desiccation. Our results raise interesting questions about physiological differences between burrowing types, and future studies should quantify desiccation tolerances in species with different ecologies.

Contrary to our predictions, temperature related variables did not significantly vary in their model contributions among the three burrowing types. This is likely due to the behavioral mechanisms crayfish have evolved to persist in environments not directly connected to a permanent water source. As ectotherms are unable to thermoregulate physiologically without large costs energetically (Bicego, Barros, and Branco, 2007), behavioral mechanisms are used to regulate body temperature (Eshky, Atkinson, and Taylor, 1995, McGaw, 2003). Behavioral thermoregulation has been observed in crayfish within burrows when temperatures approached their thermal maxima (Payette and McGaw, 2003). To avoid overheating, crayfish submerge themselves in water at the bottom of the burrow and then move back into air, regulating their body temperatures through evaporative cooling (Payette and McGaw, 2003). Hence, access to adequate water supply likely is more critical in the persistence of species than temperature per se.

Distributional changes in response to climate change

Our results suggest that the distributional ranges of crayfish in Oklahoma, regardless of burrowing type, are not negatively impacted by climate change under the three different emission scenarios considered. This pertains both to the areas covered and potential distributional shifts (i.e., movement of geographic centroids in relating to standard distance). Our models actually indicated that the majority of the species would in fact increase the area of their distributional range slightly in all scenarios. Consequently, our results contradict recent studies on other crayfish species that have suggested significant reductions in species distributional ranges and suitable habitat at broader spatial resolutions, ranging from 4.5 km^2 to 50 km^2 (Capinha *et al.*, 2012, Capinha *et al.*, 2013, Dyer *et al.*, 2013). These discrepancies could be caused by a number of factors: (1) Potential effects of climate change could vary substantially among species and/or the geographic regions examined. In this case, variation in long-term distributional trends uncovered by different studies would actually be biologically relevant, prevent researchers and conservation managers to extrapolate the findings in one species to other closely related ones, and preclude broad scale geographic and taxonomic generalizations. (2) The different results could be a consequence of different modeling methods, input variables, as well as spatial scales and resolutions used to predict future potential distributional ranges. We used a relatively conservative method at a fine spatial resolution (1 km^2) by taking the 10% threshold training values from our models and applying that value as our lowest predicted presence value, which is widely accepted and used by others (e.g., Capinha *et al.*, 2013, Pearson, Raxworthy, Nakamura *et al.*, 2007). Although this approach yielded in well-performing models based on AUC values in this and other studies, even slight differences in modeling algorithms, spatial resolutions, and climate variables included can ultimately produce different results (Rahbek, 2005). For example, some of the species used in our study (*Orconectes leptogonopodus, O. menae, O. saxatilis,* and *Procambarus tenuis*) correspond with the species used in Dyer *et al.* (2013). While their results suggested some severe reductions of suitable environmental conditions for three of the species, our results suggest slight increases or no significant changes in their distributional ranges.

Ultimately, Ecological Niche Modeling is starting point to predict future species distributions under the threat of climate change, but this approach also has limitations (Elith and Leathwick, 2009, Pearman, Guisan, Broennimann *et al.*, 2008). First and foremost, all niche based models are correlative, and they do not take into account genetic and plastic variation in organismal traits (including physiological tolerances and behavioral traits that allow for coping with environmental stressors), biotic interactions, or dispersal abilities, all of which could be critically involved in population level responses to environmental change (Kearney and Porter, 2009, Davis, Jenkinson, Lawton *et al.*, 1998, Dormann, 2007). The unanticipated low impact of climate change on crayfish projected by our analyses may be due to the fact that they already inhabit and have adapted to a broad range of environmental conditions available in the study region. Crayfish burrowing behavior may effectively allow individuals to create microenvironments with suitable conditions; even when surface temperature and precipitation conditions vary or change.

Although the lack of significant distributional changes uncovered in this study was unanticipated, it is not unprecedented. In a recent study, Collen, Whitton, Dyer *et al.* (2014) examined the global patterns of and threats to freshwater species diversity. Of the multiple mechanisms that cause species diversity declines, three disproportionally impacted freshwater species: habitat loss/degradation, water pollution, and over-exploitation. Furthermore, Collen *et al.* (2014) suggested that climate change only accounted for approximately 10% of the declines in threatened species, although the authors highlighted the lack of strong distributional data particularly of under-studied taxa (such as crayfish) and the need for studies on a regional level. Nonetheless, the results of our study at a regional scale largely coincide with their conclusion that habitat loss/degradation likely contributes more to distributional changes of crayfish than climate change.

Land cover at known crayfish locations

The greatest threats to crayfish biodiversity have been hypothesized to be linked to habitat destruction/degradation, pollutants, and invasive species (Larson and Olden, 2011, Taylor *et al.*, 2007, Welsh *et al.*, 2010). Our study confirms this notion in that the percentage of known crayfish collection localities that are categorized as developed/disturbed exceeds 30% for 21 species and even 50% for 7 species (out of a total of 28). The land use/cover changes predicted in the future under the same emission scenarios used in this study suggest that both the conversion of land into agriculture and the development of economies will continue to increase (Sleeter, Sohl, Bouchard *et al.*, 2012), suggesting that habitat destruction and degradation will accelerate and further affect the species' distributions in our study region. Matthews and Zimmerman (1990) as well as Strayer and Dudgeon (2010) both stated that human population growth and economic development in the central United States imposed a major constraint on species distributional expansions, as species are unable to migrate through large areas of unsuitable habitat, and this is especially alarming for endemic and rare species (Stranko, Gresens, Klauda *et al.*, 2010). Furthermore, threats to biodiversity in aquatic environments and their crayfish inhabitants are exacerbated by alterations of flow regimes through construction of dams and reservoirs, water removal, and channelization, as well as increasing levels of organic and inorganic pollutants (Strayer and Dudgeon, 2010, Vorosmarty, McIntyre, Gessner *et al.*, 2010). Within Oklahoma, water conservation, pollutants, and changes in flow regime have negatively impacted freshwater mussel species richness and abundances in the past decade (Allen, Galbraith, Vaughn *et al.*, 2013).

Conclusions

Our results suggest that climate change may not negatively impact crayfish distributions within our study region, but development of natural areas causing changes in land cover (e.g., habitat destruction/degradation) is likely a greater concern for the conservation of crayfish and demands more attention. As more predictions of potential species distribution under climate change are produced, it is important to combine information from multiple sources to enhance decision making processes during the implementation of conservation measures, including the establishment of refuge areas, the identification of biodiversity hotspots, and the preservation of buffer areas (i.e., riparian zones) around habitats that contain endemic or rare species. Additionally, as crayfish exhibit varying levels of burrowing behavior, the actual microclimate they encounter is likely different than the predicted climate in our models. Therefore it is important to integrate and combine correlative niche modeling with more mechanistic models that take into account empirical data on microclimate variation within crayfish burrows as well as the physiological tolerance limits of different species to produce more biologically precise predictions.

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Table 1: Results of the analyses of covariance (ANCOVA) comparing the contribution of the top six climatic variables on the predicted distribution among the three burrowing types of crayfish. Bold indicates statistically significant results; $P < 0.05$.

Climate variable	***df***	***F***	***P*-value**
Precipitation of the driest month	2,27	4.118	**0.028**
Mean temperature of the driest quarter	2,27	0.914	0.414
Precipitation of the wettest quarter	2,27	0.101	0.905
Precipitation seasonality	2,27	0.348	0.709
Mean temperature of the wettest quarter	2,27	0.299	0.744
Temperature seasonality	2,27	0.130	0.878

Table 2: Total number of occurrence points and percent of developed/disturbed land cover associated with known crayfish occurrence locations in our study region.

Crayfish Species	Number of occurrence points	% Developed/Disturbed
Primary Burrowers		
Cambarus diogenes	28	54
Cambarus ludovicianus	23	49
Fallicambarus fodiens	19	84
Procambarus gracilis	41	42
Procambarus liberorum	20	40
Secondary Burrowers		
Procambarus acutus	99	39
Procambarus clarkii	18	39
Procambarus curdi	11	36
Procambarus simulans	80	60
Tertiary Burrowers		
Cambarellus puer	12	67
Faxonella blairi	17	24
Faxonella clypeata	20	70
Orconectes causeyi	36	56
Orconectes deanae	9	44
Orconectes difficilis	16	38
Orconectes lancifer	5	60
Orconectes leptogonopodus	29	17
Orconectes macrus	45	12
Orconectes meeki brevis	41	30
Orconectes menae	40	28
Orconectes nais	92	43
Orconectes nana	62	21
Orconectes neglectus neglectus	202	30
Orconectes palmeri longimanus	262	37
Orconectes saxatilis	89	16
Orconectes virilis	219	25
Procambarus dupratzi	26	39
Procambarus tenuis	36	39

Figure 1. Occurrence points for all crayfish used within this study and extent of study area used for all ecological niche modeling analyses.

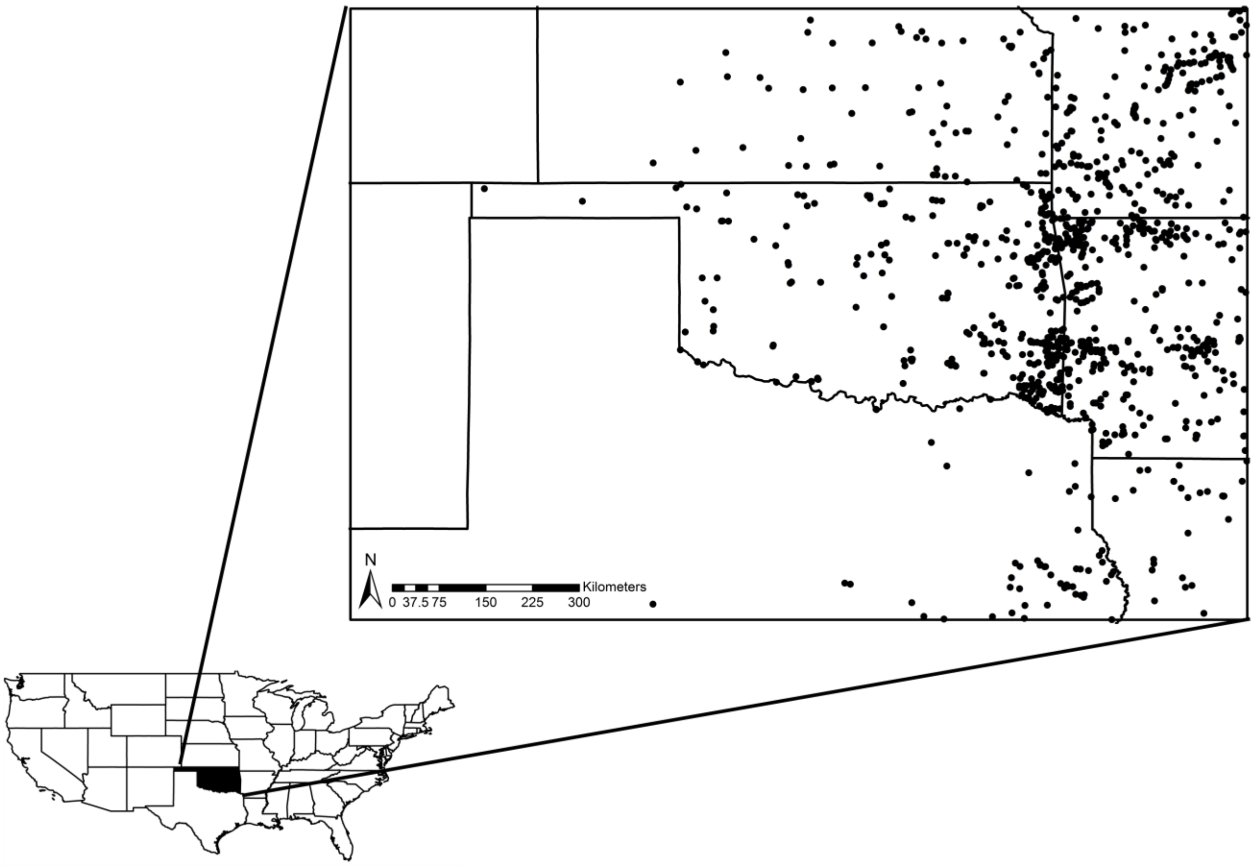


Figure 2. Diagram depicting the metrics used for analysis of distributional shifts due to climate change. Squares represent 1 km^2 of potential distributional area. Dark grey shaded squares depict the predicted area inhabited by a hypothetical species in one time period, medium grey represents the predicted area inhabited for the same species in the future year, and the light grey represents quadrants where the species is predicted present in both time periods. For our analyses, total area present was estimated by counting the number of pixels predicted inhabited. Relative area is the total area present under a future scenario and year divided by the total area present in the current model for a species. Black dots represent the geographic centroid for the present (C1) and future (C2) model prediction. Black circles with radius R around the centroids represent the standard distance for each distribution, which is a measure of the degree of concentration or dispersion of predicted occurrences around the geographic centroid. Finally, the black arrow (D) represents the Euclidean distance between the geographic centroids, providing a quantitative measure of shifts in the center of distribution across time periods.

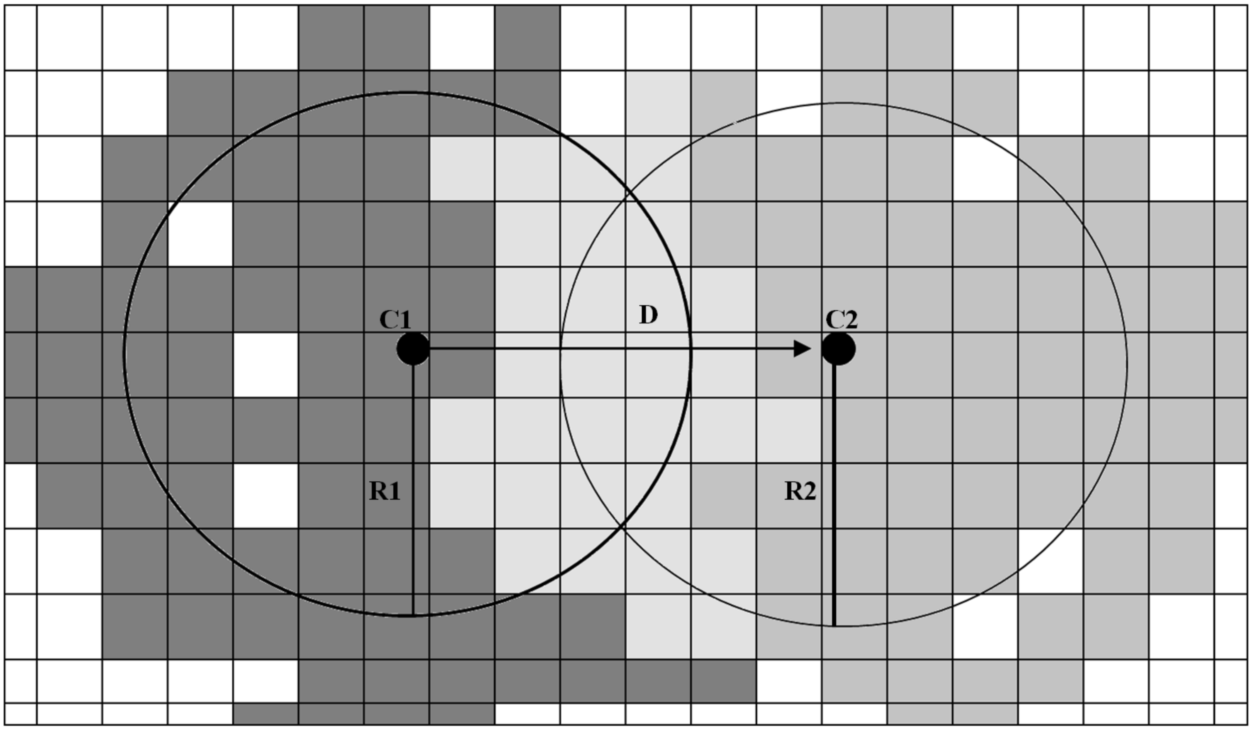


Figure 3. Percent contribution of the top six climatic variables to the crayfish distribution models categorized by burrowing type.

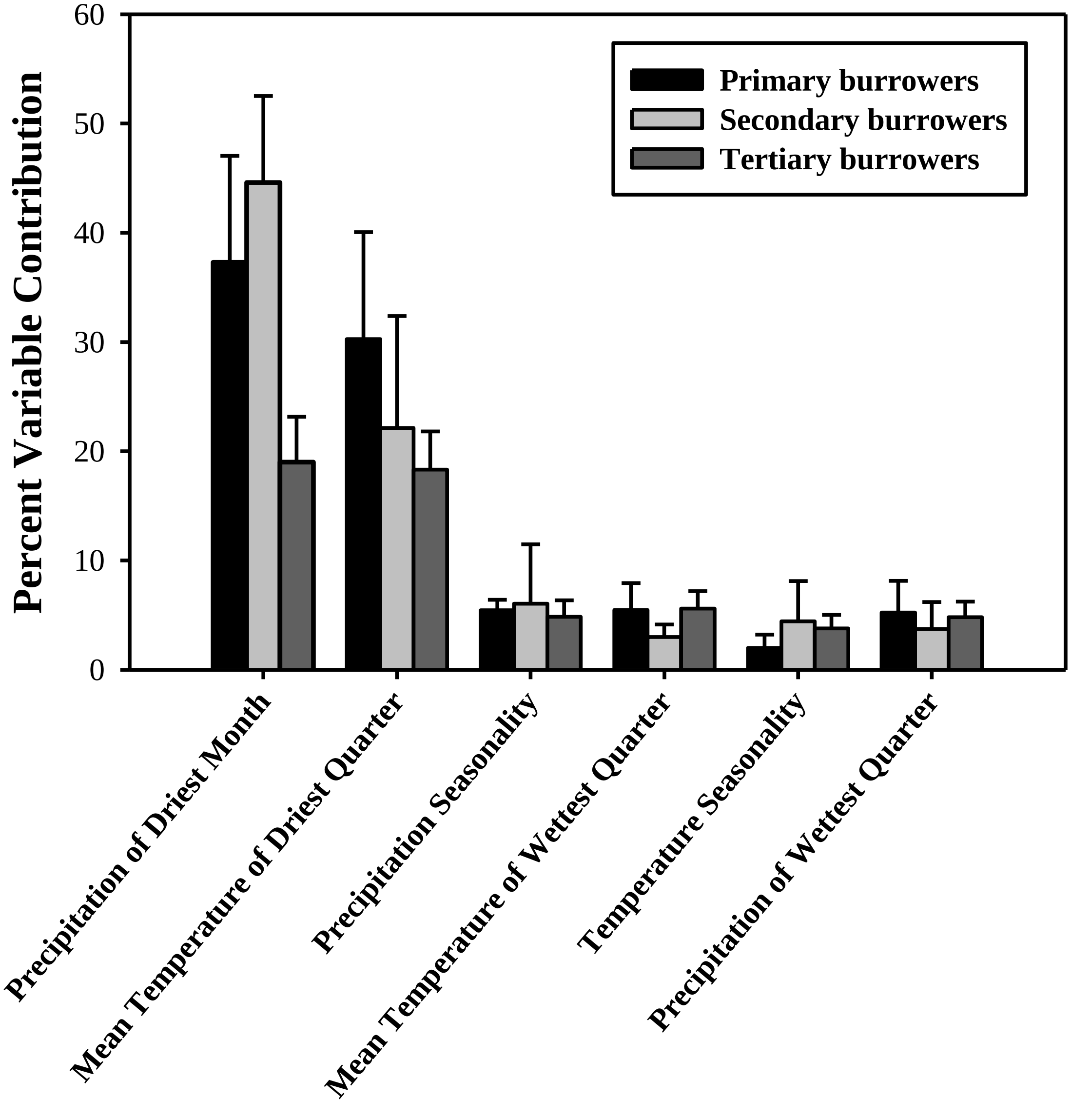


Figure 4. Estimated marginal means from the RM-ANOVA for total area and relative area predicted as suitable habitat for the three burrowing types across three emission scenarios and four years (2000, 2030, 2050, 2080). Open circles represent primary burrowing crayfish, closed circles represent secondary burrowing crayfish, and triangles represent tertiary burrowing crayfish.

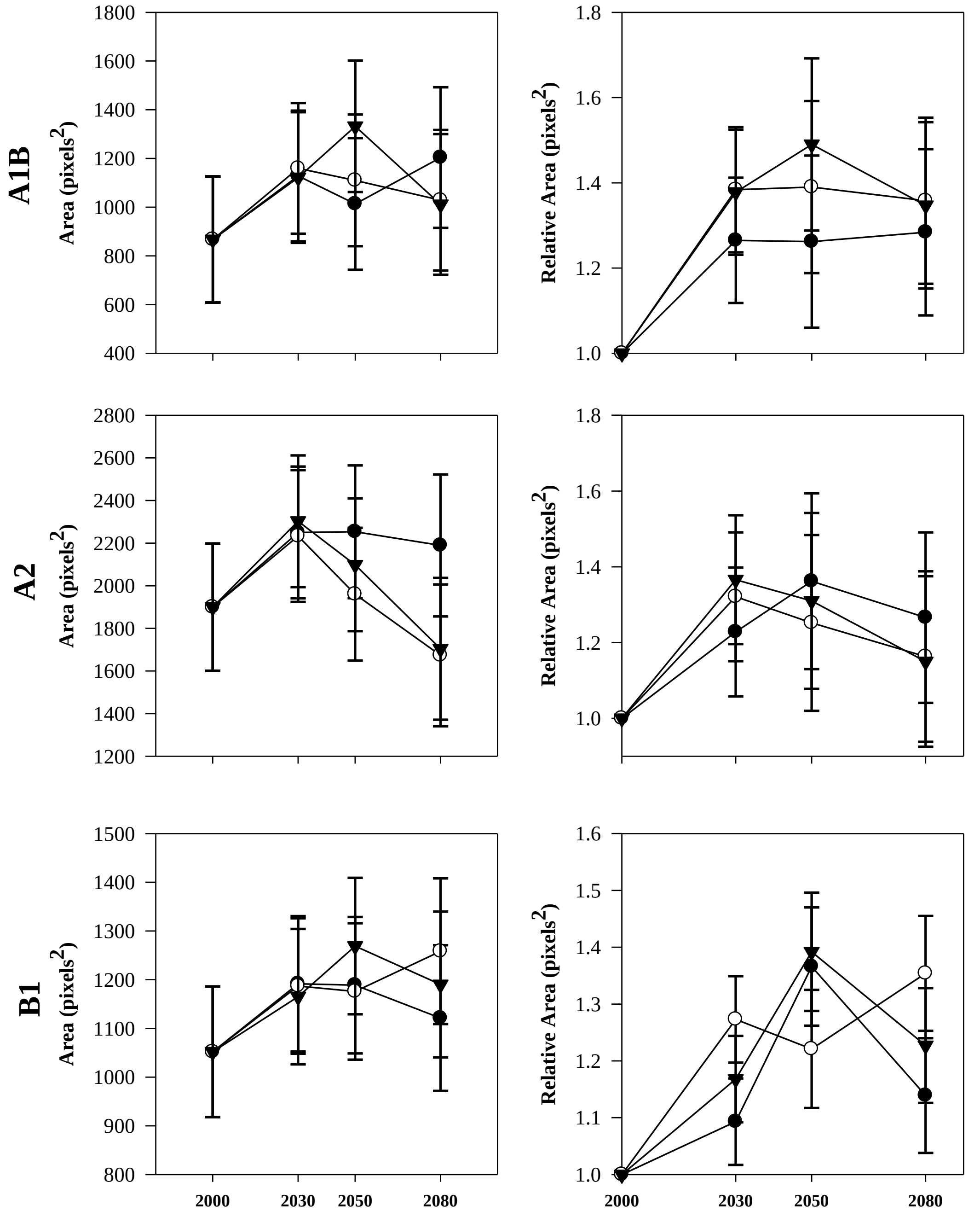
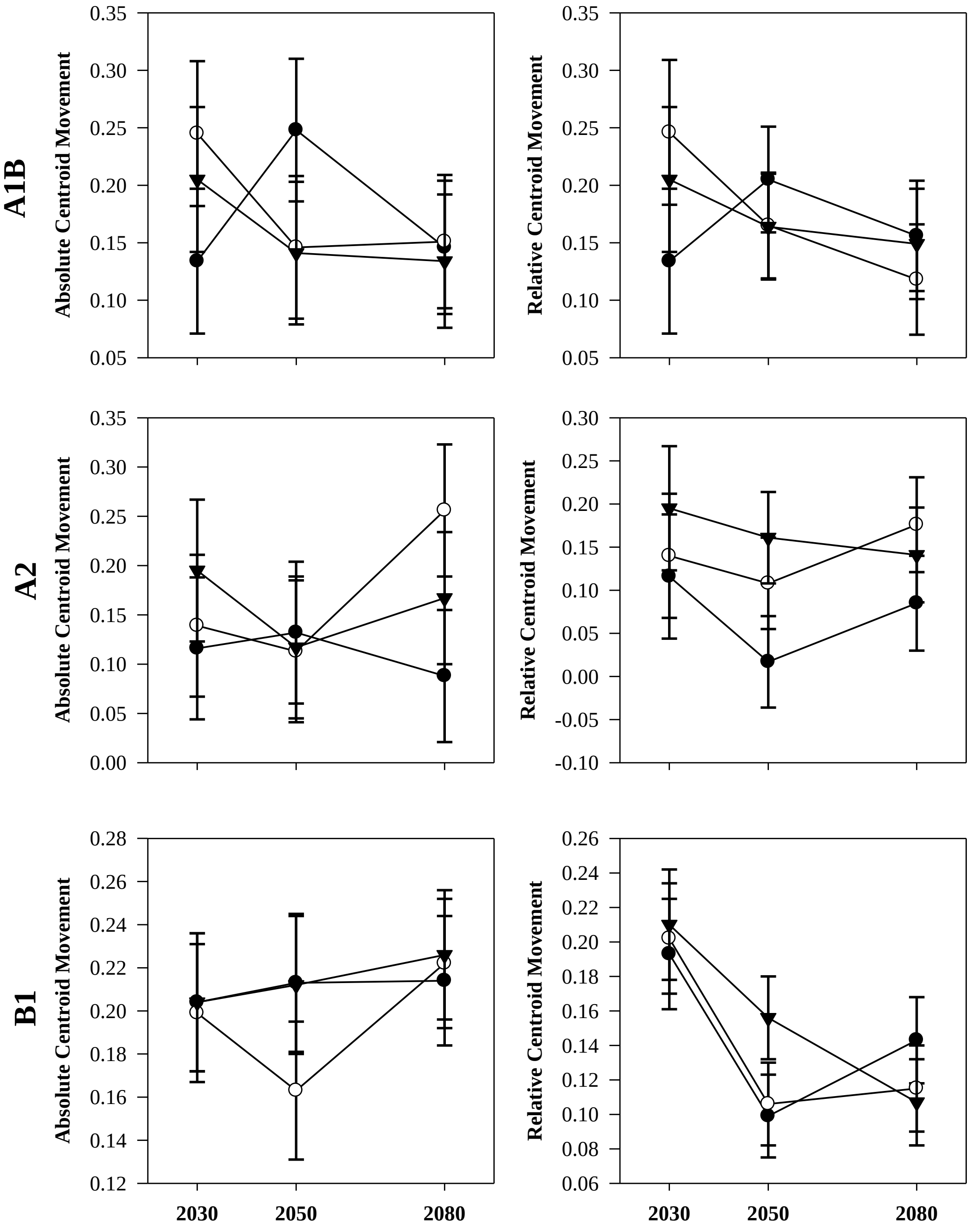


Figure 5. Estimated marginal means from the RM-ANOVA for absolute centroid movement and relative centroid movement (between years) for the three burrowing types across three emission scenarios and four years (2000, 2030, 2050, 2080). Open circles represent primary burrowing crayfish, closed circles represent secondary burrowing crayfish, and triangles represent tertiary burrowing crayfish.



CHAPTER IV

CONVERGENT EVOLUTION IN CRAYFISHES: BURROWING BEHAVIOR CORRELATES WITH ECO-MORPHOLOGICAL TRAITS

Reid L. Morehouse

Abstract

Ecological morphology (ecomorphology) investigates the relationships between organismal body morphology and ecology and is an integral part of comparative biology attempting to gain a functional understanding of adaptive evolution. We investigated ecologically relevant morphological traits in multiple species of freshwater crayfish that inhabit a variety of habitats. We particularly asked whether there are shared aspects of body morphology among species having similar ecologies by comparing morphological variation among three general ecomorphs (i.e., burrowing types). Specifically, we ask three main questions: (1) How do morphological characteristics vary among taxonomic groups (genera, subgenera, species), and are they useful for species identification? (2) Are there consistent morphological differences between the sexes and between form I (reproductive) and form II (non-reproductive) males? (3) Are there consistent – potentially convergent – morphological differences among burrowing types? Our study indicates strong morphological differences among taxonomic groups, with clear species differences except among closely related species. After correcting for morphological variation due to taxonomic affiliation, our results suggest that there are general patterns of sexual dimorphism in crayfish. In most species, females have modification of traits relevant to reproductive biology

(i.e., longer and wider abdomens with longer pleopods), and form I males have longer and thicker chelae and longer first and second walking legs, which could be related to sexual selection). Most importantly, our results show evidence for convergent evolution of morphological traits in species belonging to the same burrowing type, irrespective of taxonomic classification. Primary and tertiary burrowers were morphologically most distinct, with secondary burrowers being intermediate. Primary burrowers have shorter, bulkier chelae and shorter more narrow abdomens, smaller tails and deeper walking legs. In contrast, tertiary burrowers have longer, skinnier chelae and longer, wider abdomens with larger tails.

Introduction

Ecological morphology (ecomorphology) investigates the relationships between organismal body morphology and ecology, and is an integral part of comparative biology attempting to gain a functional understanding of adaptive evolution (Wainwright and Reilly 1994, Motta et al. 1995, Norton et al. 1995, Wainwright and Richard 1995, Maldonado et al. 2009). Relationships between morphological traits and environmental or ecological parameters have been uncovered in a multitude of taxa and in response to a variety of selective sources. For example, populations and species inhabiting lotic environments often exhibit morphological modifications compared to those in lentic habitats, allowing them to cope with elevated flow velocities (Winemiller et al. 1995, Langerhans 2008, Franssen et al. 2013a, Franssen et al. 2013b, Rivera et al. 2014). Similarly, phenotypic divergence is evident among populations and species exposed to different abiotic environmental parameters (Crispo and Chapman 2011, Tobler et al. 2011), differential trophic resource use (Hulsey et al. 2010, Lujan et al. 2011), and differential habitat use (Holomuzki and Biggs 2006, Hulsey et al. 2013, Muller-Peddinghaus and Hering 2013, Giokas et al. 2014).

The wealth of eco-morphological studies involving a diversity of taxa and environmental sources of selection illustrates the pervasiveness of convergent evolution, where independent lineages evolved similar phenotypic features in response to shared sources of selection (Foster and Baker 2004, Losos 2009, Bernatchez et al. 2010, Elmer et al. 2010). Such evolutionary convergence illustrates how adaptation by natural selection leads to predictable evolutionary outcomes (Endler 1986, Schluter 2000, Melville et al. 2006), which allows for inferences about species level ecology based on the investigation of phenotypic features (Douglas and Matthews 1992, Wainwright and Reilly 1994, Litchman and Klausmeier 2008, Green and Côté 2014). Nonetheless, there is a variety of ecological, genetic, and functional mechanisms that can potentially influence the degree of evolutionary convergence among taxa exposed to similar sources of selection, and recent studies have indicated that organisms may indeed adapt to similar environments in unique, non-convergent ways (Langerhans and DeWitt 2004, Rosenblum and Harmon 2011, Kaeuffer et al. 2012). With their ecological diversity, crayfish in the central United States provide an opportunity to test for potential convergent evolution among species spanning a broad range of phylogenetic relationships. We investigated ecologically relevant morphological traits in multiple species of freshwater crayfish that inhabit a variety of habitat types from streams and rivers, roadside ditches, wet depressional areas, to ponds, lakes, and prairies/fields. To establish a basic eco-morphological paradigm for crayfishes, we particularly asked whether there are shared aspects of body morphology among species having similar ecologies by comparing three general ecomorphs (i.e., burrowing types).

Crayfish have been classified into three main burrowing types that reflect broad aspects of species level ecology: primary, secondary, and tertiary burrowers (Hobbs 1942). Primary burrowers excavate elaborate burrows, spending most of their lives underground. They usually dig vertically into the substrate until they reach the water table, which allows them to occur in habitats with semi-permanent standing water (e.g., wet fields, ditches, and shallow ponds). Such burrows can reach up to 3 meters in depth and be composed of multiple chambers, tunnels, and surface openings (Taylor and Schuster 2004). Primary burrowers will emerge from their burrows only to forage or mate during wet spring and fall months and on warm humid nights (Walls 2009). Secondary burrowers also spend a considerable portion of their lives in burrows, but will frequently visit streams and other permanent water sources throughout the year. Their burrows are less complex than those of primary burrowers and usually have a tunnel that is connected to a permanent water body (Taylor and Schuster 2004). Secondary burrowers occur in areas that are inundated seasonally or within close proximity to permanent water bodies (Gherardi 2002). In contrast, tertiary burrowers are species that only intermittently retreat into simple, pocket-like burrows (e.g., under large rocks in streams) during periods of drought, cold temperatures, and egg brooding (Taylor and Schuster 2004). Tertiary burrowers are strictly associated with permanent water bodies and usually occur on gravel, cobble, and boulder substrates (e.g., in streams, rivers, or ponds). Interestingly, different burrowing types appear to have evolved independently multiple times during the diversification of North American crayfish, as multiple genera of crayfishes (e.g., *Cambarus*, and *Procambarus*) encompass species belonging to two or more burrowing types (Hobbs 1989, Morehouse and Tobler 2013).

While different burrowing types starkly differ in their ecologies, particularly in terms of habitat use and associated bioclimatic variables (Chapter 3, Pflieger 1996, Taylor and Schuster 2004), it remains unclear whether and how variation in ecology is correlated with morphological characteristics of crayfish in a predictable manner (i.e., whether there are convergent morphological differences among species of the same burrowing type irrespective of phylogenetic relationships). Some general morphological observations have been made based on burrowing behavior, where primary burrowers tend to have narrower abdomens and broader chelae (Holdich 2002, Riek 1972). The majority of morphological analyses in crayfish have been conducted in a taxonomic context and primarily focused on the gonopods (the copulatory organs of males formed by the first pair of pleopods) of reproductive males, because they have historically provided the key traits for species delineation (Huxley 1880, Smith 1912). A handful of recent studies that have examined morphological variation in crayfish species particularly focused on endangered species in Europe (Grandjean and Souty-Grosset 2000, Sint et al. 2005, 2007, Bertocchi et al. 2008, Scalici and Gibertini 2009, Haddaway et al. 2012). For conservation purposes and to assess relocation potential, these studies tested whether morphological features other than the structures of the gonopods are useful for population and species identification. For example, there is significant morphological variation among populations of *Austropotamobius pallipes* in relation to habitat, with individuals from lentic habitats having broader carapaces than those from lotic habitats, which could be related to variation in oxygen levels (Haddaway et al. 2012). Additionally, there appears to be sufficient variation in ecologically-relevant morphological traits that allows for the differentiation of populations and species without an investigation of the gonopods; aspects of the cephalothorax and chelae (Sint et al. 2007) and shape of the rostrum (Bertocchi et al. 2008). Consequently, and despite taxonomic research having disproportionally focused on reproductive traits or traits with unknown ecological function (i.e., areola), there is clear evidence for variation in ecologically relevant traits of crayfish. But whether and how trait variation is related to crayfish ecology across a broader taxonomic sample remains untested.

In this study, we examined 27 species of crayfish including six genera and representatives from all three burrowing types to illuminate variation in putatively ecologically-relevant traits among species and test for potential evolutionary convergence. Specifically, we ask three main questions: (1) How do morphological characteristics vary among taxonomic groups (genera, subgenera, species), and are they useful for species identification? We first accounted for effects of evolutionary relationships on morphological variation among the taxa investigated. In absence of a robust phylogeny for the core taxa of this study, we used a taxonomy-based approach to do so (Ayache and Near 2009, Koeppel and Wu 2013). We also tested whether variation in morphological traits is effective in distinguishing species that are mostly delineated by aspects of male reproductive structures. (2) Are there consistent morphological differences between the sexes and between form I (reproductive) and form II (non-reproductive) males? Besides evolutionary history and ecology, sexual selection can be a key driver of morphological variation (Andersson 1994, Butler and Losos 2002, Moczek 2005). Accordingly, we investigated the nature of sexual dimorphism in crayfish. As male crayfish also molt between reproductive forms, we further expected to find morphological differences in between form I males and form II males. We predicted that differences among reproductive groups (females and the two male forms) particularly included aspects in the morphology of chelae (which are potentially involved in both intra and intersexual selection; Stein 1976), and the abdomen (which plays a critical role during parental care for eggs and juveniles). (3) Are there consistent – potentially convergent – morphological differences among burrowing types? We addressed this question by comparing morphological variation corrected for taxonomic classification and sex across burrowing types. We predicted that secondary burrowers would exhibit intermediate morphologies between primary and tertiary burrowers. Although functional studies on aspects of crayfish morphology are largely missing, we predicted that differences in abdomen size, tail size, walking legs, and chelae characteristics should be evident based on the burrowing types' known ecology. Primary burrowing crayfish use their abdomens, tails, and chelae to burrow down to the water table (Hobbs 1942). Additionally, the walking legs for primary burrowing crayfish need to be able to support more weight, as they are not assisted by surrounding water (i.e., tertiary burrowers) causing buoyancy.

Methods

Morphological characteristics of 27 species of crayfish that occur in Oklahoma, USA were assessed (see Table 1 for a species list). Individual crayfish (approximately 10 females, 5 form I males, 5 form II males) for each species were either collected by the authors throughout the state or borrowed from the Sam Noble Museum of Natural History (Norman, OK), Illinois Natural History Survey (Urbana, IL), or Smithsonian Museum of Natural History (Washington, DC).

Specimens borrowed from museums were either located within our study area or as close as available.

Thirty morphological characteristics were measured for each specimen with digital calipers to the nearest 0.01 mm. Measured traits are illustrated in Figure 1 and included chelae length (CLL), chelae width (CLW), chelae height (CLH), length of palm (CPL), dactyl length (CFL), rostrum length (ROL), rostrum width (ROW), width of rostrum apex (TRW), distance from tip of rostrum to the cervical groove (TCL), length of carapace (HEL), width of carapace (HEW), height of carapace (HEH), width at cervical groove (CGW), maximum cephalothorax width (CPW), cephalothorax width at hind edges (CEW), areola length (ARL), areola width (CRW), abdomen length (ABL), abdomen width (ABW), abdomen height (ABH), telson length (TEL), telson width (TEW), tail width (TW), length of first pereiopod (LFP), length of second pereiopod (LSP), width of third pereiopod (WTP), depth of third pereiopod (DTP), length of first non-reproductive pleopod (PLEO), diameter of eye (EYE), and total length (TL). These morphological characteristics were chosen based on previous studies that have compared morphological characteristics among species (Sint et al. 2005, Bertocchi et al. 2008). Some of the selected traits are sexually dimorphic and also within males depending on reproductive form, and can potentially be used to uncover trait-environment correlations (Riek 1972). All bilateral measurements were taken on the crayfish's right side except when injuries or regenerations were observed (e.g., missing or regenerated chelae). In this case, measurements were taken on the left side.

Statistical Analyses

Prior to examining morphological variation in relation to ecology (i.e., among different burrowing types), it is critical to understand general patterns of morphological variation in a phylogenetic context as well as in relation to sex and male reproductive state. Consequently, we first used a multivariate analysis of covariance (MANCOVA) with all of the morphological characteristics (listed above; except total length) as the dependent variables. Total length was used as a covariate to control for multivariate allometry, and sex (female, male form I, and male form II) as an independent variable. In absence of sound phylogenetic analyses for the examined species, we used the current taxonomic classification of species into genera and subgenera (Table 1; Hobbs 1972, Hobbs and Robison 1988, Hobbs 1989) as an approximation of phylogenetic relationships (Ayache and Near 2009, Koeppel and Wu 2013). Accordingly, we included genus, subgenus (nested within genus), species (nested within subgenus nested within genus), and their interactions with sex as additional independent variables in the model. Although this approach does not account for the hierarchical relationships among the investigated species, it essentially treats the different taxonomic levels as blocks, controls for differences across taxonomic groups, and provides an intuitive metric for comparing morphological variation across groups of interest.

To illuminate general patterns of differences between sexes and male reproductive forms, we calculated divergence vector scores for each individual based on the sex divergence vector as defined by Langerhans (2009). The divergence vector was based on the sums of squares and cross products (SSCP) matrix for the sex term in the above MANCOVA and summarizes the linear combination of morphological traits that contributes most to morphological variation across the three sex categories, while simultaneously controlling for all other effects in the model.

Furthermore, we conducted a discriminant function analysis (DFA) to test whether individual specimens could be assigned to the correct species based on ecologically-relevant, morphological traits. A jack-knife (leave-one-out) sampling scheme was used for cross-validation, where each sample was classified by the functions derived from all other samples, and overall classification success was calculated. To facilitate the DFAs, the effects of the sex and allometry terms were first removed by using the residuals of a preparatory MANCOVA, in which 29 morphological variables were used as dependent variables, total length as a covariate, and sex as an independent variable.

Finally, we tested for potentially shared morphological characteristics among species with similar ecologies (i.e., belonging to the same burrowing type). We first accounted for variation due to allometry, sex, and taxonomic affiliation by subjecting all morphological variables to MANCOVA, including total length as a covariate as well as sex, genus, subgenus (within genus), and their interactions as independent variables. The residuals of this MANCOVA represent species-level morphological variation corrected for allometry, sex, and taxonomic affiliation. Residuals were then analyzed using MANOVA, with burrowing type as an independent variable. To identify traits that consistently vary among burrowing types, we calculated divergence vector scores based on the SSCP matrix for the burrowing type term as explained above.

For all MAN(C)OVAs, *F*-values were approximated using Wilks' lambda. The assumptions of normal distribution and homogeneities of variances and covariances were met for all analyses, and *P*-values reported were two-tailed. Statistical analyses were conducted in SPSS 21.

Results

Five hundred and forty-nine individual crayfish were measured for morphological analyses. MANCOVA results revealed significant effects of allometry, sex, and taxonomic affiliation (Table 2), and based on effect sizes (partial eta squared), morphological differences were particularly pronounced across genera and subgenera. The degree of sexual dimorphism was highly variable among species (Figure 2). If sexual dimorphism was present, males generally had longer 1st and 2nd legs, longer and wider chelae, longer chelae fingers and palms, shorter pleopods, as well as narrower and shorter abdomens with shorter telsons (Table 3). In some species (i.e., *C. diogenes*, *O. lancifer*, *O. difficilis*), form II males were more similar to females, while in others they were more similar to form I males (i.e., *C. puer*, *F. blairi*, *O. macrus*, *O. nana*; see Figure 2).

DFA indicated that over 81% of cross-validated specimens were correctly assigned to the correct species based on morphological measurements (Table 4). Of the 27 species examined, 17 species had classification success above 90%. Of the species that had a classification success below 90%, a few species pairs stand out. Nearly half of *O. deanae* and half of *O. difficilis* specimens were classified as each other. This is not surprising as these species are classified in the same subgenus and have allopatric distributions in adjacent river drainages. Additionally, we see a similar pattern with *O. macrus*, *O. nana*, and *O. meeki brevis*. As *O. macrus* and *O. nana* are sister species and in the same subgenus, their resemblance is not surprising, but *O. meeki brevis* is in a different subgenus. *O. meeki brevis* is a sympatric species with *O. macrus* and *O. nana* in all of their known locations, and it is possible that the environment is playing a role in shaping their morphological characteristics resulting in similar traits across all three species. All cross-validation results for individual species can be found in Table 5.

Finally, we found significant differences in morphological characteristics among burrowing types after correcting for allometry, sex, and taxonomic affiliation ($F_{58,1036} = 3.747$; $P < 0.001$). Secondary burrowers exhibited an intermediate morphology between primary and tertiary burrowers (Figure 3). Along the morphological gradient from primary to tertiary burrowers, primary burrowers exhibited shorter carapace heights, width at hind edges of cephalothorax, telson width, abdomen width, carapace width, abdomen length, abdomen height, and rostrum length, as well as longer 1st and 2nd legs, chelae width, pleopods, chelae length, areola, heads, chelae palms, and chelae heights (Table 3).

Discussion

This study investigated morphological variation in 27 species of crayfish encompassing six genera and representatives from all three burrowing types to uncover patterns across taxonomic groups (e.g., genus, subgenus, and species), sex and male reproductive forms, as well as broad ecological groups (burrowing type). Overall, we found significant variation among taxonomic groups. Morphological differences were pronounced among genera and subgenera, and we also uncovered clear species differences in ecologically-relevant morphological characteristics. These results illustrate that – in addition to gonopod structure – other traits are useful for species delineation and identification. These results coincide with studies on European crayfish species that have successfully established the use of morphological traits to differentiate between species and populations (Sint et al. 2005, 2007, Haddaway et al. 2012). In particular, inclusion of morphological characteristics not commonly used in crayfish taxonomy allowed for the discrimination of previously cryptic species in the *Austropotamobius pallipes* complex without the use of molecular techniques (Bertocchi et al. 2008). Nonetheless, it is important to note that misclassifications occurred in our analyses particularly between closely related species (e.g., between *O. macrus* and *O. nana*, which are sister species; Williams and Leonard 1952, Dillman et al. 2010). Hence, morphological data as assessed here ultimately can provide a complimentary – rather than an alternative – approach to traits more commonly used in species delineation.

Our analyses also revealed significant variation between the sexes as well as between reproductive and non-reproductive male, although sexual dimorphism was not present in all species. In addition, in species with sexual dimorphism, form II males either resembled females or form I males. These results provide fruitful grounds to further investigate mechanisms underlying among species variation in morphological differences among reproductive categories. Specifically, patterns of intra- and intersexual selection that could shape morphological features over evolutionary time remain understudied in crayfish, although previous studies have documented sexual selection on chelae size in different species (Stein 1976, Galeotti et al. 2006). Overall, female crayfish generally were characterized by having larger (length and width) abdomens and longer pleopods. Form I males (and in some species form II males) have larger chelae is all aspects measured (i.e., total length, width, height), as well as larger heads and eyes. These results support earlier findings of (Grandjean et al. 1997a, Grandjean et al. 1997b, Streissl and Hodl 2002), which all reported form I males with large chelae and females with longer and wider abdomens. Specifically, for some species a positive allometric growth of chelae in males has been reported, whereas females chelae growth was isometric to total length (Mason 1979, Streissl and Hodl 2002). Simultaneously, female abdomen width and length were greater relative to males (also see Lowery 1988). Larger abdomens and longer pleopods are likely related to the reproductive biology of crayfish. Females carry eggs and juveniles underneath their abdomen (attached to the pleopods), and an elaboration of these structures may potentially increase the carrying capacity for eggs and juveniles (Kato and Miyashita 2003).

Most importantly, our study also found consistent morphological differences among species belonging to different burrowing types with vastly different ecologies. Compared to tertiary burrowers, primary burrowers generally had shorter, more narrow and flatter abdomens with broader, shorter tails and longer pleopods. The chelae in primary burrowers were also bulkier and heavier relative to the other burrowing types and primary burrowers had larger heads and smaller eyes. In general, tertiary burrowers were more streamlined, with longer more slender bodies and chelae, although some species (i.e., *Orconectes macrus*, *O. nana*) had thicker more blunt chelae. Overall, the differences listed above are likely adaptations to burrowing and spending the majority of time in semi-aquatic, subterranean habitats. The shorter, stouter abdomens with broader short tails maybe used to help excavate burrows. The longer pleopods may be primarily used for keeping the attached eggs and juveniles aerated in poor oxygenated water at the base of the burrow (Grow and Merchant 1980). Additionally, the larger, more blunt chelae are likely used during burrowing to move mud out of the burrow, and for offensive/defensive behaviors (Holdich 2002). The depth of the third pereiopod was also the deepest relative to secondary and tertiary burrowing crayfish. Along with burrow construction, primary crayfish have to support more body weight, as they do not have water and buoyancy factors to help alleviate the effects of gravity. The third pereiopod is used for walking and the main support of body weight (Holdich 2002), so being deeper than secondary and tertiary burrowers suggests an adaptation for burrowing activity and having a semi-terrestrial lifestyle. As predicted, secondary burrowers were intermediate in morphological characteristics between primary and tertiary burrowers. Since secondary burrowers inhabit both burrows and permanent water sources, they likely evolved to have morphological characteristics that balance the trade-offs associated with performance at either end of the spectrum and allow them to adequately perform in either environment. Clearly, functional studies testing the adaptive value of traits divergent among burrowing types are highly warranted to understand trait differences from a mechanistic perspective.

In conclusion, we have shown that different taxa and burrowing types significantly differ in their morphology. More rigorous morphological analyses could thus provide informative traits for describing species level biodiversity, particularly in species complexes that are difficult to distinguish because of subtle or gradual variation in gonopod structure (i.e., *Orconectes virilis* and *O. causeyi*; Hobbs 1989). Additionally, this study has provided evidence that disparate taxa of crayfish have converged on similar morphological phenotypes based on their burrowing behavior. Such convergent evolution of cambarids, among genera as well as subgenera, has been hypothesized by other studies when phylogenetic studies based on morphological traits and molecular markers have produced conflicting results (Breinholt et al. 2012, Pedraza-Lara et al. 2012, Taylor et al. 2014). Overall, adaptation to different ecological and environmental conditions may be a driving force in crayfish diversification (e.g., Schluter , Schluter 2000), and future studies will need to integrate phylogenetic, phenotypic, distributional, and ecological analyses to elucidate the evolutionary mechanisms that have led to the staggering species and functional diversity in the crayfish of North America.

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Figure 1. Description of the morphological characteristics measured in this study. Note that the figure does not include eye width, length of first and second pereiopod, width and depth of third pereiopod, and pleopod length. The figure was modified from Sint et al. (2005).

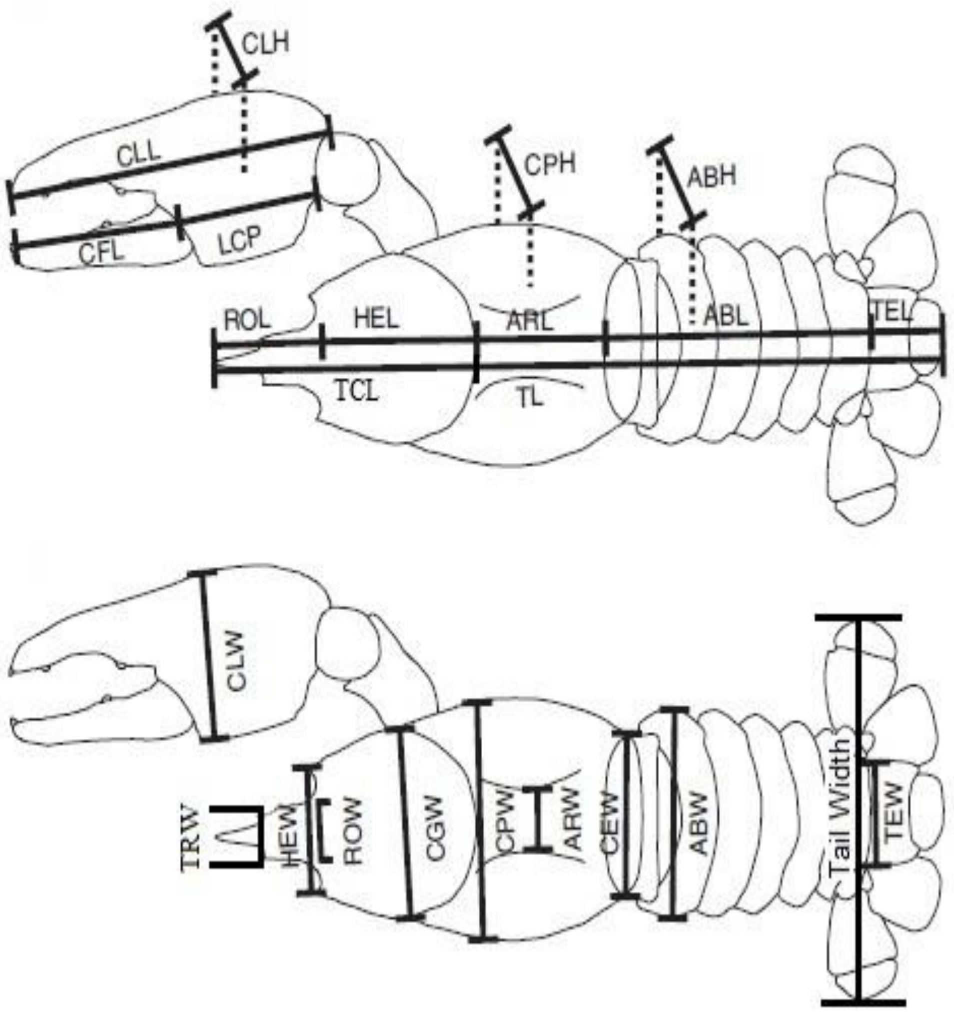

Figure 2. Estimated marginal means of the sex divergent vector scores for females, form I males, and form II males of all species investigated. Morphological traits correlated with the sex divergent vector are listed in Table 3.

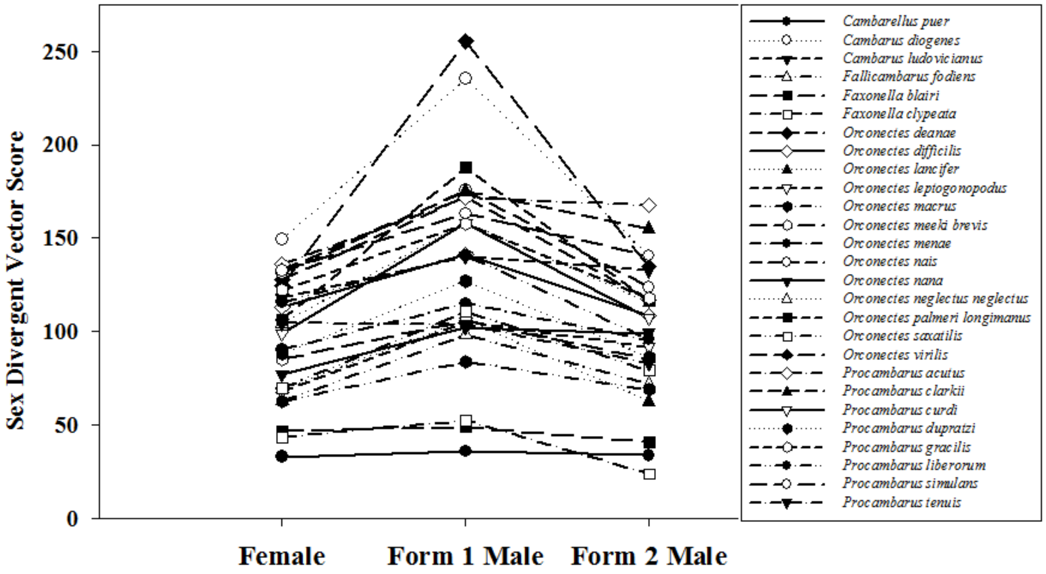

Figure 3. Estimated marginal means (± SEM) of the burrowing type divergence vector scores for each of the three burrowing types. Morphological traits correlated with the burrowing type divergent vector are listed in Table 3. Letters above bars indicate significant difference between burrowing types (*P* < 0.05).

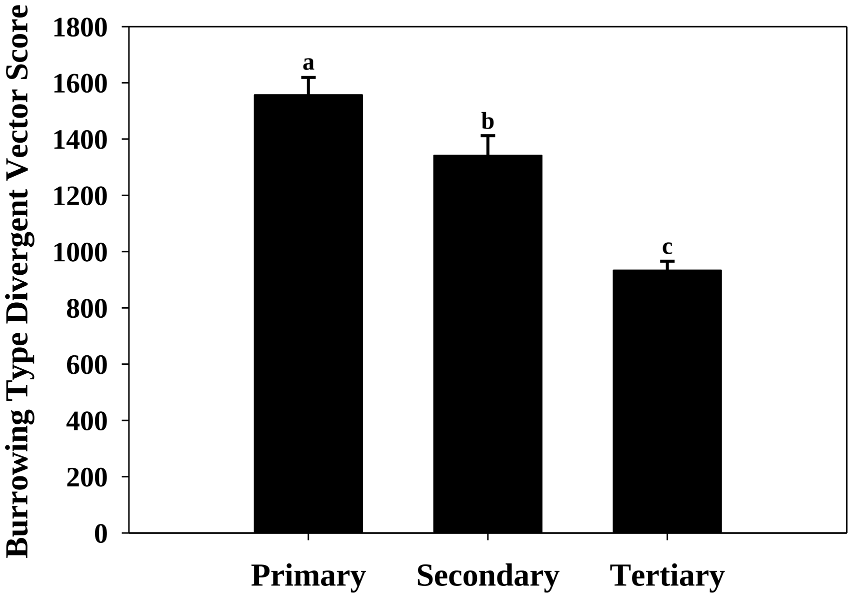

Table 1. List of species used in the current study, organized by genus and subgenus (in parentheses). For each species, we list its burrowing type as well as sample sizes for form I and form II males as well as females.

Species	**Burrowing type**	**Form I Males**	**Form II Males**	**Females**
Cambarellus (*Pandicambarus*)				
C. puer	Tertiary	5	5	10
Cambarus (*Lacunicamabrus*)				
C. diogenes	Primary	5	5	10
C. ludovicianus	Primary	5	5	10
Fallicambarus (*Creaserinus*)				
F. fodiens	Primary	5	5	10
Faxonella (*Faxonella*)				
F. blairi	Tertiary	5	5	10
F. clypeata	Tertiary	5	5	10
Orconectes (*Baunnulifictus*)				
O. meeki brevis	Tertiary	5	5	10
O. palmeri longimanus	Tertiary	7	5	10
Orconectes (*Gremicambarus*)				
O. nais	Tertiary	5	5	10
O. virilis	Tertiary	5	5	10
Orconectes (*Hespericambarus*)				
O. deanae	Tertiary	5	5	10
O. difficilis	Tertiary	5	5	10
Orconectes (*Procericambarus*)				
O. leptogonopodus	Tertiary	6	5	10
O. macrus	Tertiary	8	5	10
O. menae	Tertiary	5	5	10
O. nana	Tertiary	7	5	10
O. neglectus neglectus	Tertiary	5	5	10
O. saxatilis	Tertiary	6	5	10
Orconectes (*Tragulicambarus*)				
O. lancifer	Tertiary	5	5	10
Procambarus (*Girardiella*)				
P. curdi	Secondary	5	5	10
P. gracilis	Primary	5	5	10
P. liberorum	Primary	5	5	10
P. simulans	Secondary	5	5	10
Procambarus (*Pennides*)				

P. dupratzi	Tertiary	5	5	10
<u>*Procambarus* (*Scapulicambarus*)</u>				
P. acutus	Secondary	5	5	10
P. clarkii	Secondary	5	5	10
<u>*Procambarus* (*Tenuicambarus*)</u>				
P. tenuis	Tertiary	5	5	10

Table 2. Results of MANCOVA investigating morphological variation across 27 species of crayfish. *F*-values were approximated using Wilks' lambda, and effect sized were estimated based on partial eta squared (η_p^2).

Effect	**Hypothesis *df***	**Error *df***	***F***	***P***	**η_p^2**
Intercept	29.0	439.0	19.016	<0.001	0.557
Total length	29.0	439.0	1189.261	<0.001	0.987
Sex	58.0	878.0	14.747	<0.001	0.493
Genus	145.0	2174.2	39.271	<0.001	0.719
Subgenus(Genus)	203.0	3007.6	30.974	<0.001	0.667
Species(Subgenus(Genus))	406.0	5598.9	7.787	<0.001	0.332
Sex * Genus	290.0	4187.8	3.540	<0.001	0.188
Sex * Subgenus(Genus)	406.0	5598.9	2.961	<0.001	0.161
Sex * Species(Subgenus(Genus))	812.0	8996.2	2.117	<0.001	0.118

Table 3. Canonical correlations between morphological traits and divergent vectors for the sex and crayfish burrowing type terms from MAN(C)OVA models (see methods). Bold values represent the highest absolute correlations between specific traits and each morphological gradient.

Variables	**Sex DV**	**Burrowing Type DV**
1st leg length	**1167.929**	**-35.201**
2nd leg length	**326.813**	**-16.02**
3rd leg depth	18.042	-3.835
3rd leg width	11.685	1.175
Abdomen height	-3.683	**19.106**
Abdomen length	**-42.088**	**16.347**
Abdomen width	**-99.654**	**14.091**
Areolar length	50.463	**-13.996**
Areolar width	-6.119	9.528
Carapace height	39.182	**11.16**
Carapace width	47.399	**15.313**
Chelae finger length	**464.811**	-3.683
Chelae height	161.67	**-11.575**
Chelae length	**787.597**	**-17.453**
Chelae palm length	**253.246**	**-12.015**
Chelae width	**227.165**	**-27.68**
Eye diameter	10.611	4.044
Head length	-9.583	**-13.151**
Head width	13.304	2.204
Length from tip of rostrum to cervical groove	11.936	5.911
Pleopod length	**-222.442**	**-19.481**
Rostrum length	6.585	**19.428**
Rostrum width	4.778	10.622
Tail fan width	-13.315	10.41
Telson length	**-29.145**	6.185
Telson width	-8.297	**13.812**
Width at cervical groove	4.589	3.257
Width at hind edges of cephalothorax	7.255	**11.763**
Width of rostrum at apex	-4.529	-7.019

Table 4. Results of the discriminant function analysis (DFA) used to test for the utility of eco-morphological traits for species identification. Overall, over 81% of cross-validated specimens were correctly assigned to the correct species.

Variable	Function 1	Function 2	Function 3	Function 4
Abdomen length	0.088	-0.043	-0.037	0.019
Abdomen width	0.071	-0.337	0.107	0.144
Abdomen height	0.134	0.056	0.133	-0.074
Areolar length	-0.213	0.013	-0.078	0.253
Areolar width	0.347	0.255	0.704	-0.384
Width at hind edges of cephalothorax	-0.037	0.024	-0.005	-0.042
Chelae finger length	-0.226	0.265	0.224	0.590
Width at cervical groove	0.142	-0.426	0.011	0.100
Chelae length	0.581	-0.622	0.154	-0.530
Chelae width	-0.103	-0.965	-0.291	-0.705
Chelae height	-0.291	-0.065	0.131	0.574
Chelae palm length	0.126	1.124	-0.339	0.273
Carapace width	0.193	-0.097	0.140	0.545
Carapace height	0.075	0.565	0.118	0.162
Head length	-0.483	0.305	-0.060	-0.306
Head width	0.292	0.024	-0.176	-0.039
Rostrum length	0.570	-0.040	-0.399	0.352
Rostrum width	0.054	0.501	0.130	0.299
Length from tip of rostrum to cervical groove	-0.057	0.054	-0.100	-0.379
Telson length	-0.028	0.112	-0.217	0.001
Telson width	-0.153	-0.123	0.313	0.145
Width of rostrum at apex	-0.060	-0.064	-0.119	-0.164
1st leg length	-0.160	-0.014	-0.008	-0.279
2nd leg length	-0.071	0.051	0.060	-0.027
3rd leg width	-0.035	-0.139	-0.017	-0.073
3rd leg depth	-0.063	0.032	-0.093	0.004
Pleopod length	0.006	0.126	-0.145	0.029
Eye diameter	0.244	-0.113	0.043	-0.080
Tail fan width	0.020	0.162	0.132	0.047
Canoncial correlation	0.970	0.959	0.898	0.874
Eigenvalue	15.757	11.422	4.142	3.235
% of Variance	36.700	26.618	9.653	7.538
Chi-square	7422.431	5956.656	4646.537	3795.061

df	754.000	700.000	648.000	598.000
P-value	<0.001	<0.001	<0.001	<0.001

Variable	Function 5	Function 6	Function 7	Function 8
Abdomen length	0.080	-0.324	-0.033	0.252
Abdomen width	-0.023	0.353	0.085	-0.218
Abdomen height	-0.234	-0.114	-0.417	-0.357
Areolar length	0.449	0.518	0.175	-0.175
Areolar width	0.456	0.172	0.068	-0.030
Width at hind edges of cephalothorax	-0.063	-0.005	-0.044	-0.316
Chelae finger length	-0.397	-0.069	0.186	0.221
Width at cervical groove	0.310	0.265	-0.014	0.474
Chelae length	-0.478	-0.334	-0.654	0.046
Chelae width	-0.341	0.602	0.189	0.479
Chelae height	0.723	-0.887	0.316	-0.449
Chelae palm length	0.049	0.262	-0.095	-0.332
Carapace width	0.060	0.202	-0.085	0.048
Carapace height	-0.011	-0.152	-0.426	0.121
Head length	-0.374	-0.090	0.032	0.111
Head width	-0.128	0.212	0.245	-0.168
Rostrum length	0.413	0.001	-0.109	-0.084
Rostrum width	-0.309	-0.217	0.381	-0.047
Length from tip of rostrum to cervical groove	-0.079	0.322	0.322	0.157
Telson length	0.134	-0.334	0.248	0.045
Telson width	-0.202	-0.341	0.304	-0.187
Width of rostrum at apex	0.024	0.123	0.339	-0.077
1st leg length	0.125	0.196	-0.305	-0.131
2nd leg length	0.310	0.019	-0.201	-0.106
3rd leg width	0.173	-0.261	0.214	-0.032
3rd leg depth	0.053	0.046	-0.027	-0.054
Pleopod length	0.166	-0.252	-0.209	0.196
Eye diameter	0.125	0.027	-0.023	0.488
Tail fan width	-0.088	0.312	-0.227	0.521
Canoncial correlation	0.820	0.771	0.712	0.690
Eigenvalue	2.049	1.464	1.028	0.908
% of Variance	4.775	3.411	2.396	2.117
Chi-square	3044.548	2464.876	1996.030	1628.314
df	550.000	504.000	460.000	418.000
P-value	<0.001	<0.001	<0.001	<0.001

Variable	Function 9	Function 10	Function 11	Function 12
Abdomen length	0.279	0.252	0.063	0.163
Abdomen width	0.041	0.014	0.568	-0.023
Abdomen height	0.029	0.213	0.202	0.139
Areolar length	0.431	0.503	-0.160	0.248
Areolar width	0.223	0.217	-0.272	0.045
Width at hind edges of cephalothorax	-0.035	0.260	0.016	0.220
Chelae finger length	0.220	0.473	-0.897	-1.627
Width at cervical groove	-0.353	0.264	0.483	-0.207
Chelae length	0.345	0.017	0.248	1.946
Chelae width	-0.588	0.652	-0.221	1.491
Chelae height	0.901	-1.021	0.593	-1.138
Chelae palm length	-0.868	0.089	-0.139	-0.526
Carapace width	-0.166	-0.476	-0.327	0.141
Carapace height	-0.201	0.017	-0.109	-0.171
Head length	-0.115	-0.144	0.091	0.087
Head width	0.636	-0.527	-0.323	-0.103
Rostrum length	0.115	0.246	-0.013	-0.084
Rostrum width	0.321	-0.223	0.181	0.333
Length from tip of rostrum to cervical groove	-0.083	0.465	0.103	0.241
Telson length	-0.029	0.303	0.085	-0.007
Telson width	-0.558	0.029	-0.381	-0.181
Width of rostrum at apex	0.007	0.089	-0.061	-0.197
1st leg length	-0.084	-0.117	0.330	0.111
2nd leg length	0.110	-0.082	-0.011	-0.591
3rd leg width	-0.063	-0.035	0.100	-0.059
3rd leg depth	-0.111	-0.052	0.051	0.056
Pleopod length	-0.080	-0.167	-0.203	0.125
Eye diameter	-0.379	-0.375	-0.014	0.169
Tail fan width	0.233	0.137	0.330	-0.149
Canoncial correlation	0.641	0.573	0.518	0.487
Eigenvalue	0.699	0.488	0.366	0.312
% of Variance	1.628	1.137	0.854	0.726
Chi-square	1292.298	1016.814	810.159	647.867
df	378.000	340.000	304.000	270.000
P-value	<0.001	<0.001	<0.001	<0.001

Variable	Function 13	Function 14	Function 15	Function 16
Abdomen length	0.121	0.215	0.174	-0.120
Abdomen width	-0.193	0.251	0.300	0.136
Abdomen height	0.389	-0.206	-0.110	0.346
Areolar length	0.431	0.063	0.102	0.339
Areolar width	-0.008	0.036	0.052	0.045
Width at hind edges of cephalothorax	-0.073	-0.189	-0.224	-0.173
Chelae finger length	0.638	0.560	0.459	0.053
Width at cervical groove	0.046	0.058	-0.498	-0.136
Chelae length	-0.475	0.026	-0.500	-0.372
Chelae width	-0.958	0.529	-0.055	0.786
Chelae height	1.112	-1.942	0.437	-0.552
Chelae palm length	0.164	1.070	0.573	-0.095
Carapace width	-0.080	-0.091	0.023	-0.640
Carapace height	-0.469	-0.406	-0.238	0.161
Head length	0.144	-0.240	0.317	-0.439
Head width	0.236	0.345	0.109	0.077
Rostrum length	0.034	-0.353	0.070	-0.390
Rostrum width	-0.071	0.322	-0.012	0.136
Length from tip of rostrum to cervical groove	0.550	-0.016	0.218	0.272
Telson length	-0.166	-0.054	-0.048	-0.236
Telson width	0.049	-0.067	0.348	0.217
Width of rostrum at apex	-0.361	0.152	-0.122	0.077
1st leg length	-0.414	-0.027	-0.245	0.210
2nd leg length	0.079	0.007	-0.154	0.087
3rd leg width	0.578	0.426	-0.510	-0.034
3rd leg depth	0.038	-0.006	0.285	0.018
Pleopod length	0.176	0.112	0.207	0.002
Eye diameter	-0.020	-0.046	-0.068	0.423
Tail fan width	-0.119	-0.130	0.197	0.212
Canoncial correlation	0.432	0.397	0.361	0.338
Eigenvalue	0.229	0.187	0.150	0.129
% of Variance	0.534	0.436	0.349	0.300
Chi-square	506.821	399.500	310.402	237.780
df	238.000	208.000	180.000	154.000
P-value	<0.001	<0.001	<0.001	<0.001

Variable	Function 17	Function 18	Function 19	Function 20
Abdomen length	-0.271	0.306	0.039	0.303
Abdomen width	-0.383	-0.184	0.210	-0.170
Abdomen height	0.146	-0.027	0.096	0.231
Areolar length	-0.111	0.183	-0.065	0.035
Areolar width	0.011	-0.081	0.004	-0.059
Width at hind edges of cephalothorax	-0.313	0.020	0.310	-0.158
Chelae finger length	-1.189	-0.896	0.347	-0.322
Width at cervical groove	0.453	0.226	-0.191	-0.262
Chelae length	1.421	0.675	-0.191	0.541
Chelae width	0.040	0.072	0.867	0.439
Chelae height	0.072	-0.207	-0.387	-0.484
Chelae palm length	-0.609	-0.411	0.213	-0.011
Carapace width	-0.123	-0.242	-0.287	0.571
Carapace height	-0.308	0.333	0.402	-0.134
Head length	-0.179	0.177	0.476	0.665
Head width	-0.011	0.541	0.277	-0.141
Rostrum length	0.166	0.285	0.606	0.384
Rostrum width	0.184	-0.300	0.086	-0.040
Length from tip of rostrum to cervical groove	-0.044	-0.352	-0.607	-0.527
Telson length	0.043	0.074	0.102	0.111
Telson width	0.395	0.215	-0.147	-0.179
Width of rostrum at apex	0.264	-0.113	0.274	0.131
1st leg length	0.234	0.485	-0.718	-0.741
2nd leg length	0.247	-0.234	0.109	0.352
3rd leg width	0.023	0.050	-0.015	-0.009
3rd leg depth	0.204	0.262	-0.230	0.450
Pleopod length	0.502	0.142	0.351	-0.451
Eye diameter	-0.259	-0.022	0.083	0.131
Tail fan width	0.124	-0.199	-0.115	0.066
Canoncial correlation	0.305	0.277	0.239	0.178
Eigenvalue	0.103	0.083	0.061	0.033
% of Variance	0.240	0.193	0.141	0.076
Chi-square	174.722	123.790	82.427	51.807
df	130.000	108.000	88.000	70.000
P-value	0.005	0.142	0.648	0.949

Variable	Function 21	Function 22	Function 23	Function 24
Abdomen length	0.142	0.041	0.034	-0.169
Abdomen width	0.182	0.095	-0.039	0.334
Abdomen height	0.018	-0.343	-0.322	0.116
Areolar length	0.391	-0.080	0.153	-0.022
Areolar width	0.098	0.041	-0.008	0.115
Width at hind edges of cephalothorax	-0.093	0.338	0.066	-0.381
Chelae finger length	-0.218	0.198	-1.406	0.180
Width at cervical groove	0.353	-0.027	-0.536	-0.599
Chelae length	0.752	-0.617	1.675	-0.698
Chelae width	-1.364	0.755	0.266	0.213
Chelae height	1.066	-0.393	-0.197	-0.213
Chelae palm length	-0.470	-0.191	-0.652	-0.346
Carapace width	-0.345	-0.524	0.099	0.399
Carapace height	-0.182	0.003	-0.094	0.053
Head length	0.690	0.089	0.295	0.314
Head width	-0.136	0.029	0.089	0.013
Rostrum length	0.435	0.449	0.185	0.285
Rostrum width	0.025	0.337	-0.185	-0.121
Length from tip of rostrum to cervical groove	-0.660	-0.290	0.058	-0.064
Telson length	-0.301	-0.225	-0.072	0.347
Telson width	0.056	0.104	0.310	-0.148
Width of rostrum at apex	0.143	-0.242	0.051	0.092
1st leg length	-0.020	0.341	0.230	1.091
2nd leg length	0.087	0.511	0.233	-0.118
3rd leg width	-0.314	-0.031	0.318	0.043
3rd leg depth	-0.178	0.367	-0.439	0.025
Pleopod length	0.077	-0.116	-0.257	0.052
Eye diameter	0.320	-0.116	0.037	-0.091
Tail fan width	-0.253	0.027	0.316	-0.259
Canoncial correlation	0.151	0.134	0.121	0.080
Eigenvalue	0.023	0.018	0.015	0.006
% of Variance	0.054	0.043	0.035	0.015
Chi-square	35.141	23.121	13.698	6.014
df	54.000	40.000	28.000	18.000
P-value	0.978	0.985	0.989	0.996

Variable	Function 25	Function 26
Abdomen length	0.088	-0.614
Abdomen width	-0.131	0.041
Abdomen height	-0.176	-0.030
Areolar length	0.048	0.193
Areolar width	0.057	0.084
Width at hind edges of cephalothorax	-0.155	-0.090
Chelae finger length	0.267	0.324
Width at cervical groove	-0.012	0.279
Chelae length	-0.134	0.162
Chelae width	-0.165	0.133
Chelae height	0.634	-0.466
Chelae palm length	-0.028	0.237
Carapace width	-0.056	-0.395
Carapace height	0.435	-0.103
Head length	0.077	0.415
Head width	-0.156	0.222
Rostrum length	0.398	0.550
Rostrum width	-0.090	0.078
Length from tip of rostrum to cervical groove	-0.115	-0.889
Telson length	-0.489	0.292
Telson width	0.085	-0.035
Width of rostrum at apex	0.414	-0.285
1st leg length	0.097	-0.035
2nd leg length	-0.566	-0.454
3rd leg width	0.188	0.251
3rd leg depth	0.179	0.063
Pleopod length	-0.248	-0.216
Eye diameter	-0.183	0.095
Tail fan width	0.235	0.197
Canoncial correlation	0.055	0.046
Eigenvalue	0.003	0.002
% of Variance	0.007	0.005
Chi-square	2.710	1.124
df	10.000	4.000
P-value	0.987	0.890

Table 5. Cross-validation table from the discriminant function analysis (DFA) of crayfish morphological characteristics. Numbers represent the counts for each species.

Species	*C. puer*	*C. diogenes*	*C. ludovicianus*	*F. fodiens*	*F. blairi*	*F. clypeata*	*O. deanae*
Cambarellus puer	20	0	0	0	0	0	0
Cambarus diogenes	0	19	1	0	0	0	0
Cambarus ludovicianus	0	4	16	0	0	0	0
Fallicambarus fodiens	0	0	0	20	0	0	0
Faxonella blairi	0	0	0	0	20	0	0
Faxonella clypeata	0	0	0	0	0	20	0
Orconectes deanae	0	0	0	0	0	0	10
Orconectes difficilis	0	0	0	0	0	0	7
Orconectes lancifer	0	0	0	0	0	0	0
Orconectes leptogonopodus	0	0	0	0	0	0	0
Orconectes macrus	0	0	0	1	0	0	0
Orconectes meeki brevis	0	0	0	0	0	0	0
Orconectes menae	0	0	0	0	0	0	0
Orconectes nais	0	0	0	0	0	0	0
Orconectes nana	0	1	0	0	0	0	0
Orconectes neglectus	0	0	0	0	0	0	0
Orconectes palmeri longimanus	0	0	0	0	0	0	0
Orconectes saxatilis	0	0	0	0	0	0	0
Orconectes virilis	0	0	0	0	0	0	0
Procambarus acutus	0	0	0	0	0	0	0
Procambarus clarkii	1	0	0	0	0	0	0

Procambarus curdi	0	0	0	0	0	0	0
Procambarus dupratzi	0	0	0	0	0	0	0
Procambarus gracilis	0	0	0	0	0	0	0
Procambarus liberorum	0	0	0	2	0	0	0
Procambarus simulans	0	0	1	0	0	0	0
Procambarus tenuis	0	0	0	0	0	0	0

Species	*O. difficilis*	*O. lancifer*	*O. leptogonopodus*	*O. macrus*	*O. meeki brevis*	*O. menae*	*O. nais*
Cambarellus puer	0	0	0	0	0	0	0
Cambarus diogenes	0	0	0	0	0	0	0
Cambarus ludovicianus	0	0	0	0	0	0	0
Fallicambarus fodiens	0	0	0	0	0	0	0
Faxonella blairi	0	0	0	0	0	0	0
Faxonella clypeata	0	0	0	0	0	0	0
Orconectes deanae	9	0	0	0	0	0	1
Orconectes difficilis	9	0	0	0	0	0	0
Orconectes lancifer	0	20	0	0	0	0	0
Orconectes leptogonopodus	0	0	18	0	0	1	0
Orconectes macrus	0	0	0	18	1	0	0
Orconectes meeki brevis	0	0	1	1	12	0	0
Orconectes menae	0	0	4	0	0	11	0
Orconectes nais	1	0	0	0	1	0	18
Orconectes nana	0	0	0	6	2	0	0

Orconectes neglectus	0	0	0	0	1	0	0
Orconectes palmeri longimanus	1	0	0	0	0	0	1
Orconectes saxatilis	0	0	0	0	0	1	0
Orconectes virilis	0	0	0	0	0	0	5
Procambarus acutus	0	0	0	0	0	0	0
Procambarus clarkii	0	0	0	0	0	0	0
Procambarus curdi	0	0	0	0	0	0	0
Procambarus dupratzi	0	0	0	0	0	0	0
Procambarus gracilis	0	0	0	0	0	0	0
Procambarus liberorum	0	0	0	0	0	0	0
Procambarus simulans	0	0	0	0	0	0	0
Procambarus tenuis	0	1	0	0	0	0	0

Species	*O. nana*	*O. neglectus*	*O. palmeri longimanus*	*O. saxatilis*	*O. virilis*	*P. acutus*	*P. clarkii*
Cambarellus puer	0	0	0	0	0	0	0
Cambarus diogenes	0	0	0	0	0	0	0
Cambarus ludovicianus	0	0	0	0	0	0	0
Fallicambarus fodiens	0	0	0	0	0	0	0
Faxonella blairi	0	0	0	0	0	0	0
Faxonella clypeata	0	0	0	0	0	0	0
Orconectes deanae	0	0	0	0	0	0	0
Orconectes difficilis	0	0	4	0	0	0	0
Orconectes lancifer	0	0	0	0	0	0	0

Orconectes leptogonopodus	0	2	0	0	0	0	0
Orconectes macrus	3	0	0	0	0	0	0
Orconectes meeki brevis	6	0	0	0	0	0	0
Orconectes menae	0	1	0	4	0	0	0
Orconectes nais	0	0	0	0	0	0	0
Orconectes nana	13	0	0	0	0	0	0
Orconectes neglectus	1	18	0	0	0	0	0
Orconectes palmeri longimanus	0	0	20	0	0	0	0
Orconectes saxatilis	0	1	1	18	0	0	0
Orconectes virilis	0	2	0	0	13	0	0
Procambarus acutus	0	0	0	0	0	18	0
Procambarus clarkii	0	0	0	0	0	0	19
Procambarus curdi	0	0	0	0	0	0	0
Procambarus dupratzi	0	0	0	0	0	0	0
Procambarus gracilis	0	0	0	0	0	0	0
Procambarus liberorum	0	0	0	0	0	0	0
Procambarus simulans	0	0	0	0	0	2	0
Procambarus tenuis	0	0	0	0	0	0	0

Species	*P. curdi*	*P. dupratzi*	*P. gracilis*	*P. liberorum*	*P. simulans*	*P. tenuis*	Total Count
Cambarellus puer	0	0	0	0	0	0	20
Cambarus diogenes	0	0	0	0	0	0	20
Cambarus ludovicianus	0	0	0	0	0	0	20

Fallicambarus fodiens	0	0	0	0	0	0	20
Faxonella blairi	0	0	0	0	0	0	20
Faxonella clypeata	0	0	0	0	0	0	20
Orconectes deanae	0	0	0	0	0	0	20
Orconectes difficilis	0	0	0	0	0	0	20
Orconectes lancifer	0	0	0	0	0	0	20
Orconectes leptogonopodus	0	0	0	0	0	0	21
Orconectes macrus	0	0	0	0	0	0	23
Orconectes meeki brevis	0	0	0	0	0	0	20
Orconectes menae	0	0	0	0	0	0	20
Orconectes nais	0	0	0	0	0	0	20
Orconectes nana	0	0	0	0	0	0	22
Orconectes neglectus	0	0	0	0	0	0	20
Orconectes palmeri longimanus	0	0	0	0	0	0	22
Orconectes saxatilis	0	0	0	0	0	0	21
Orconectes virilis	0	0	0	0	0	0	20
Procambarus acutus	0	0	0	0	2	0	20
Procambarus clarkii	0	0	0	0	0	0	20
Procambarus curdi	19	0	0	0	1	0	20
Procambarus dupratzi	0	20	0	0	0	0	20
Procambarus gracilis	0	0	16	4	0	0	20
Procambarus liberorum	0	0	7	11	0	0	20
Procambarus simulans	4	0	2	0	11	0	20
Procambarus tenuis	0	0	0	0	0	19	20

CHAPTER V

DO SYMPATRIC CRAYFISH SPECIES PARTITION TROPHIC RESOURCE USE?

Reid L. Morehouse

Abstract

Stream ecosystems support diverse communities of fish and macroinvertebrates, and resource partitioning is a key mechanism facilitating stable coexistence of functionally similar species. Crayfish are a very diverse group of macroinvertebrates, play important roles in ecosystem functioning, and can comprise the majority of invertebrate biomass. Despite multiple species often co-occurring in the same habitat, mechanisms facilitating coexistence of different crayfish remain largely unknown. We utilized stomach content and stable isotope ($\delta^{13}C$ and $\delta^{15}N$) analyses to test whether sympatric species across three different geographic regions occupy distinct trophic niches. We found substantial among site variation in stomach contents and stable isotope signatures. This likely reflects spatial variation in resource availability, because crayfish isotopic signatures were significantly correlated with those of resources at the base of the food web (fine particulate organic matter). More importantly, we uncovered significant differences both in stomach contents and in isotopic signatures ($\delta^{15}N$) between sympatric species in some – but not all – investigated streams, suggesting that species partition food resources by feeding on different dietary items. We discuss these findings in the context of concrete hypotheses that could explain the varying degree of niche partitioning in sympatric crayfish across sites and outline future steps required to understand coexistence of crayfish species.

Keywords: Crayfish, Niche partitioning, Stable Isotopes, Sympatric Species, Trophic Resources

Introduction

Stream ecosystems support diverse communities of fish and macroinvertebrates. While fish dominate freshwater vertebrate diversity worldwide, macroinvertebrate diversity exceeds vertebrate diversity at any one locale (Allan and Flecker 1993). Ecological theory predicts that stable coexistence of competing or functionally similar species is mediated through niche partitioning and according differentiation along some niche axis that reduces overlap among species (Colwell and Fuentes 1975; Hardin 1960; Pianka 1974, 1976). Indeed, empirical evidence supports niche partitioning in coexisting aquatic macroinvertebrates (Atkinson et al. 2010; Behmer and Joern 2008; Khelifa et al. 2013) and in fish (Barili et al. 2011; Correa and Winemiller 2014; Guo et al. 2014; Lujan et al. 2011), including differentiation in both microhabitat and trophic resource use. For example, sympatric dragonfly species partitioned niches through occupying different microhabitats (i.e., open areas *vs.* heavy vegetation) to avoid direct competition (Khelifa et al. 2013), while filter-feeding freshwater bivalves selectively fed on microorganisms with certain elemental ratios (Atkinson et al. 2010). Similar results have been found in fish, where even apparently similar sympatric species selectively feed on different food resources (Lujan et al. 2011; Polačik et al. 2014).

Crayfish (Cambaridae) are a diverse group of decapods with over 400 species occurring throughout large portions of North America, particularly east of the Rocky Mountains (Taylor et al. 2007). They play important roles in aquatic ecosystem functioning and can comprise the majority of invertebrate biomass (Momot et al. 1978; Rabeni et al. 1995). As keystone species, crayfish have the ability to alter food web structure, and cause trophic cascades (Evans-White et al. 2001; Evans-White et al. 2003), ultimately having complex impacts on their ecosystems that can be difficult to predict (Renai and Gherardi 2004). Despite their abundance and critical role in aquatic habitats, relatively little is known about variation in trophic resource use and trophic interactions within and among crayfish species. Typically considered omnivores, crayfish as a group have been documented to exploit a diversity of food sources from particulate organic matter to aquatic vertebrates, and they occupy an intermediate trophic position between non-crayfish macroinvertebrate and fish consumers (Schofield et al. 2001; Taylor and Soucek 2010; Whitledge and Rabeni 1997). The classification of crayfish as omnivores, however, has lead to a lack of knowledge about variation in dietary preferences and potential mechanisms of trophic niche differentiation that could contribute to the stable coexistence of multiple species in the same habitat.

Previous studies have produced contrasting results about trophic resource use in crayfish. Some species have been found to predominantly feed on algae and detritus (Evans-White et al. 2001), while others incorporate substantial proportions of macroinvertebrates into their diet (Parkyn et al. 2001). In addition, some crayfish species appear to be active predators or scavengers (Taylor and Soucek 2010; Thomas and Taylor 2013; Whitledge and Rabeni 1997). For example, Taylor and Soucek (2010) inferred that fish comprised approximately 12% of the diets of three species of crayfish (*Orconectes propinquus*, *O. rusticus*, and *O. virilis*) by using stable isotope based mixing models, but were unable to determine if crayfish actively preyed upon live fish and fish eggs, or whether they scavenged carcasses. Nonetheless, laboratory and field experiments indicated that – even relatively small – crayfish species are capable of actively capturing fish and other vertebrates at natural densities (Gherardi et al. 2001; Thomas and Taylor 2013; Z. Culumber unpublished data). The role of crayfish as active predators has also been implied by studies documenting inverse correlations between crayfish and benthic fish densities (Thomas and Taylor 2013), negative recruitment in centrarchid fishes due to crayfish nest predation (Dorn and Mittelbach 2004), and declines in macroinvertebrate biomasses (Usio and Townsend 2004). While crayfish as a group undoubtedly exploit a wide variety of trophic resources, the major factors driving within and among species variation in diet still remain poorly understood. This is in part caused by many studies focusing on single species and/or single streams (e.g., Perry et al. 2000; Rabeni et al. 1995; Rosenthal et al. 2006; Whitledge and Rabeni 1997).

Local resource availability likely plays a critical role in shaping crayfish diets. For example, Parkyn et al. (2001) documented substantial intraspecific variation in trophic resource use driven by land use patterns surrounding streams. When investigating *Paranephrops planifrons* occurring in forested and pasture streams, specimens from pasture streams consistently exhibited a higher trophic position as inferred both by a higher proportion of macroinvertebrates *vs*. leaf litter present in gut contents, and by a higher $\delta^{15}N$ value in stable isotope analyses (Parkyn et al. 2001). In addition, interspecific competition might affect crayfish resource use. However, despite multiple species of crayfish often coexisting in the same (micro) habitats (Morehouse and Tobler 2013; Taylor et al. 2007), it remains largely unclear whether and how sympatric species partition trophic resource use to minimize competitive interactions and prevent competitive exclusion.

The goal of this study was to examine trophic resource use in multiple species of crayfish occurring in the states of Oklahoma and Missouri. We specifically used stomach content and stable isotope analyses to ask whether sympatric species across three different geographic regions occupy distinct trophic niches. Based on the competitive exclusion principle (Hardin 1960), we predicted sympatric species to exploit different dietary resources, which should be reflected in among species variation in gut contents and in the stable isotope composition of the body. Finding substantial variation in stable isotope ratios among sites (even within the same species), we also asked whether such variation is indicative of vastly different dietary preferences among sites, or whether among site differences in stable isotope ratios at the base of the food web (fine particulate organic matter, FPOM) predicts isotopic composition of crayfish consumers.

Methods

Study sites, sample collection, and preparation

We collected crayfish from three separate geographic regions, two in Oklahoma (Ozark Mountains, sampled in 2011, and Ouachita Mountains, sampled in 2012) and one in Missouri (sampled in 2013) (Figure 1). In each region, between three and six stream sites were sampled (Table 1). All streams were first to third order streams surrounded by forested riparian zones with various types of agricultural fields within the watersheds. Crayfish were collected by flipping rocks, hand netting, and backpack electrofishing within a 100-meter segment of stream at each sampling location. Overall, we collected 12 species of crayfish, which occurred in different combinations across study sites. Collected crayfish were placed on ice and returned to the laboratory, where carapace length (tip of rostrum to the posterior edge of carapace) was measured to the nearest 0.01 mm and samples for gut content and stable isotope analyses were extracted. For select sampling locations in the two Oklahoma regions (see Table 1), we also collected fine particulate organic matter (FPOM) to test for a correlation between stable isotope composition at the base of the food web and in crayfish consumers. FPOM was filter from 500 ml of water onto 20 mm Whatman GF/F microfibre glass filters. Below, we first describe the methods of data collection and then the analytical approaches to address our questions.

Stomach contents

Crayfish were dissected for stomach contents to evaluate variation in trophic resource use. Stomachs were dissected from specimens and fixed in 70% ethanol. Stomach contents were then removed, distributed across a Petri dish, and examined using a dissecting microscope. We identified the contents to one of six categories following Taylor and Soucek (2010): (1) detritus; (2) crayfish parts; (3) unidentified organic matter; (4) fish parts (i.e., bones, scales); (5) algae/periphyton; and (6) macroinvertebrates (non-crayfish). The presence or absence of each food type was recorded for each specimen.

Stable isotope analyses

Extracted crayfish abdominal muscle tissue and FPOM samples were dried at 60°C for 48 hours, and the crayfish tissue was ground into a powder using a mortar and pestle. Sub-samples (approximately 0.1 mg) were then packed into tin capsules and sent to the University of California at Davis' Stable Isotope Facility for carbon (^{13}C) and nitrogen (^{15}N) isotope analysis. Stable isotope composition was determined using a PDZ Europa 20-20 isotope ratio mass spectrometer. Stable isotope ratios are expressed in δ notation as parts per thousand according to the following equation:

$$\delta(‰) = [(R\text{sample} - R\text{standard}) - 1] * 1000,$$

where R represents the molar ratio of the heavy to light isotopes of an element. The standard ratio used was atmospheric nitrogen and Vienna PeeDee Belemnite for ^{15}N and ^{13}C, respectively. Examining the relative amount of carbon isotope reveals the source of carbon being utilized by consumers as less than 1‰ of carbon is fractionated across trophic levels (Post 2002). In contrast, ^{15}N is fractionated between 3-5‰ across trophic levels; hence, $\delta^{15}N$ values allow inferences about trophic positions of consumers to be made (Vander Zanden and Rasmussen 1999).

Statistical analyses

To test whether sympatric crayfish species differentially feed on available food items, presence and absence data for each dietary category present in crayfish stomachs were first subjected to a correspondence analysis (CA) to reduce data dimensionality. We retained three CA axes explaining 55% of variation (Table 2) and calculated CA scores for each individual for quantitative analysis. CA scores for the three axes were then used as dependent variables in a multivariate analysis of variance (MANOVA), in which site and species (nested within site) served as independent variables. In addition to stomach content data, stable isotope ratios were used as a complimentary approach to infer potential trophic niche differentiation. $\delta^{13}C$ and $\delta^{15}N$ isotopic signatures were used as the dependent variables in a MANOVA, and as in the previous analysis, we used site and species (nested within site) as the independent variables. If crayfish are occupying distinct trophic niches, we expected to find significant species differences in $\delta^{13}C$ and/or $\delta^{15}N$ isotopic signatures.

Due to stark among site variation, particularly in stable isotope signatures (see results), we also asked whether stable isotope ratios of consumers were affected by the stable isotope ratios of FPOM, representing availability at the bottom of the food web. To do so, we calculated site-specific estimated marginal means of $\delta^{13}C$ and $\delta^{15}N$ both for crayfish consumers and for FPOM samples. We then used a linear regression to test whether crayfish stable isotope signatures were related to FPOM stable isotope signatures across sites. If baseline stable isotope signatures are significant predictors for among site variation in consumer signatures, it is unlikely that among site variation in crayfish stable isotopes are indicative of stark differences in trophic resource use.

For all MANOVAs, *F*-values were approximated using Wilks' lambda and effect strengths by use of partial eta squared (η_p^2). The assumptions of normal distribution and homogeneities of variances and covariances were met for all analyses, and all *P*-values reported were two-tailed. Statistical analyses were conducted in SPSS 20, except for CA, which was conducted in Canoco 5.

Results

Two hundred and twenty seven crayfish were collected and used for all subsequent analyses. Overall, unidentified organic matter (92%) and detritus (84%) dominated stomach contents of the crayfish species investigated. Detritus occurrence ranged from 33 - 100%, crayfish parts 0 - 7%, unidentified organic matter 73 - 100%, fish parts 0 - 31%, algae/periphyton 0 - 18%, and macroinvertebrates 0 - 33% for all species combined (see Figure 2 for summaries of each species' diet). Despite the high prevalence of detritus and unidentified organic matter, CA revealed substantial variation in stomach contents that was summarized in three CA axes (Table 2). Stomach contents varied significantly among collections sites ($F_{36,568} = 1.841$, $P = 0.002$, $\eta_p^2 =$

0.103) particularly along the second CA axis (Figure 3A). More importantly, there was also a significant effect of species ($F_{42,570} = 1.519$, $P = 0.021$, $\eta_p^2 = 0.100$) both along the second and third CA axes, indicating at least some degree of differential diet use between sympatric species. *Post-hoc* comparisons, however, revealed that the significant species term in the multivariate analysis was primarily driven by two sites with significant species differences (Pearson's Creek with *O. n. chaenodactylus* and *O. ozarkae*; Tributary to Flint Creek with *O. n. neglectus*, *O. m. brevis*, and *O. nana*; Table 3). At two additional sites, species differences were marginally non-significant (Luksuklo Creek with *O. p. longimanus* and *O. menae;* Honey Creek with *O. n. neglectus* and *O. macrus*; Table 3). For all other sites, *post-hoc* species comparisons were clearly non-significant ($P > 0.100$; see Table 3 for details).

Analysis of stable isotopes corroborated results from stomach content analysis, albeit with clearer results. We found significant differences in stable isotope signatures among sites ($F_{26,432} = 187.761$; $P < 0.001$, $\eta_p^2 = 0.919$) both for $\delta^{13}C$ and $\delta^{15}N$, as well as between species nested within site ($F_{32,432} = 3.756$; $P < 0.001$, $\eta_p^2 = 0.218$) for $\delta^{15}N$ (Figure 3B). *Post-hoc* comparisons indicated significant differences ($F \geq 4.904$, $P \leq 0.028$; see Table 3) between sympatric species at the following sites: Tributary to Flint Creek (*O. n. neglectus*, *O. m. brevis*, and *O. nana*), Cucumber Creek (*O. leptogonopodus* and *O. menae*), Blackbird Creek (*O. n. neglectus* and *O. m. brevis*), Honey Creek (*O. n. neglectus* and *O. macrus*), Big Eagle Creek (*O. menae* and *O. p. longimanus*), and Sawyer Creek (*O. n. chaenodactylus* and *O. ozarkae*). In contrast, no evidence for differentiation in stable isotope signatures ($F \leq 1.700$, $P \geq 0.212$) was found at Ross Branch (*O. n. neglectus* and *O. m. brevis*), Lost Creek (*O. n. neglectus* and *O. nais*), South Fork Dry Sac (*O. luteus* and *O. virilis*), Pearson's Creek (*O. n. chaenodactylus* and *O. ozarkae*), as well as sites Rock Creek, Luksuklo Creek, and Beach Creek (all with *O. menae* and *O. p. longimanus;* see Table 3 for details).

Finally, analyzing the stable isotope signature of FPOM in a sub-sample of sites analyzed above indicated that stable isotope ratios at the base of the food web significantly predicted the signatures of the crayfish consumers. δ^{13}C values in FPOM were not significant, but δ^{15}N values in FPOM were significantly and positively correlated with those quantified in crayfish ($F_{1,4}$ = 28.703; P = 0.013; R^2 = 0.905) (Figure 4).

Discussion

This study examined the trophic ecology of twelve species of crayfish in three regions of Oklahoma and Missouri. Consistent with previous studies examining stomach contents in stream and lake dwelling crayfishes (Momot et al. 1978; Parkyn et al. 2001; Taylor and Soucek 2010; Whitledge and Rabeni 1997), detritus and unidentified organic matter dominated crayfish stomach contents. Nonetheless, both stomach content and stable isotope analyses revealed significant among site variation. More importantly, we uncovered evidence for differential resource use in sympatric crayfish species, suggesting potential trophic niche partitioning.

Among site variation in trophic resource use

The factor "site" explained the bulk of variation especially the stable isotope data, with differences both along the δ^{13}C and δ^{15}N axes. These strong patterns of variation among sites were not driven by the fact that different species (combinations) were investigated, because analyses of among site variation in individual species (data not shown) produced the same results. Based on a δ^{15}N fractionation rate of 3-5‰ per trophic level (Post 2002), these data were suggestive of trophic levels varying from one to four positions within the same species across different sites. While such intraspecific differences in trophic position have previously been reported in the literature (Beatty 2006; Johnston et al. 2011), and at first glance, stark differences in stable isotope signatures may be indicative of variation in trophic resource use, the correspondence of isotope signatures of FPOM (a major contributor of energetic input into the low-order streams we investigated; Whitledge and Rabeni 1997) and crayfish tissues indicates that among site variation is likely driven by local availability in food resources. That is, among site variation in stable isotope signatures is not driven by crayfish consuming radically different dietary items, but by similar dietary items present across sites having different stable isotope signatures due to differential input at the base of the ecosystem. Similar to our study, Johnston et al. (2011) observed differences among sites in carbon and nitrogen isotopes for all of the crayfish species examined, and attributed $\delta^{15}N$ enrichment at some locations to a waterbird rookery at one of their sites that elevated dissolved nitrogen concentrations (Baxter and Fairweather 1994) and $\delta^{15}N$ values (Stenroth et al. 2008). Our results coincide with these findings as the sampling locations in northeastern Oklahoma and Missouri are located in agricultural areas, and poultry manure is frequently used as fertilizer for surrounding fields (Haggard et al. 2001), likely affecting the stable isotope signatures of baseline nutrients like FPOM.

Trophic niche partitioning in sympatric crayfish species

Stomach content and stable isotope analyses revealed evidence for significant differences in trophic resource use in sympatric crayfish species. Significant differences were found in two species pairs using stomach contents and six pairs using stable isotope analyses. Differentiation in stable isotope signatures exclusively occurred along the $\delta^{15}N$ axis, suggesting that niche partitioning particularly involves crayfish occupying different trophic levels. A lack of differentiation along the $\delta^{13}C$ axis is not surprising; the sites sampled in this study were all first to third order streams surrounded by trees in the riparian zone, and the carbon source in such streams is almost entirely allochthonous (Vannote et al. 1980).

Despite the evidence for trophic niche partitioning this study has uncovered, it is important to note that this pattern was by no means universal, as there were multiple sites harboring sympatric crayfish species lacking any significant differences in stomach contents and stable isotope signatures. This finding parallels a study by Johnston et al. (2011), which examined three sympatric species across multiple sites and suggested that one species predominantly consumes plant materials, while the other two species also feed on animal material, with large overlap in trophic resource use in the latter two. We propose three alternative, but not mutually exclusive, hypotheses that could explain the observed variable degree of niche partitioning. (1) The degree of niche partitioning could be dependent on the species combination present in any given stream. Overall, our data provides little evidence for this hypothesis, because in most species pairs for which we had replicates across multiple sites (e.g., *O. menae* and *O. longimanus*, *O. m. brevis* and *O. n. neglectus*, as well as *O. n. chaenodactylus* and *O. ozarkae*), there were sites with and sites without evidence for trophic differences. The only exception may include the midget crayfishes (*O. macrus* and *O. nana*), which consistently exhibited elevated δ^{15}N values and relatively low proportions of detritus in their diet compared to larger bodied, sympatric congeners. These observations are consistent with Lorman (1975), showing that smaller bodied crayfish species have higher growth rates (requiring protein rich diets), but have reduced total energy requirements relative to larger bodied crayfish, leading to an increased consumption of animal based foods as opposed to detritus (also see Whitledge and Rabeni 1997).

(2) Trophic niche partitioning in crayfish may be temporally variable. Indeed, there is much evidence for such temporal variation in dietary differentiation in fishes inhabiting seasonal environment. Overlap in trophic resource use has been shown to be high when resources are abundant and competitive interactions relatively low, but decreased during periods of reduced resource availability and intensified competition (Colwell and Futuyma 1971; Correa and Winemiller 2014; Komonen et al. 2004; Winemiller et al. 2005). Our current sampling scheme, with sites being visiting only once, does not allow testing for potential temporal variation in dietary overlap, and future studies will need to address this question by rigorously sampling multiple crayfish assemblages across seasons or periods of differential resource availability.

(3) Trophic niche partitioning may be critically dependent on spatial variation in resource availability. In some stream habitats, resource availability both in terms of quality and

quantity may be relatively low, and niche partitioning in sympatric crayfish species accordingly pronounced (Brewer et al. 2009; DiStefano et al. 2003). In contrast, resource availability may not be limiting at other sites, potentially allowing for the coexistence of multiple crayfish species without differentiation in resource use. Availability driven diets with large overlap between functionally similar species have been documented in other systems (Martin and Genner 2009). In fact, detritus is frequently abundant in aquatic ecosystems (Moyle and Light 1996), such that there may be little competition for resources and accordingly little opportunity or necessity for niche differentiation among detritivores (Scharnweber et al. 2011), including crayfishes investigated here.

Conclusions

Overall, this study indicated that sympatric crayfish species do partition food resources in some locations both based on stomach content and stable isotope analyses. Ecological theory predicts that if two species are indistinguishable ecologically, one species should stochastically drift to extinction (Hubbell 2001), or suffer competitive exclusion through the dominant species in the shared niche (Hardin 1960). While the trophic niche partitioning therefore could contribute to the stable coexistence of sympatric crayfish species, additional research is clearly required to fully understand the level of niche differentiation in the taxa examined. This not only includes additional aspects of trophic ecology (including temporal variation in resource use), but it also remains unclear whether and how sympatric crayfish partition microhabitat use (Clark et al. 2013; Flinders and Magoulick 2007).

Acknowledgements

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Table 1. List of sampling sites including location (stream name, county, and state) as well as latitude and longitude GPS coordinates. For each site, we also list the crayfish species present and the sample size (*N*) for each species. Asterisks indicate sites that were included in the analysis of FPOM isotope signatures.

Location	**Latitude; Longitude**	**Crayfish species present (*N*)**
South Fork Dry Sac (Greene County, MO)	37.265545; -93.249031	*O. luteus* (10)/ *O. virilis* (7)
Pearson Creek (Greene County, MO)	37.17131; -93.19672	*O. n. chaenodactylus* (10)/ *O. ozarkae* (3)
Sawyer Creek (Greene County, MO)	37.193142; -93.107075	*O. n. chaenodactylus* (10)/ *O. ozarkae* (9)
Ross Branch (Cherokee County, OK)*	35.89271; -94.95650	*O. n. neglectus* (10)/ *O. m. brevis* (10)
Blackbird Creek (Cherokee County, OK)*	36.02812; -95.04919	*O. n. neglectus* (10)/ *O. m. brevis* (10)
Tributary to Flint Creek (Delaware County, OK)*	36.18657; -94.70946	*O. n. neglectus* (10)/ *O. m. brevis* (9)/ *O. nana* (9)
Tributary to Lost Creek (Ottawa County, OK)	36.84374; -94.65531	*O. n. neglectus* (5)/ *O. nais* (11)
Honey Creek (Delaware County, OK)*	36.54886; -94.68359	*O. n. neglectus* (8)/ *O. macrus* (9)
Rock Creek (LeFlore County, OK)	34.511456; -94.61645	*O. p. longimanus* (10)/ *O. menae* (5)
Luksuklo Creek (McCurtain County, OK)	34.036050; -94.58098	*O. p. longimanus* (10)/ *O. menae* (10)
Cooper Creek (LeFlore County, OK)	34.06447; -94.64572	*O. p. longimanus* (10)/ *O. menae* (3)
Big Eagle Creek (McCurtain County, OK)	34.52182; -94.72274	*O. p. longimanus* (9)/ *O. menae* (5)
Pigeon Creek (LeFlore County, OK)*	34.645375; -94.539311	*O. p. longimanus* (10)
Cucumber Creek (LeFlore County, OK)*	34.55612; -94.707275	*O. menae* (5)/ *O. leptogonopodus* (11)

Table 2. Correspondence Analysis (CA) results from crayfish stomach contents. Eigenvalues, percent variation explained by each axis, and response variables for each food source. Response variables indicate the position along the axes for each food source.

	Axis 1	**Axis 2**	**Axis 3**
Eigenvalues	0.5382	0.269	0.0853
Explained variation (cumulative)	33.18	49.77	55.03

	Resp.1	**Resp.2**	**Resp.3**
Detritus	2.8707	0.7437	0.7737
Crayfish parts	0	1.3045	1.1671
Unidentified OM	2.9394	1.906	2.0292
Fish parts	4.7509	3.1808	0
Algae/Periphyton	4.3937	-0.7437	3.2771
Macroinvertebrates	1.5395	0.0659	1.2572

Table 3. *Post-hoc* comparisons of sympatric crayfish species from the results of the multivariate analysis of variance (MANOVA) on stomach contents and stable isotopes. Bold indicates significant values (*P*<0.05). df represents the hypothesis df and error df in each MANOVA.

Stream name	Species	Stomach Contents			Stable Isotopes		
		df	*F*	*P*-value	df	*F*	*P*-value
Pearson Creek	*O. n. chaenodactylus/O. ozarkae*	2,10	7.981	**0.008**	2,10	1.320	0.310
Sawyer Creek	*O. n. chaenodactylus/O. ozarkae*	4,14	0.645	0.640	2,17	5.958	**0.011**
South Fork Dry Sac	*O. luteus/O. virilis*	3,13	1.02	0.416	2,14	1.097	0.361
Tributary to Flint Creek	*O. n. neglectus/O. m. brevis/O. nana*	8,44	2.676	**0.017**	4,54	5.407	**0.001**
Ross Branch	*O. n. neglectus/O. m. brevis*	4,15	1.82	0.177	2,17	1.700	0.212
Blackbird Creek	*O. n. neglectus/O. m. brevis*	4,14	0.944	0.468	2,17	4.486	**0.027**
Honey Creek	*O. n. neglectus/O. macrus*	4,12	2.585	0.091	2,16	16.686	**<0.001**
Lost Creek	*O. n. neglectus/O. nais*	4,11	1.806	0.198	2,12	0.107	0.900
Cucumber Creek	*O. menae/O. leptogonopodus*	2,13	0.593	0.567	4,26	3.567	**0.019**
Rock Creek	*O. p. longimanus/O. menae*	3,8	0.327	0.806	2,12	0.610	0.559
Luksuklo Creek	*O. p. longimanus/O. menae*	3,15	2.697	0.083	2,17	1.450	0.262
Cooper Creek	*O. p. longimanus/O. menae*	2,9	2.068	0.182	2,10	1.178	0.347
Big Eagle Creek	*O. p. longimanus/O. menae*	1,11	0.967	0.347	2,12	4.904	**0.028**

Figure 1. Map of the study region in Oklahoma (Ozark Mountains on the north side of the state, and Ouachita Mountains in the south) and Missouri. Dots indicate the location of specific sampling locations.

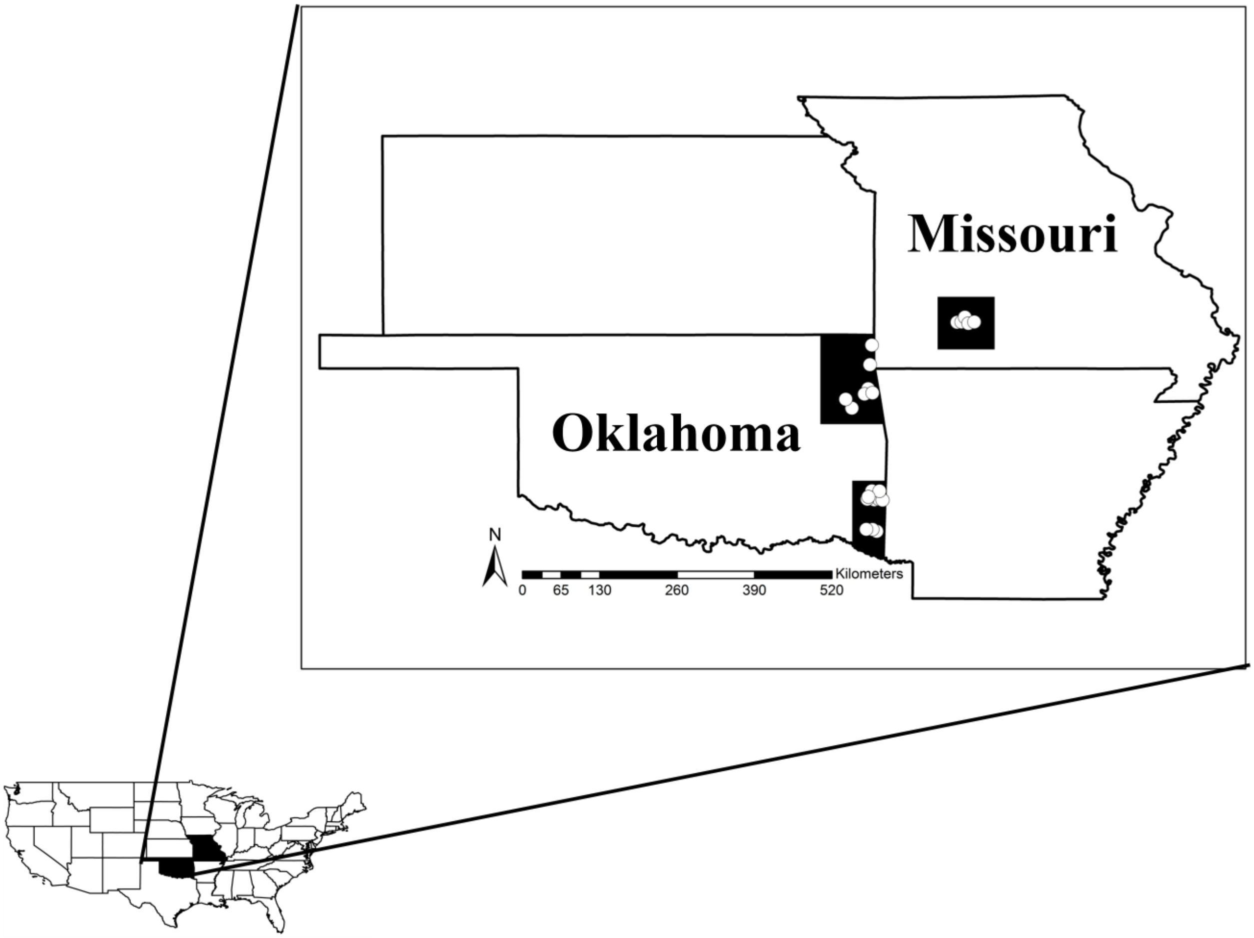


Figure 2. Percent occurrence of stomach contents for each crayfish species investigated.

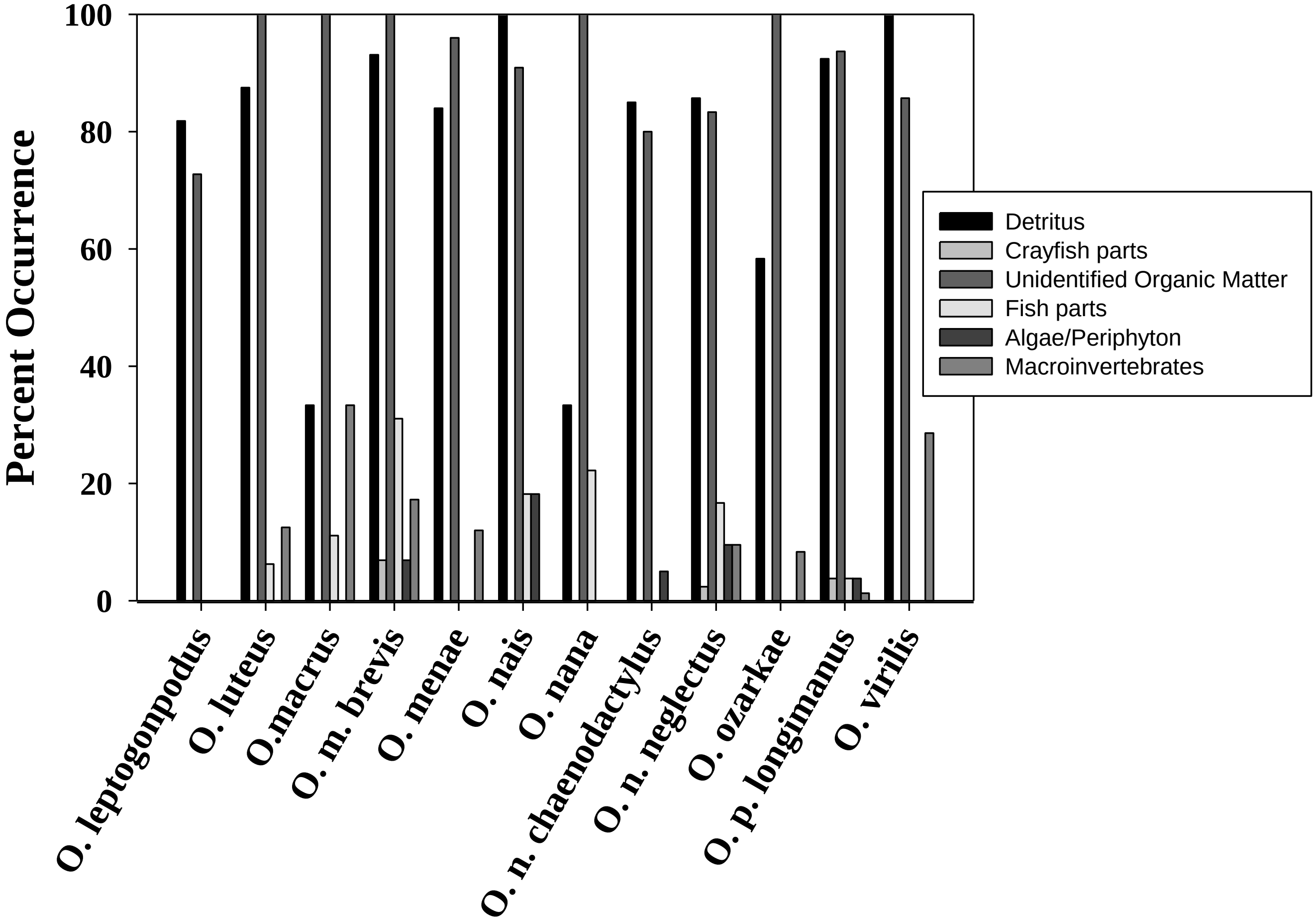


Figure 3. A) Correspondence Analysis (CA) axes 2 and 3 from stomach contents results. Triangles represent food resources and dots represent the estimated marginal means of individual crayfish species. Bars represent the standard error of the mean. B) Stable isotope ($\delta^{13}C$, $\delta^{15}N$) bi-plot of the estimated marginal means for sympatric crayfish species pairs. The same symbol and color represent sampling location and each individual symbol represents a separate species. Bars represent the standard error of the mean.

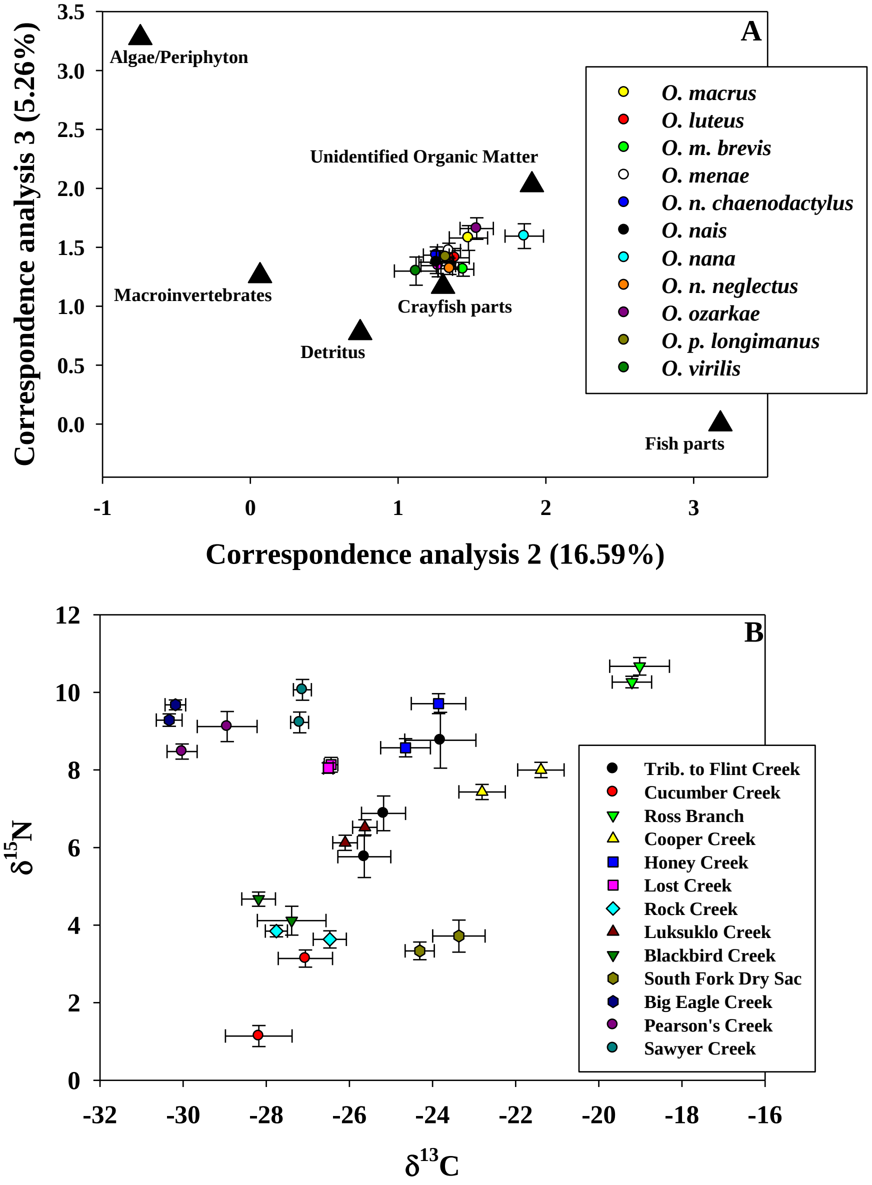
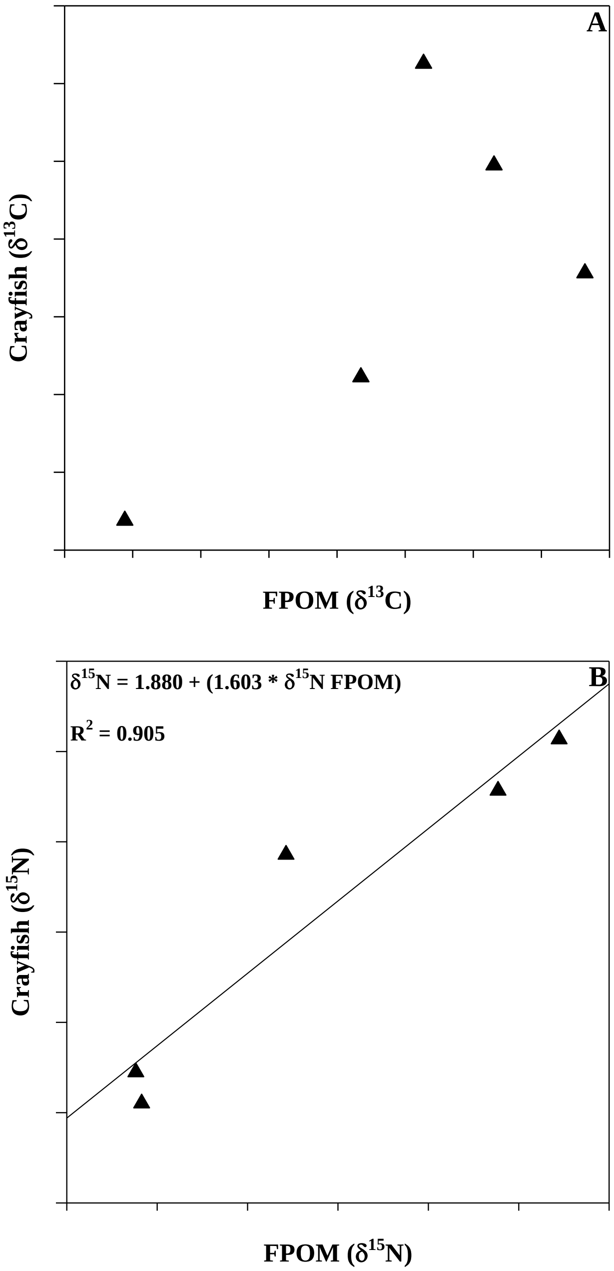


Figure 4. Bi-plot of stable isotope signatures (A; $\delta^{13}C$) and (B; $\delta^{15}N$) for crayfish and fine particulate organic matter (FPOM) across sampling locations. Solid line represents the regression line.



VITA

Reid Landen Morehouse

Candidate for the Degree of

Doctor of Philosophy

Thesis: SPECIES DISTRIBUTIONS AND TRAIT-ENVIRONMENT CORRELATIONS: IMPLICATIONS FOR THE EVOLUTIONARY ECOLOGY OF CRAYFISH (DECAPODA: CAMBARIDAE)

Major Field: Zoology

Biographical:

Education:

Completed the requirements for the Doctor of Philosophy in Zoology at Oklahoma State University, Stillwater, Oklahoma in July, 2014.

Completed the requirements for the Master of Science in Zoology at Oklahoma State University, Stillwater, Oklahoma in May 2010.

Completed the requirements for the Bachelor of Science in Fisheries and Aquatic Sciences at Purdue University, West Lafayette, Indiana in December 2006.

Experience: Research Assistant at Oklahoma State University investigating Tier listed fish and crayfish in northeast Oklahoma.
Teaching Assistant for Introduction to Biology and Ecological Niche Modeling: Applications and Processes.

Professional Memberships: Freshwater Science, Southwestern Association of Naturalists, American Fisheries Society, Oklahoma-Texas Aquatic Research Group, Great Plains Limnological Society.