

ASSESSING THE DISTRIBUTION AND HABITAT
NEEDS OF THE LEAST DARTER AND SYMPATRIC
SPECIES OF THE OZARK HIGHLANDS AND
ARBUCKLE MOUNTAIN ECOREGIONS

By

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Abstract: There are more than 700 freshwater fish species considered vulnerable, threatened, or endangered making fish one of the most imperiled taxa in North America. Several of these species are found exclusively or primarily in lotic or semi-lotic systems. The hierarchical nature of lotic systems convolutes the quantification of species-habitat relationships necessary for development of successful management or conservation strategies. This hierarchical nature means it is fundamentally important to understand population persistence and patch dynamics at multiple spatial and temporal scales. Groundwater dependent streams often have unique assemblages adapted to their unique thermal and physicochemical conditions. The Least Darter (*Etheostoma microperca*) is an isolated spring-obligate species with disjunct southern populations in the Ozark Highlands and Arbuckle Uplift ecoregions. Though Least Darter are considered a spring-associated species, the habitat conditions which regulate their distributions are relatively unknown at all spatial and temporal scales. Understanding these relationships will be integral for developing management and monitoring strategies. I sampled habitat at coarse (reach) and fine (sub-reach) scales in the Ozark Highlands and Arbuckle Uplift ecoregions of Oklahoma in 2018 and 2019. At the reach scale Least Darter and Southern Redbelly Dace occupancy probabilities are inversely related to temperature, whereas Redspot Chub and Smallmouth Bass increase with increases in drainage area. Furthermore, Southern Redbelly Dace and Smallmouth Bass sub-adult occupancy was influenced by sample year. In addition to the reach-scale occupancy, sub-reach observations were made to determine fine-scale Least Darter habitat associations. A reach in the Arbuckle Uplift and a reach in the Ozarks Highlands were sampled in winter and summer to determine Least Darter seasonal patch use. Our fine-scale observations showed Least Darter are generally associated with microhabitats containing fine substrates and use shallower higher-velocity areas with less vegetation in winter when compared to summer. The results of this study may be used to help develop year-round baseflow guidelines that support necessary groundwater inputs for these species. The development of such guidelines will be integral in maintaining variable yet suitable thermal and physical conditions for groundwater associated species to persist in these lotic environments.

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CHAPTER I

INTRODUCTION

There are more than 700 freshwater fish species considered vulnerable, threatened, or endangered making fish one of the most threatened taxa in North America (Jelks et al. 2008). In the southern United States, 28% of fishes are considered vulnerable, threatened or endangered (Warren Jr. et al. 2000). Over-exploitation, water pollution, habitat degradation, species invasion, and flow modification are the greatest threats affecting freshwater fishes (Dudgeon et al. 2006). The physical and biological processes of streams are altered by anthropogenic activities such as dams, agriculture, water overconsumption, toxic chemicals and exotic species (Karr et al. 1985). Particularly in southern United States streams, channelization, impoundments, sedimentation, and flow modification are significant alterations leading to species declines (Etnier 1997; Warren Jr. et al. 2000). Many fish species in the southern United States have narrow ranges and are geographically isolated (Burr and Mayden 1992), thereby exacerbating the effects of habitat degradation on these species (Eaton and Scheller 1996). Fish populations may become isolated because of geocliological phenomena, which can result in separation of populations with different environmental and resource needs (Lesica and Allendorf 1995;

Marsh-Matthews and Matthews 2000; Hoagstrom et al. 2014). Peripheral populations are often smaller when compared to core populations, which can lead to increased extirpation risk, but also increased evolution potential (Lesica and Allendorf 1995). Separated populations were isolated by glaciation (Berendzen et al. 2010), stream capture (Buth and Mayden 1981), and tectonic lifts (McKeown et al. 1988) sometimes leaving only small suitable habitat patches. For example, in the southern United States there are isolated thermal patches due to springs, providing refuge for fishes requiring cooler water temperatures (Bergey et al. 2008; Seilheimer and Fisher 2010), such as the Arkansas Darter (*Etheostoma cragini*) and Watercress Darter (*Etheostoma nuchale*, Duncan et al. 2010). Isolated populations are more vulnerable to environmental perturbations where the likelihood of population persistence decreases via habitat degradation (e.g., water withdraws and impoundments, Poole and Berman 2001).

Groundwater dominated streams have relatively stable discharge conditions and are typified by relatively constant annual water temperatures near hyporheic and spring inflows (Hubbs 1995; Poff 1996; Mcmanamay et al. 2014). Low variation in discharge leads to an increase in predictability of high and low-flow events increasing refugia availability for organisms (Moyle and Vondracek 1985; Schlosser 1990). Groundwater dominated streams have cooler thermal regimes during the summer, and warmer temperatures during winter when compared to streams regulated by surface runoff (Whitledge et al. 2006). Groundwater dependent streams often have unique assemblages adapted to these unique conditions (Hubbs 1995; Farless and Brewer 2017). However, temperature changes can affect the distribution and persistence of fishes (Last et al. 2011) causing fish to seek out temperature refuge near seeps and springs (Snyder et al. 2015).

The thermally more stable groundwater sources can isolate associated species because surrounding habitat is not suitable for persistence.

Temperature has a myriad of effects on fish ecology (i.e., lethal, stressing, controlling, masking, limiting and directing, Coutant 1976). Temperature can alter the range and persistence of fish populations (Last et al. 2011). Temperature, alone or in concert with other environmental factors, is a primary driver altering fish distributions (Taniguchi et al. 1998; Buisson et al. 2008). Mollenhauer et al. (2019) showed the relationship between fish assemblage structure and groundwater contributions in the Ozark Highlands of Oklahoma and Missouri. Additionally, species may associate themselves with microhabitat patches having different thermal characteristics than the surrounding stream (Baltz et al. 1987; Ebersole et al. 2001). Fish-patch associations may also vary with time of day (i.e., diel, Young 1999; Armstrong et al. 2013), season (i.e., summer, (Ingersoll and Claussen 1984; Brewer et al. 2006; Wolf et al. 2019) or life stage (Holland 1986; Dolomatov et al. 2013). Species with patchy distribution could benefit from habitat relationships emphasizing temperature to identify species persistence and range shifts under the current climatic conditions (Matthews and Zimmerman 1990; Eaton and Scheller 1996; Mohseni et al. 2003; Comte and Grenouillet 2013). Though temperature can restrict fish distributions (Caissie 2006), other factors (environmental and anthropogenic) also contribute to their spatial and temporal arrangement.

Because of the hierarchical nature of streams, it is fundamentally important to understand population persistence and patch dynamics across space and time (Frissell et al. 1986; Gido et al. 2006). Habitat patches can provide suitable refuge locations for populations during disturbances and become sources for recolonization thereafter

(Townsend 1989; Schlosser 1991). These multiscale interactions can reveal patterns obscured when limiting observations to either fine (e.g., channel unit) or coarse scales (e.g., ecoregion) (Wiens 1989; Levin 1992). Understanding why and how fish use patchy environments and the role occupied patches play in species stability is critical for the development of meaningful conservation strategies of stream fishes (Falke and Fausch 2010). Identifying critical habitat relationships can become more complex when studying species having restricted but patchy distributions due to anthropogenic processes occurring at multiple scales (e.g., Arkansas Darter *Etheostoma mihleze*, (Smith and Fausch 1997; Groce et al. 2012).

The Least Darter (*Etheostoma microperca*) is an isolated spring-obligate species with disjunct southern populations in the Ozark Highlands and Arbuckle Uplift ecoregions (Burr and Page 1979; Pflieger et al. 1997; Wagner et al. 2012). Least Darter populations also occur in the streams and lakes of northern United States (Figure 1), where they are more generally distributed and less associated with springs. Southern and northern populations are genetically divergent and isolated (Echelle et al. 2015), so the two groups likely would require somewhat different conservation and management strategies. In the southern extent of the range, Least Darter appears to have an affinity for calm headwater streams and springs, but they also occupy vegetated margins of larger stream runs and pools (Burr and Page 1979; Pflieger et al. 1997; Hargrave and Johnson 2003; Bergey et al. 2008). Though Least Darter is considered a spring-associated species, other local factors may regulate their distributions and should be considered prior to implementing management or monitoring plans. The overarching goal of this thesis is to describe the physicochemical habitat necessary for Least Darter and other spring-

associated species persistence. My thesis objectives are to (1) determine the physicochemical factors related to reach-scale occurrences of Least Darter and sympatric Southern Redbelly Dace (*Phoxinus erythogaster*) and Redspot Chub (*Nocomis asper*) in the Arbuckle Uplift and Ozark Mountain ecoregions (Woods et al. 2005), and (2) assess how Least Darter habitat use is affected by fine-scale environmental features (e.g., temperature, depth, velocity). My first objective examines the physicochemical factors related to Least Darter occurrences among stream reaches in two ecoregions of Oklahoma. My second objective builds on the first by examining how Least Darter use within-site habitat patches during contrasting seasons (summer and winter). Broad patterns of distribution are spatial arrangements that develop, typically, over a longer temporal scale, whereas local patch use develops over finer temporal time frames and often indicates behavioral responses by fishes to their immediate biotic and abiotic surroundings (e.g., seeking out cooler thermal patches during hotter summer months). The latter is informative for understanding how the species responds to changing conditions and in identifying their immediate habitat needs. Ideally, fish occupy energetically profitable locations and documenting use of those patches is helpful for developing conservation.

STUDY AREA

Fish and habitat conditions were sampled in both the Ozark Highlands and Arbuckle Uplift ecoregions (Figure 2). Both ecoregions are influenced by karst topography (i.e., dissolved carbonate terrains) and spring flow characteristics (see also Chapter 2 Study Area, Woods et al. 2005). Springs of the Ozark Highlands vary

substantially in size (Vineyard and Feder 1982) and erupt within the stream channel or manifest themselves as hyporheic flow (Zhou et al. 2018), whereas those of the Arbuckle Uplift ecoregion are typically isothermic (Osborn 2009; Christenson et al. 2011) and located on small spring branches. The Ozark Highlands ecoregion is relatively humid (102-122 cm precipitation annually, Woods et al. 2005), limestone dominated, and comprises mixed deciduous forest with lowland grassland and pasture areas (Woods et al. 2005). The Arbuckle Uplift ecoregion receives 96-109 cm precipitation annually, and is dominated by dolostone, limestone and granite lithologies (Woods et al. 2005). Land cover comprises tallgrass prairie and oak savannas, with both cropland and pasture occurring in lowland areas (Woods et al. 2005). Threats to riverine biota in both ecoregions include impoundments, land-uses including (Christenson et al. 2011), poultry pollution (Olsen et al. 2012), altered flows, degraded water quality, and accelerated streambank erosion (Woods et al. 2005).

CHAPTER II

ESTIMATING OCCUPANCY OF LEAST DARTER AND SYMPATRIC SPRING-ASSOCIATED SPECIES IN THE OZARKS HIGHLANDS AND THE ARBUCKLE UPLIFTS OF OKLAHOMA

ABSTRACT

Least Darter is a species of conservation concern in Oklahoma that was historically sampled from a few stream locations with high groundwater inputs. The sparsity of these historical observations and lack of corresponding habitat information made estimating of habitat associations difficult and did not allow for the determination of a realized Least Darter distribution. My study objective was to estimate occupancy for Least Darter relative to other common spring-associated species, specifically the Southern Redbelly Dace, Redspot Chub, and Smallmouth Bass adults and sub-adults in the Ozark Highlands and Arbuckle Uplift ecoregions. I sampled in summer 2018 and 2019 using repeat surveys with both snorkeling and seining. At each site, I measured a variety of physicochemical conditions hypothesized to affect species occupancy. Detection probability for all species was relatively high (i.e., > 0.5) at occupied sites when snorkeling. Detection probability increased with increases in visibility and water depth. Least Darter and Smallmouth Bass sub-adults were more

likely to occur in the Arbuckle Uplift ecoregion. The occupancy probabilities of Least Darter and Southern Redbelly Dace increased as water temperature decreased. Redspot Chub and Smallmouth Bass (adult and sub-adult) occupancy probabilities increased as drainage area increased. Southern Redbelly Dace occupancy was lower in reaches with proportionally less pool habitat. Redspot Chub and Southern Redbelly Dace occurrence probability increased as depth increased, whereas Southern Redbelly Dace and Smallmouth Bass sub-adult occupancy varied between sample years. This information will be integral in identifying the current Least Darter distribution in Oklahoma and improving stream fish conservation strategies in areas of high groundwater influence.

INTRODUCTION

Identifying the factors driving species distributions is important for meaningful conservation and management actions for threatened stream fauna (Hopkins and Burr 2009), especially as human disturbance increases across the landscape (Allan and Flecker 1993; Jelks et al. 2008; Ellis 2015). Human landscape disturbance alters fish assemblages (Wang et al. 2006b), interspecies relationships (Meffe 1984), and species-habitat relationships (Wang et al. 2011). Distribution data are useful for a variety of conservation and management needs including identifying habitat refugia over time (Peterson and Rabeni 1996; Torgersen et al. 1999; Lake 2000; Magoulick and Kobza 2003), identifying locations to manage with limited resources (Rabeni and Sowa 1996; Gore et al. 2001; Dauwalter and Rahel 2008; Gardner et al. 2013; Park et al. 2003; Wilson et al. 2005), determining conservation status of a species (e.g., Goldline Darter *Percina aurolineata*, Albanese et al. 2004; Potoka et al. 2016), and identifying areas of reintroduction (Bearlin et al. 2002; Wall et al. 2004). Determining distributions and habitat needs for stream fishes can result in more informed management decisions and conservation planning

for threatened species, especially species with narrow or patchy ranges (Richter et al. 1997; Jelks et al. 2008; Strayer and Dudgeon 2010).

The distribution of stream fauna is related to physicochemical relationships occurring at multiple spatial and temporal scales (Hynes 1975; Vannote et al. 1980; Poff et al. 1997). Coarse-scale distributions of stream fishes are constrained primarily by long-term factors such as climate and geological history (Hynes 1975; Marsh-Matthews and Matthews 2000), whereas a myriad of physicochemical factors determine how fish are distributed at finer spatial and temporal scales such as catchment, stream segments, and reach (Southwood 1977; Vannote et al. 1980; Poff et al. 1997; Goldstein and Meador 2004). For example, groundwater (Power et al. 1999; Brewer 2013a) and water temperature (Constantz 1998; Wehrly et al. 2006; Last et al. 2011; Wolf et al. 2019) affect habitat selection by stream fishes at different spatial and temporal scales (e.g., patch or reach and seasonally). Groundwater sources in streams create suitable habitat patches for some species across multiple temporal and spatial scales (Brewer 2013a). Groundwater species with narrow distributions, such as Watercress Darter *Etheostoma nuchale* (Duncan et al. 2010) or patchy distributions like that of the Arkansas Darter *Etheostoma cragini* (Groce et al. 2012) often occupy locations with above average stream quality and provide areas of focus for conservation management (Fausch et al. 1990).

Groundwater-associated species can be indicators of high-quality habitats essential for stream ecosystem function (Fausch et al. 1990; Soto-Galera et al. 2008). Stream reaches influenced by groundwater are important determinants of a stream's thermal regime (Caissie 2006). Groundwater can create important thermal habitat for stream organisms (Glazier 1991; Hubbs 1995; Caissie 2006; Farless and Brewer 2017). These habitats often have different water chemistry, temperature and ecological structure and function within the stream network (Hubbs

1995). Spring-associated species tend to be characteristic of karst regions (Matthews et al. 1985; Hubbs 2001; Bergey et al. 2008); however, these species also tend to occupy diminutive spatial extents and are typically understudied and lacking distribution and habitat association data (Matthews et al. 1985; Bergey et al. 2008; Kollaus and Bonner 2012; Spitale 2012).

Groundwater-associated species play an important ecological role as they are often the primary consumers of invertebrates such as herbivorous insects (Cordes and Page 1980). The lack of top-level piscivorous fish in many headwater streams and springs can increase the functional importance of insectivorous fish species (Matthews et al. 1985; Bergey et al. 2008).

The Least Darter is a spring-obligate fish with patchy southern populations in both the Ozark Highlands and Arbuckle Uplift ecoregions (see Introductory Chapter for an overview). Based on a perceived decline in collections over the past 50 years the conservation status of the species is in question. Therefore, my first thesis objective was to determine the physicochemical factors related to the distribution of Least Darter and three co-occurring, spring-associated species in Oklahoma (Southern Redbelly Dace *Phoxinus erythogaster*, Redspot Chub *Nocomis asper*, and Smallmouth Bass *Micropterus dolomieu*). This species assemblage occupied two upland ecoregions in Oklahoma, the Ozark Highlands and the Arbuckle Uplift. Least Darter populations in the two regions are genetically divergent (Echelle et al. 2015). I hypothesized Least Darter, Southern Redbelly Dace, Smallmouth Bass and Redspot Chub occupy similar habitats at multiple spatial scales with occurrence related to cooler water temperatures during summer. However, I hypothesized species occurrence would also reflect other physicochemical factors at multiple spatial scales. For example, the two relatively large predatory species, Smallmouth Bass and Redspot Chub should occur at sites with larger catchments and higher quantities of cover.

STUDY AREA

I sampled fish and habitat from streams of the Arbuckle Uplift and Ozark Highland ecoregions (Figure 1). Both ecoregions are characterized by karst topography with a variety of spring habitats (see Chapter 1 for an overview, Woods et al. 2005). I sampled streams from July through October in 2018 and 2019 under base-flow conditions (0.00-5.00 m³/s) and relatively warm water temperatures (16.1-28.9 °C). My sites were riffle-pool complexes nested within stream reaches approximately 200-500 m long; thus, multiple sample sites shared reach-scale attributes. Sample locations were selected to include 1) locations previously documented to support Least Darter, and 2) previously unsampled stream reaches or reaches where prior sampling did not detect Least Darter (Figure 2 and 3). Historical records revealed locations where Least Darter was previously collected or observed, but it was important for me to sample locations where previous detections were not reported to avoid sampling bias in my analyses.

METHODS

Target Species

I determined occurrence probabilities for Least Darter and Southern Redbelly Dace, Redspot Chub, and Smallmouth Bass. Species were chosen based on hypothesized importance of spring habitats to their occurrences and ecological and economic importance. Southern Redbelly Dace and Redspot Chub were selected because they are considered spring associates (Seilheimer and Fisher 2010). I also sampled adult and sub-adult Smallmouth Bass because of their importance as a sportfish and top-level predator (Brewer and Orth 2014). Additionally, Smallmouth Bass offers an interesting comparison because the species is native in the Ozark

Highlands ecoregion and non-native in the Arbuckle Uplift ecoregion (Miller and Robison 2004). Including a few sympatric species added perspective on ecological relationships for this assemblage and increased the robustness of my ecological model.

Study Design

At each site (riffle-pool complex), two temporally replicated surveys were conducted to account for imperfect detection by obtaining a modelling coefficient reflecting the probability of detecting a species when it is present at a site (Mackenzie et al. 2002; Tyre et al. 2003). Because Least Darter is patchily distributed but also considered locally abundant (Pflieger et al. 1997), I anticipated an average detection probability of 0.50 (the species was equally likely to be observed as not observed) when designing my study. Two surveys at each site would be adequate to account for average detection, allowing more sampling to be devoted to different sites rather than increasing the number of surveys. Increasing the number of sites is more important when sampling rare species and disjunct populations (Guillera-Aroita et al. 2010).

Fish Sampling

I used both snorkeling and seining to sample Least Darter. The funding agency did not approve use of electrofishing due to the perceived rarity of the species. Seining and snorkeling are commonly used to sample Least Darter (Burr and Page 1979; Bergey et al. 2008; Wagner et al. 2012). Using two approaches allowed for more sampling flexibility because it was not possible to sample all sites with both methods (i.e., too shallow to snorkel or too deep to seine). Lastly, sampling with two gears allowed me to identify and account for sources of detection variability with both approaches.

Sites were sampled using two temporally replicated snorkel surveys on separate days to both minimize disturbance on habitat and biota and ensure heterogeneity in the detection probability estimates (MacKenzie et al. 2006; Dunham et al. 2009). The snorkeling approach followed the methods of Dunham et al. (2009). Snorkel surveys were conducted when the horizontal visibility was > 1 m and between 0800 hours and 1800 hours (i.e., when daylight was most conducive to sampling, Spyker and Vandenberghe 1995). Snorkel surveys were completed by 1-2 people (depending on channel width, Thurow 1994). Each snorkeler was randomly assigned to a snorkel lane. Snorkel lanes varied in width depending on water depth and habitat complexity (i.e., narrower lanes in complex habitat). Snorkelers swam upstream in their designated lanes at approximately 2 m/min, spending more time in complex habitats. In areas too shallow for completely submerging their mask, snorkelers walked slowly upstream and visually scanned the stream bottoms. If a target species was observed using above-water observation, the identity was confirmed by partially submerging the mask and viewing the individual. When snorkelers encountered a target species, they recorded the species, enumerated individuals and referenced the channel unit (see below) used on a polyvinyl chloride (PVC) writing cuff.

On the day of each snorkel survey, I resampled wadeable habitat at each site using a standardized seining protocol (Rabeni et al. 2009). Seining was completed following the temporally replicated snorkel surveys to ensure independent surveys (MacKenzie and Royle 2005). Seining began at the downstream end of each site. Similar to snorkel surveys, only Least Darter and other target species were counted via each seine haul. Only one seining event (multiple sein hauls) through each site was completed because seining was intrusive (e.g., removal of vegetation); therefore, detection probability would be expected to change if I used a second pass on the same day.

Physicochemical Conditions

Channel units were classified as riffles, runs, pools and backwaters following the general classification of Rabeni and Jacobson (1993). Riffles were characterized by higher gradients, faster velocities, and coarser substrates compared to the surrounding habitat. Runs were transitional habitats of intermediate depths and velocities with lower gradients. Pools were depositional habitats under base-flow conditions and were typified by slower velocities, low gradients, and finer substrates. Similarly, backwaters shared pool characteristics (i.e., depositional, slack water habitat with fine substrates) but were located off the main channel.

I measured site (i.e., riffle-pool complex) covariates hypothesized to relate to the detection of Least Darter and sympatric species (Table 1). Velocity and substrate were measured following methods of Dodd et al. (2008). Average water-column velocity (0.1 m/s, 0.6 of water depth at depths < 1.0 meters, Gordon et al. 2004) of each site was measured along three, evenly spaced transects perpendicular to streamflow using a Marsh McBirney Flo-mate (Hach, Loveland, Colorado). Depth (1.0 cm) was measured at the same points along the transects. The number of velocity and depth points measured depended on channel width (~1 measurement for every 1-2 m wide). Velocity and depth measurements were averaged to represent the general conditions at each site. Coarse substrate was estimated as a percent of the available substrate \geq 90-mm diameter (Wentworth 1922). Percent coverage of coarse wood (1.0 m²; i.e., circumference > 10 cm, Dodd et al. 2008) was visually estimated at each site. I also estimated the percent cover of floating and emergent vegetation at each site and during each survey. Because water clarity is related to fish detection (Thurow 1994), I measured horizontal clarity using a Secchi disk. The Secchi disk was positioned downstream of a snorkeler, and clarity was determined by the maximum distance (to the nearest 0.1 m) at which the snorkeler could

distinguish the bands on the disk (Tyler 1968). A single value was applied to multiple sites if they occurred within the same reach because I did not expect or observe clarity varying between nested sites.

I quantified both site and reach-scale occupancy covariates to determine the multiscale factors associated with species occurrence (Table 1). First, the surface area (1.0 m^2) of each channel unit (i.e., pool, riffle, run and backwater) at each site was estimated by measuring wetted width and length. Additionally, I quantified percent of sand and silt at each site because Least Darter has been associated with finer substrates (Burr and Page 1979). Percent coarse wood, percent vegetation, and average site velocity were quantified as described for the detection covariates (previous paragraph). Residual pool depth (RPD) of each site was measured as described by Lisle (1987), where the difference between channel depth at the riffle crest and the deepest point of the downstream pool were quantified. A temperature logger was placed approximately mid pool within each reach to account for mean daily stream temperature ($0.1 \text{ }^\circ\text{C}$) over the same 2-week period. The same water temperature value was applied to each site within the reach. Discharge ($0.1 \text{ m}^3/\text{sec}$) was measured at the downstream and upstream end of each site with a Marsh McBirney Flo-mate (Hach, Loveland Colorado) using the velocity-area method (Gordon et al. 2004). Groundwater contribution was quantified using seepage runs following Zhou et al. (2018). The seepage contributions or losses (to the nearest $0.01 \text{ m}^3/\text{sec}$) were calculated by taking the difference between the downstream and upstream discharge calculations to estimate a net gain or loss (gaining or losing stream discharge) for each site (Riggs 1972). Lastly, percent vegetation and percent coarse wood were calculated from the detection covariates by averaging the values from the two surveys.

Existing geospatial data were used to calculate several reach-scale covariates and were applied to multiple sites if they occurred with the same reach (i.e., nested). I calculated drainage area for each reach as it is a primary factor structuring fish distributions (Schlosser 1995; Fausch et al. 2002). I calculated the drainage area (km²) upstream of each reach using the software NHDPlus version 2 (Dewald et al. 2016) to help determine the position of the stream within the network (headwater or higher stream orders). A landscape development intensity index (hereafter LDI) was calculated using the 2016 National Land Cover Dataset (Homer et al. 2015) to represent a cumulative disturbance upstream from each site in the catchment. The disturbance index was calculated by simplifying the landscape development intensity index (LDI) of Brown and Vivas (2005) to include only the four land cover categories occurring in my study area (see Mouser et al. 2019): developed (coefficient = 7.31), cultivated crops (4.54), hay/pasture (2.99), and forested/wetland (1.00). For instances where Brown and Vivas have multiple categories for a land-use type such as hay/pasture: woodland pasture (2.02), pasture without livestock (2.77), low intensity pasture (3.41), high intensity pasture (3.74), these categories values were averaged and assigned the same average value for each land category (see Mouser et al. 2019). I also designated all forested or wetland areas as being in a relatively “natural state.” The final coefficients for a site can range from one to ten and a higher LDI coefficient reflected increased land cover disturbance but in my data set they ranged from 1 to 3.

Occupancy modeling and validation

I developed a single-season, multispecies occupancy model for my five target species to determine relationships related to both detection and site-level occupancy as described by MacKenzie et al. (2002). Repeat survey data are needed to account for species detection probability associated with habitat covariates (Mackenzie et al. 2002; Tyre et al. 2003). I used

data where fish were both detected and not detected, allowing me to relate detection probability to the covariates measured at each site (MacKenzie et al. 2006). Occupancy modelling requires four assumptions: 1) occupancy state does not change at a site over the study season 2) constant occurrence probability across sites 3) constant detection probability among surveys, and 4) independence between detection histories. The first assumption was met by limiting my study season between July and October after spring floods and before winter cool down. The second and third assumptions were satisfied by using covariates hypothesized to explain differences in occurrence and detection probabilities (Mackenzie et al. 2002). The fourth assumption was met using temporally replicated surveys instead of multiple seining or snorkeling events on the same day (Mackenzie et al. 2002).

I made several data transformations and checked correlations among my detection covariates. Coarse substrate, velocity and depth were log-transformed because they were right-skewed. I checked the continuous detection covariates for high correlations ($|r| > 0.50$) using the Pearson correlation coefficients (Table 4). If two covariates were correlated, I retained only one to avoid redundancy. However, detection covariates showed no significant correlations ($|r| < 0.26$). Also, categorical covariates were examined for independence by determining the frequency at which covariates occurred together at the sites. My most complex detection model contained a quadrature depth term and four continuous detection covariates: percent coarse substrate, average water column velocity, water clarity, water temperature, depth.

I first built a detection model accounting for some species-specific relationships, but also more general relationships expected to be shared among species. I fit species-specific relationships with gear and ecoregion to determine how each species differed between ecoregions and with gear. I assumed species would have similar detection relationships with

continuous covariates to avoid an overly complex detection model (i.e., place the emphasis on occupancy). My most complex model included six continuous covariates and a gear and ecoregion factor where seining and the Arbuckle Uplift ecoregion were references. I included interactions with each of the five continuous covariates and gear to account for a gear effect with differing habitat conditions. Additionally, I used stream reach as a grouping factor to account for unexplained variation and spatial correlation of the sites nested within a stream reach (Gelman and Hill 2006; Wagner et al. 2006).

The detection model can be written as:

$$\text{logit}(p_{ij}) = \sum_{k=1}^5 \alpha_{0k} + \sum_{k=1}^5 \alpha_{GEARK[ij]} + \sum_{k=1}^5 \alpha_{ECOK[ij]} + \sum_{m=1}^8 \sum_{n=1}^8 \beta_m X_n[ij] * GEAR_{[ij]},$$

for $i = 1, 2..N$, for $j = 1,..J$

$$\alpha_{0k}, \alpha_{GEARK} \text{ and } \alpha_{ECOK[ij]} \sim t(\mu, \sigma^2, \nu),$$

$$\beta_m \sim t(\mu, \sigma^2, \nu),$$

where p_{ij} is the species detection probability for survey j at site i , α_{0k} is the species mean k deflection from the group mean intercept, α_{GEARK} is the gear factor for species k , where seine is the reference, α_{ECOK} is the ecoregion factor for species k , β_m is the group-mean slope for m , X_n are detection covariates (see habitat section).

After the most complex detection model was fitted, I simplified the model using an iterative process where I first tested interactions and then main effects by removing any covariates overlapping zero via the 95% highest-density intervals (HDIs: Kruschke 2014; Kery and Royle 2015). First, two-way interactions overlapping zero were removed, followed by rerunning the model and removing any main effects overlapping zero or not included in a critical (not overlapping zero) two-way interaction. All significant interactions (i.e., not overlapping zero) and corresponding main effects were retained in the detection model. The model was then

refitted to determine if the 95% highest-density intervals of the main effects overlapped zero. The final detection model covariates were then included in the occupancy models to determine which environmental factors related to species occurrence.

I made several data transformations and checked correlations among occurrence covariates (Table 5). Percent fine, discharge, RPD, drainage area, percent vegetation, average two-week temperature, and percent coarse wood were all log transformed due to skewness. All continuous occupancy covariates were standardized for each survey to a mean of zero and a variance of one to improve model interpretation and convergence (MacKenzie and Royle 2005). I chose drainage area over two other highly correlated variables (discharge and total area, Table 5) to minimize redundancy between variables. All other correlations were $|r| \leq 0.54$.

Next, I fit the most complex occupancy model, while including the detection relationships in my model. Incorporating the detection portion of the model allowed me to interpret physicochemical relationships at sites without species specific occurrence. The most complex occurrence model contained the following continuous covariates: drainage area, average two-week temperature, percent fine substrate, catchment-scale LDI, proportion pool area, RPD, seepage run, percent vegetation, and percent coarse wood. I additionally included three interaction terms I hypothesized could be important: average water temperature and residual pool depth, total vegetation and residual pool depth, and a total vegetation-pool area interaction. Occurrence probability of smaller-bodied species (i.e., Southern Redbelly Dace and Least Darter) would be higher in shallow areas with warmer water temperature because larger-bodied predators tend to have lower thermal tolerances and occupy moderate depths (Peck et al. 2013). I predicted, at cooler water temperatures, occurrence probability of the smaller-bodied species would be independent of residual pool depth. Next, I hypothesized occurrence

probability in areas of high vegetation (i.e., refuge from a variety of predators) would remain relatively constant across pool depths, whereas low vegetation in shallow water could reduce occupancy due to increased avian predation and lack of suitable habitat. Deeper water, however, even with limited vegetation reduces the risk of avian predation (Savino and Stein 1982; Rozas and Odum 1988). Lastly, I hypothesized occurrence probability in highly vegetated areas would be consistent regardless of pool area. However, if vegetation occurs in low quantities, occurrence should be lower for the small bodied species in larger pools because of the increased likelihood of predators (Burr and Page 1979a; Johnson and Hatch 1991; Hargrave and Johnson 2003).

I allowed each species to be modeled around the group mean (i.e., all species) and interpreted the results as the deflection of individual species from the group mean relationship with covariates. This model structure shifts the attention to individual species rather than differences among species (the reference approach), similar to a “random-slopes” model (Jamil et al. 2013). Additionally, a grouping factor of stream reach was included in my model to account for the hierarchical structure of streams, with multiple sites within the same reach. Adding grouping factors, accounts for the inherent pseudoreplication between nested sites (Wagner et al. 2006). The occupancy model can be written as:

$$\text{logit}(\Psi_i) = \sum_{k=1}^5 \alpha_{0k} + \sum_{k=1}^5 \alpha_{ECOK[i]} + \sum_{k=1}^5 \alpha_{YEARK[i]} + \sum_{m=1}^{10} \sum_{k=1}^5 \sum_{n=1}^{10} \beta_{mk} X_{n[i]} +$$

$$\sum_{m=21}^{13} \sum_{k=1}^5 \sum_{c=1}^3 \beta_{mk} X_{c[i]} + \sum_{k=1}^5 \gamma_{t[i]}, \text{ for } i = 1, 2..N,$$

$$\alpha_{0k}, \alpha_{YEARK}, \alpha_{ECOK} \sim t(\mu, \sigma^2, \nu),$$

$$\beta_{mk} \sim t(\mu, \sigma^2, \nu),$$

$$\gamma_t \sim t(0, \sigma^2, \nu), \text{ for } t = 1, 2....61,$$

where Ψ_i is species occurrence probability for survey j at site i , α_{0k} is the species k deflection from the group-mean intercept, $\alpha_{ECO k}$ is the ecoregion factor for species k with Arbuckle Uplift as the reference, $\alpha_{YEAR k}$ is the year factor for species k with 2018 as the reference, β_{mk} is the species k deflection from the group mean for slope m , X_n is an occurrence environmental covariate (see above), X_c is an occurrence environmental covariate interaction of the following: total vegetation \times residual pool depth, total vegetation \times proportion of pool habitat, and average temperature \times residual pool depth. γ_t is the grouping factor for the stream reach t .

I used a backward selection approach to simplify my overall model. First, I fit my most complex model including all three-way interactions. I retained only significant three-way interactions (i.e., 95% HDIs that did not overlap zero) and then refit the model and examined two-way interactions. I again omitted any non-significant interactions by examining HDIs and removing non-significant interactions. Lastly, I fit a model that included significant three-way, and two-way interactions, and all main effects. In the last iteration, I retained only significant main effects and those variables that were part of a higher order interaction.

Priors were used to give the models starting points to begin estimation for posterior distributions used to assess model fit and estimate parameters. Broad uniform priors were used for main effects and species covariates and vague gamma priors for associated standard deviations (Kery and Royle 2015). The use of broad and vague priors is common when previous research gives no useful initial estimates (Kruschke and Liddell 2018). Broad priors follow a distribution (i.e., normal) and gives the model a basis for estimating parameters. Because the range of the prior is wide, its effect on the model outcome is minimal. Posterior distribution for covariates were estimated using Markov chain Monte Carlo methods with 60,000 iterations (first 10,000 = burn-in). Convergence was determined by applying the Brooks-Gelman-Rubin statistic

(\hat{R} , Gelman and Rubin 1992), for which values <1.1 indicate adequate mixing of chains for all parameters.

I used MacKenzie and Bailey (2004) chi-squared goodness-of-fit test to assess the fit of my final model, where \hat{c} ranging from 1.00 to 1.02 is considered acceptable (Kery and Royle 2015). The chi-squared goodness-of-fit test uses a factor to account for overdispersion and helps yield more reliable inferences when using overdispersed data common for occupancy models (MacKenzie and Bailey 2004). Models were fit using the program JAGS (Plummer 2003) called from the statistical software R (version 3.5.3; R Developments Core Team 2019) using the package jagsUI (Kellner 2019). Detection and occurrence probability were determined by using the inverse logit of a parameter, while holding all other parameters at mean levels.

RESULTS

Fish sampling

I sampled 153 sites nested within 61 stream reaches in the Arbuckle Uplift and Ozark Highland ecoregions (Table 2; Figure 2) during 2018-2019. Of the 153 sites, 42% ($n=64$) were in the Arbuckle Uplift ecoregion, whereas 58% ($n= 89$) were in the Ozark Highlands ecoregion (Table 2). During the two summers of sampling, I conducted 284 seining surveys and 264 snorkel passes across all sites (Table 2). During summer 2018, 69 sites were sampled: 26 sites in the Arbuckle Uplift and 43 in the Ozark Highlands (Table 2). During summer 2019, I sampled 84 sites: 38 sites sampled in the Arbuckle Uplift and 46 sites sampled in the Ozark Highlands.

Commonness of my target species differed by ecoregion, and some species were easier to sample using one of the two gears (Table 3). Least Darter was the rarest of the five target species. Redspot Chub was common across both ecoregions. Both Smallmouth Bass life-history stages (adult and subadult) were relatively uncommon in the Arbuckle Uplift, but common in the

Ozark Highlands. Least Darter was detected at more sites in the Arbuckle Uplift ecoregion ($n = 15$) than in the Ozark Highlands ecoregion ($n = 3$), whereas Redspot Chub, Smallmouth Bass adults and Smallmouth Bass sub-adults occurred at more than twice as many sites in the Ozark Highlands compared to the Arbuckle Uplift. Least Darter was detected at about the same number of sites when seining ($n = 18$) or snorkeling ($n = 24$). Smallmouth Bass, Redspot Chub and Southern Redbelly Dace were typically 2-3 times more likely to be detected by snorkeling than by seining, regardless of ecoregion (Table 3). Redspot Chub and Smallmouth Bass subadults were exceptions as the frequency of detection was similar in the Arbuckle Uplift regardless of gear used (Table 3).

Physicochemical Conditions

The physicochemical conditions associated with my surveys varied across sites but were similar between ecoregions and sample year (Table 6). Sites in both ecoregions had moderate amounts (~25%) of coarse substrates and coarse wood (~15%). Average temperature (~23 °C), depth (~0.30 m), and average water column velocity (~ 0.17 m/s) were similar across sites in each ecoregion. Percent vegetation and water clarity were more variable at sites in the Arbuckle Mountain ecoregion. Additionally, sites in the Arbuckle Uplift tended to have higher percentages of vegetation and lower water clarity than those in the Ozark Highlands.

Site-level occupancy covariates were variable across sites and between the two ecoregions but similar among sample years (Table 7). Water temperature, seepage runs, and LDIs were, on average, similar between ecoregions. The most notable differences between sites in the two ecoregions was the percent of fine substrates (Arbuckle Uplift, 39%; Ozark Highlands, 10%). Similar to my detection covariates, average percent vegetation was higher in the Arbuckle

Uplift (25%) than in the Ozark Highlands (15%). Lastly, residual pool depth was greater in the Ozark Highlands (0.74 m) than in the Arbuckle Uplift (0.54 m). Average physicochemical conditions between 2018 and 2019 were similar with little variation except average water-column velocities were slightly higher in 2019 (0.21 m/s) than in 2018 (0.11 m/s).

Occupancy modeling and validation

The final occupancy model had appropriate model fit and adequate mixing of chains. The final model had an average \hat{c} of 1.0 indicating appropriate model fit (Kery and Royle 2015). Additionally, all model parameters successfully converged at \hat{R} of 1.0 with of an effective sample size of at least 7,847 suggesting the model had appropriate mixing.

Relationships between my target species and detection covariates were often shared among species, but some relationships were species-specific. The final model included water clarity and water depth interactions with gear (two-way interactions) as the only common slope among species, and the HDIs did not overlap zero for any predictor variable (Table 7). Southern Redbelly Dace, Redspot Chub and Smallmouth Bass had higher average detection probabilities when snorkeling compared to seining; however, detection was similar between the two gears when sampling Least Darter (Table 7). Detection increased with water clarity while snorkeling (i.e., seining as the reference) (Table 7, Figure 4). Similarly, detection probability was higher in deeper water when snorkeling (Table 7, Figure 5). Detection probability was not significantly different between ecoregions, but I retained an ecoregion factor in my model to account for unexplained spatial variation (Table 7).

I found both common and species-specific occurrence relationships with my predictor variables (Table 8). Occurrence probability of Least Darter in the Ozark Highlands was

significantly lower than in the Arbuckle Uplift, whereas the reverse was seen for Smallmouth Bass sub-adults (Table 8). Occurrence probability was higher for Smallmouth Bass sub-adults and Southern Redbelly Dace in 2018 than in 2019 (Table 8). Occurrence probabilities of both Least Darter and Southern Redbelly Dace increased with cooler water temperatures (Figure 6). Redspot Chub and both Smallmouth Bass life-stages were associated with larger drainage areas (Figure 7). Southern Redbelly Dace was negatively associated with sites having a higher proportion of pool habitat (Figure 8). Lastly, occurrence probabilities of Smallmouth Bass sub-adults and Redspot Chub were higher in deeper pools (Figure 9).

DISCUSSION

Two of the rarer species across my study area were associated with cooler summer water temperatures. Southern Redbelly Dace and Least Darter are commonly sampled in areas of cooler water across their range (Johnson and Hatch 1991; Walker et al. 2013). Walker et al. (2013) hypothesized Southern Redbelly Dace movement was related to both hydrology (i.e., connectivity) and temperature. Although movements by Least Darter is unknown, they occur in streams with cooler water temperatures in Oklahoma and Arkansas (Wagner et al. 2012). Smaller headwater streams tend to be cooler and provide refuge from a host of perturbations (Meyer et al. 2007), whereas backwaters and side channels also tend to be cooler in the summer because of hyporheic flow (Arrigoni et al. 2008). Temperature interacts with several other physicochemical stream properties related to fish habitat such as vegetation, (Barko and Smart 1981), dissolved oxygen (Ostrand and Wilde 2001), substrate (Johnson 2004), and pools (Matthews and Berg 1997). Additionally, Least Darter and Southern Redbelly Dace both use areas of vegetation (Burr and Page 1979; Johnson and Hatch 1991; Slack et al. 1997; Hargrave and Johnson 2003). However, I did not find a relationship with vegetation suggesting either it may become more

important at finer spatial scales (Scheidegger and Bain 1995; Sand-Jensen and Mebus 1996) or simply covary with a coarse-scale landscape factor (Houser et al. 2005). Both species have low critical thermal maximum temperatures (Least Darter 34.4°C; Southern Redbelly Dace 34.9°C) when compared to congeneric species (Farless and Brewer 2017). My findings suggest the constraints of temperature contribute to the patchy distribution of these species (see also Buisson et al. 2008).

The more common species sampled across my study area, Smallmouth Bass and Redspot Chub, were associated with larger drainage areas and deeper pool habitat. Larger predators such as these typically do not exhibit high abundances in springs (Matthews et al. 1985). However, smaller streams can be important rearing habitats even for top-level predators (Rosenfeld et al. 2002; Meyer et al. 2007), but spatial proximity can be a driving factor (Smith and Kraft 2005). For example, Miller and Brewer (In Press) found smaller streams of the Ozark Highlands located near larger streams could support relatively large populations of young-of-year Smallmouth Bass. Larger streams provide heterogenous habitats including thermal patchiness (Arrigoni et al. 2008; Westhoff and Paukert 2014), diverse foraging opportunities (Sabo et al. 1996), and refuge from disturbance, predation, and density-dependent effects (Lukas and Orth 1995; Letcher et al. 2015). I also found subadult Smallmouth Bass and Redspot Chub were positively associated with residual pool depth. Similar to larger streams, deeper pools tend to offer increased habitat complexity (Danehy et al. 1998). For subadult Smallmouth Bass and smaller-bodied Redspot Chub, deeper habitats may be favorable in relatively smaller streams where avian predators predominate (Allouche and Gaudin 2001), whereas deeper habitats were less favorable in larger streams due to larger fish predators (Steinmetz et al. 2008). Adult Smallmouth Bass, alternatively, tend to be associated with moderate depths (Dauwalter et al. 2007; Brewer 2011),

however, depth relationship can change depending on stream size (Zorn et al. 2002; Brewer et al. 2007; Dauwalter et al. 2007; Miller et al. In Press).

Differences in occurrence probability between ecoregions and year occurred for some of my target species. Differences in occurrence between ecoregions is common and habitat relationships can differ between ecoregions (Larsen et al. 1986; Heitke et al. 2006; Wang et al. 2006a; Dauwalter et al. 2007). In the Arbuckle Uplift, Smallmouth Bass is introduced, and the lack of juveniles could be indicative of minimal suitable spawning or rearing habitat below spring sources in my Arbuckle Uplift study area (Pflieger 1966). To my knowledge, no research has been conducted on Smallmouth Bass in the upper Blue River and its tributaries, so the status of the population is unknown. I only sampled the upstream portion of the Blue River drainage which is considerably different than the downstream section (Li et al. 2012) that hosts a recreational Smallmouth Bass fishery. For Least Darter, however, a patchy distribution across its range and the difference in occurrence probability between the two ecoregions could be a function of suitable habitat. In the Arbuckle Uplift, Least Darter was presumed to only occur in a relatively small section of river on or adjacent to the mainstem Blue River where springs erupt regularly (Seilheimer and Fisher 2010). This differs from the Ozark Highlands where there were broadly distributed occurrences historically (Figure 3). The Ozark Highlands boasts karst topography but has more patchy cool-water upwelling rather than the isothermic springs of the Arbuckle Uplift. I found occurrence probability for Smallmouth Bass sub-adults and Southern Redbelly Dace was lower in 2019 compared to 2018. The year effect for Smallmouth Bass juveniles could be a product of higher precipitation in spring 2019 compared to 2018 (National Weather Service Data 2020). The high flows could have affected spawning or rearing of Smallmouth Bass leading to lower abundance (Ridgway and Friesen 1992; Lukas and Orth 1995;

Miller et al, In Press), which in, could affect occupancy (Royle et al. 2005). The higher flows could have led to more runoff reducing suitable water quality and resulting in lower occurrences of Southern Redbelly Dace (Slack et al. 1997). Additionally, higher 2018/2019 winter and spring flows could reduce recruitment of summer 2019 individuals (Settles and Hoyt 1978).

I detected Least Darter at three new locations in the Arbuckle Uplift and two new locations in the Ozark Highlands during the summer of 2018 and 2019. Two of the locations in the Arbuckle Uplift were farther north in the Blue River than previously documented for the species (Figure 2; 34°35'47.0"N 96°42'28.5"W and 34°37'20.8"N 96°46'26.8"W). Both occurrences were detected in early July when water temperature was cooler but were not detected on the following visit at the end of July. The landowner mentioned a spring on the property (Thomas Stevens, personal communication); however, I found no noticeable spring during my site visits. The third site with a new detection of Least Darter in the Arbuckle Uplift was on the Nature Conservancy's Oka' Yanahli Nature Preserve (west portion; 34°27'03.2"N 96°39'17.8"W); to my knowledge, this is the first ever documentation of the species from that section of Blue River on the nature preserve. The two new localities in the Blue River headwaters suggests isolated populations or metapopulations could occur in other areas of the Blue River and may contribute to the overall population of Least Darter (Falke and Fausch 2010). However, locating these small, isolated population is difficult due to sampling detection (MacKenzie et al. 2006). The two new localities within the Ozark Highlands both occurred near previous collections of Least Darter: 1) Rock Creek (36°58'57.9"N 94°37'13.5"W), a second order tributary to Fivemile Creek, and 2) Snake Creek (36°09'07.2"N 95°10'11.9"W). A previous collection was made on Fivemile Creek (Oklahoma Water Resource Board 2017) upstream of the confluence with Rock Creek. However, no records of Least Darter occurrences have been

documented for Rock Creek in Oklahoma or Missouri. I also detected Least Darter in a backwater approximately 70 m from the mainstem of Snake Creek downstream of previous location at the Highway 82 bridge south of Locust Grove, Oklahoma. At the time of sampling, the backwater was completely disconnected from the main source expect for hyporheic flow keeping the water cool (Arrigoni et al. 2008; Zhou et al. 2018). The section of Snake Creek near Highway 82 has several historical Least Darter collections and should be a focus area for future sampling. Future research would benefit from examination of seasonal habitat shifts by this species as the overall range may be broader based on seasonal trends. However, before we can begin to understand seasonal shifts, we first need to understand the overall distribution and how it might change annually.

The apparent decrease in suitable habitats for Least Darter at several of the known historic locations could be due to many factors outlined for all North American fish species in Jelks et al. (2008) including altered flow regimes (Poff et al. 1997; Lynch et al. 2018), climate change (Hu et al. 2005), or introduced species (Rahel et al. 2008). The Least Darter could have once been more widespread in the Ozarks as historic collections before 1970 suggest. The species may have become more isolated and rarer after human landscape changes as documented for other species (Tejerina-Garro et al. 2005). Sand mines have become common in the Arbuckle Uplift area, causing base-flow concerns including disconnection between surface and in the Arbuckle Simpson Aquifer (Christenson et al. 2011). Least Darter and other groundwater-associated species rely on the groundwater contribution in the Upper Blue River drainage (Seilheimer and Fisher 2010). However, temperature was the likely surrogate but the springs affects likely occurred across segments and were not captured at reaches with my seepage run measurement.

Habitat alterations due to landscape changes not captured by my disturbance index may be of concern for species in both ecoregions including Least Darter (Seilheimer and Fisher 2010; Christenson et al. 2011). The Ozark Highland sites were more disturbed based on my LDI values (land use coefficients), and human landscape activities can intensify patchy distributions at range edges (Sagarin et al. 2006). The LDI coefficients used in this study were derived from land use types in Florida based on energy consumption (Brown and Vivas 2005) and may not extrapolate well to my study area. However, Mouser et al. (2019) used a similar method and found occurrence probability of *Faxonious* crayfish were negatively related to higher LDI coefficients (i.e., more disturbed) in the Ozark Highlands. Watershed characteristics (geology or topography), groundwater withdrawals, and surface runoff were not represented by my LDI coefficient but may be important to species that rely on cooler-water temperatures and relatively stable flows often associated with springs (Labbe and Fausch 2000; Duncan et al. 2010; Seilheimer and Fisher 2010). Future research would benefit direct examination of these landscape perturbations, and perhaps the development of a similar land disturbance index focused on stressors affecting streams of the southern United States.

My findings support the overall importance of accounting for incomplete detection if underlying ecological relationships are the focus. Accounting for incomplete detection is important to prevent Type I errors (species reported absent when present; (Reid and Dextrase 2017; Reid and Haxton 2017; Mollenhauer et al. 2018). For example, Gwinn et al. (2015) documented several examples where incomplete detection led to erroneous conclusions about the underlying ecological relationships. My results support snorkeling for as the preferred and most reliable method in species occurrence assessments for warmwater fishes in clear groundwater-

fed streams (Brewer and Ellersieck 2011; Chamberland et al. 2014; Mollenhauer and Brewer 2018).

Multiscale studies of spring-associated and other lotic warmwater species are important for biologist developing conservation plans (Labbe and Fausch 2000; Wang et al. 2001; Torgersen et al. 2006). For example, occupancy relationships of Least Darter and Southern Redbelly Dace could be used in management plans to identify areas of critical habitats for other species that rely on groundwater contributions and cooler water temperatures (Caissie 2006; Brewer 2013b; Mollenhauer et al. 2019). The unique thermal regimes of groundwater habitats and their associated assemblages are under immense anthropogenic pressure due to changing stream structure and function (Hynes 1975; Ward 1989; Fausch et al. 2002; Caissie 2006). Longitudinal stream management is important for groundwater associated species because headwaters are often cooler and contribute flow and nutrients to downstream reaches (Moore and Richardson 2003). Protection of headwater streams could also provide refugia for small bodied fishes from predators and extreme temperatures (Schlosser 1995; Peterson and Rabeni 1996; Torgersen et al. 1999) and help maintain habitat complexity (cover, deeper pools, etc.). Restoration of riparian habitats and application of best management practices to catchments would reduce thermal pollution from runoff (Nelson and Palmer 2007) and agriculture pollutants that could contaminate an already limited and patchy environment (Osborne and Kovacic 1993; Johnson et al. 1997). Additionally, riparian habitats help mitigate the effects floods have on species by decreasing water column velocities and providing refugia during high flows (Swanson et al. 1998; Tockner and Stanford 2002). Watershed disturbances can also lead to stream channels widening and pools becoming shallower resulting in an increase in stream temperatures (Harvey et al. 2003; Poff 2018). Conservation of groundwater-associated species would benefit

from regional efforts to protect critical aquifers by regulating groundwater withdrawals (Labbe and Fausch 2000; Seilheimer and Fisher 2010). Protecting base flows would also protect against stream channels drying and compacting reducing hyporheic exchange resulting in increased stream temperatures (Cardenas 2009). Such species rely on springflows because the constant water temperature minimizes extreme fluctuations, creates thermal refugia and helps maintain baseflows (Matthews et al. 1985; Peterson and Rabeni 1996; Torgersen et al. 1999; Schaefer et al. 2003; Bergey et al. 2008).

Table 1. Detection and occupancy parameters and the measured spatial scale (Scale) used in this study. Hypothesized effects on Least Darter: negative (−), positive (+), or null (∅) indicating no expected effect. Justification is the rationale for inclusion in the model building process.

Detection			
<i>Scale</i>	<i>Covariate</i>	<i>Hypothesized effect</i>	<i>Justification</i>
Site	Gear type	Snorkeling > seining	Detection probabilities can be different between the two methods. ^{1,2}
Site	Water velocity (m/s)	−	Detection probability is reduced with increasing flow. ³
Site	Structure (+/-)	−	Presence of structure can lower detection. ⁴
Site	Substrate (%)	−	Larger substrates can reduce detection of stream fishes. ⁵
Site	Temperature (°C)	−	Warmer temperature make fish increasingly active and harder to detect
Site	Vegetation (%)	−	Vegetation reduces detectability. ⁶
Reach	Water clarity (m)	−	Lower water clarity can reduce detection. ⁷
Occupancy			
<i>Scale</i>	<i>Covariate</i>	<i>Hypothesized effect</i>	<i>Justification</i>
Reach	Temperature (°C)	−	Least Darter most commonly documented in cooler waters. ^{8,9,10}
Reach	Ecoregion	∅	Used to account for unexplained variation between Ecoregions
Reach	Year	∅	Account for unexplained variation between years
Reach	Landcover/Use	−	No riparian and disturbed landscape can alter fish assemblages. ¹²
Reach	Drainage Area (km ²)	−	Least Darter reported more commonly from smaller headwater areas. ¹⁰
Reach	Discharge (m ³ /s)	−	Least Darter documented from smaller streams (i.e. lower discharge streams). ^{10,13,14}
Site	Seepage Run (m ³ /s)	+	Net gain of water from spring input represents occurrence of a cold-water spring. ^{8,9,10}
Site	Silt/Sand (%)	+	Least Darter often observed over fine substrate. ^{10,13,14}

Site	Percent Structure (%)	+	Least Darter often observed in relation to some structure ^{10,13,14}
Site	Percent Vegetation (%)	+	Documented Least Darter prefers vegetated areas. ^{10,13,14}
Site	Channel Unit Area (m ²)	+	Least Darter have an affinity for pools but also use runs. ^{10,13,14}
Site	RPD (m)	+	Stream permanence for spawning has been documented for Least Darter. ¹⁴

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1. Goldstein 1978
 2. Hagler et al. 2011
 3. Mcmanamay et al. 2014
 4. Thurow et al. 2004
 5. Thurow et al. 2006
 6. Bayley and Austen 2002
 7. Mollenhauer et al. 2018
 8. Bergey et al. 2008
 9. Burr 1977
 10. Pflieger 1997
 11. Woods et al. 2005
 12. Jones et al. 1999
 13. Burr and Page 1979
 14. Johnson and Hatch 1991

Table 2. Number of sites and reaches sampled in 2018 and 2019 in the Arbuckle Uplift (Arbuckle) and Ozark Highlands (Ozark) ecoregions.

	<i>2018</i>	<i>2018</i>	<i>2019</i>	<i>2019</i>	<i>Total</i>	
<i>Ecoregion</i>	<i>Reaches</i>	<i>Sites</i>	<i>Reaches</i>	<i>Sites</i>	<i>Reach</i>	<i>Total Sites</i>
Arbuckle	12	26	13	38	25	64
Ozark	18	43	18	46	36	89
Total	30	69	31	84	61	153

Table 3. Species detections by gear type and sampling method (i.e., snorkeling or seining) by ecoregion: Arbuckle Uplift (Arbuckle) and Ozark Highlands (Ozarks) ecoregions. Numbers for species and ecoregion represent the number of surveys the species was detected in by using either snorkeling or seining; occupied sites refers to the number of sites the species were recorded.

	Total	Least Darter		Redspot Chub		Smallmouth Bass (Adult)		Smallmouth Bass (Subadult)		Southern Redbelly Dace	
		<i>Ozark</i>	<i>Arbuckle</i>	<i>Ozark</i>	<i>Arbuckle</i>	<i>Ozark</i>	<i>Arbuckle</i>	<i>Ozark</i>	<i>Arbuckle</i>	<i>Ozark</i>	<i>Arbuckle</i>
Seine	284	3	15	35	32	4	0	29	8	37	15
Snorkel	264	2	22	130	30	96	13	97	8	57	26
Occupied Sites		3	15	72	30	55	8	59	10	36	18

Table 4. Correlation matrix for all continuous detection probabilities across all sites.

Percent coarse wood (Coarse Wood), percent coarse substrate (Substrate), percent vegetation (Vegetation), average water column velocity (Velocity), average water depth (Depth), and water temperature were all measure at the site level. Water clarity (Clarity) was measured at the reach and applied to all sites within the reach.

	Coarse Wood	Substrate	Vegetation	Velocity	Depth	Clarity
Substrate	-0.07					
Vegetation	-0.53	-0.37				
Velocity	-0.06	-0.06	-0.20			
Depth	0.43	0.01	-0.45	0.10		
Clarity	-0.34	-0.31	0.15	-0.23	-0.42	
Temperature	0.04	0.06	-0.16	-0.37	-0.15	-0.32

Table 5. Pearson's correlation matrix for occurrence covariates across all sites. Variables measured at the reach scale: Water temperature (Temp, the two-week average water temperature), land use disturbance index (LDI), drainage area (Drain), and seepage run (Seep). Fine substrates (Fines), coarse wood (Wood), and vegetation (Veg) are expressed as percent coverage for each site. Pool area (Pool) is the proportion of total area (Total) represented by pool habitat. Discharge (Q) was recorded at the reach scale; residual pool depth (RPD) recorded for each site.

	Temp	LDI	Drain	Seep	Fine	Wood	Veg	Pool	RPD	Total
LDI	0.19									
Drain	0.21	0.10								
Seep	-0.32	0.07	0.05							
Fines	-0.18	-0.91	-0.27	-0.19						
Wood	-0.03	-0.06	0.09	-0.26	0.04					
Veg	-0.19	-0.45	-0.43	-0.07	0.54	-0.51				
Pool	-0.37	-0.32	-0.23	-0.13	0.17	0.29	-0.31			
RPD	-0.24	-0.06	0.50	-0.13	-0.17	0.39	-0.53	0.56		
Total	-0.12	-0.08	0.82	0.34	-0.14	-0.05	-0.34	0.04	0.56	
Q	0.00	0.10	0.89	0.35	-0.29	0.11	-0.53	-0.16	0.46	0.86

Table 6. Summary statistics of covariates included in the detection or occupancy model:

N is the sample size, Mean is the average, SD is standard deviation, Min is minimum, and Max is the maximum value. Data are reported for sites in each ecoregion (Ozark Highlands and Arbuckle Uplift). LDI is the land disturbance index, and occupancy model temperature refers to the 2-week average temperature.

Ozark Highlands					
<i>Detection</i>	N	Mean	SD	Min	Max
Coarse Wood (%)	1805	16.00	16.51	0.00	75.00
Coarse Substrate (%)	1805	28.00	20.40	5.00	85.00
Vegetation (%)	1805	14.00	18.60	0.00	95.00
Average Velocity (m/s)	1805	0.16	0.13	0.00	0.64
Depth (m)	1805	0.27	0.14	0.06	0.72
Clarity (m)	1805	4.40	1.61	1.60	11.20
Temperature (°C)	1805	23.84	2.73	17.00	28.80
<i>Occupancy</i>					
Fine Substrate (%)	470	10.00	11.78	0.00	85.00
Residual Pool Depth (m)	470	0.74	0.53	0.02	2.20
Seepage Run (m/s ³)	470	0.03	0.15	-0.24	1.26
Average Temp (°C)	470	23.15	2.52	16.14	27.77
Drainage Area (km ²)	470	92.56	94.91	15.82	543.90
LDI	470	1.99	0.33	1.12	2.50
Proportion Pool	470	0.54	0.26	0.00	0.96
Vegetation (%)	470	14.73	18.63	0.00	90.00
Coarse Wood (%)	470	15.67	16.13	0.00	70.00
Arbuckle Uplift					
<i>Detection</i>	N	Mean	SD	Min	Max
Coarse Wood (%)	955	14.00	13.18	0.00	65.00
Coarse Substrate (%)	955	25.00	18.71	0.00	70.00
Vegetation (%)	955	25.00	29.17	0.00	95.00
Average Velocity (m/s)	955	0.17	0.11	0.00	0.47
Depth (m)	955	0.30	0.16	0.09	0.97
Clarity (m)	955	2.70	2.08	0.20	11.50
Temperature (°C)	955	22.96	3.87	14.20	30.80

Occupancy

Fine Substrate (%)	295	39.00	26.65	0.00	90.00
Residual Pool Depth (m)	295	0.54	0.40	0.00	1.95
Seepage Run (m/s ³)	295	0.02	0.09	-0.14	0.45
Average Temp (°C)	295	23.40	3.56	17.07	28.85
Drainage Area (km ²)	295	73.65	110.25	1.00	329.08
LDI	295	1.42	0.18	1.06	1.76
Proportion Pool	295	0.59	0.24	0.00	0.98
Vegetation (%)	295	25.00	29.39	0.00	93.00
Coarse Wood (%)	295	14.00	12.56	0.00	52.00

Table 7. Final detection model results containing all significant coefficients (i.e., those with HDIs not overlapping zero). Species by gear relationships were estimated using seining as the reference, whereas ecoregion was referenced to the Arbuckle Uplift and was retained in the detection model to account for unexplained variation. Water depth and clarity were modeled as a common relationship among all species; reported as the mean with the lower (Low) and upper (High) 95% credibility intervals.

	Mean	Low	High
<i>Species by gear</i>			
Least Darter	0.76	-0.29	1.82
Redspot Chub	2.57	2.04	3.13
Smallmouth Bass Adult	4.49	3.52	5.63
Smallmouth Bass Sub-adult	2.34	1.76	2.96
Southern Redbelly Dace	1.41	0.79	2.06
<i>Species by ecoregion</i>			
Least Darter	-0.61	-2.73	0.57
Redspot Chub	-0.44	-1.04	0.14
Smallmouth Bass Adult	0.20	-0.77	1.31
Smallmouth Bass Sub-adult	0.14	-0.64	1.06
Southern Redbelly Dace	0.34	-0.32	1.06
<i>Detection intercept by gear</i>			
Depth	0.61	0.28	0.95
Clarity	0.65	0.37	0.93

Table 8. Final occurrence model results containing all significant coefficients model as deflections from the group mean. Ecoregion and year are categorical covariates using Arbuckle Uplift and 2018 as references. Two-week average water temperature, drainage area, proportion pool, and residual pool depth are covariates having at least one species-specific relationship. All covariates are reported as the mean occurrence probability with the lower (Low) and upper (High) 95% credibility intervals. Value are all reported on the logit scale.

	Mean	Low	High
<i>Ecoregion</i>			
Least Darter	-2.77	-5.29	-0.17
Redspot Chub	0.79	-1.01	2.50
Smallmouth Bass Adult	1.45	-0.47	3.41
Smallmouth Bass Sub-adult	2.09	0.40	3.82
Southern Redbelly Dace	0.37	-1.28	2.04
<i>Year</i>			
Least Darter	-1.13	-2.61	0.32
Redspot Chub	-0.84	-2.16	0.57
Smallmouth Bass Adult	-0.98	-2.38	0.43
Smallmouth Bass Sub-adult	-1.61	-3.15	-0.33
Southern Redbelly Dace	-1.26	-2.64	-0.01
<i>2-week average temperature</i>			
Least Darter	-1.38	-2.58	-0.34
Redspot Chub	0.36	-0.50	1.20
Smallmouth Bass Adult	0.23	-0.84	1.27
Smallmouth Bass Sub-adult	0.93	-0.06	1.95
Southern Redbelly Dace	-2.53	-4.31	-1.41
<i>Drainage area</i>			
Least Darter	-0.18	-1.37	0.98
Redspot Chub	0.98	0.01	2.11
Smallmouth Bass Adult	3.09	1.25	5.91
Smallmouth Bass Sub-adult	1.44	0.41	2.63
Southern Redbelly Dace	-0.02	-1.11	1.21
<i>Proportion pool area</i>			
Least Darter	-0.36	-1.18	0.44
Redspot Chub	-0.41	-1.08	0.22
Smallmouth Bass Adult	0.75	-0.16	1.77
Smallmouth Bass Sub-adult	0.07	-0.56	0.70

Southern Redbelly Dace	-0.77	-1.55	-0.07
<hr/>			
<i>Residual pool depth</i>			
Least Darter	0.39	-0.50	1.08
Redspot Chub	0.61	0.04	1.24
Smallmouth Bass Adult	0.59	-0.04	1.27
Smallmouth Bass Sub-adult	0.66	0.08	1.36
Southern Redbelly Dace	0.40	-0.33	1.01
<hr/>			

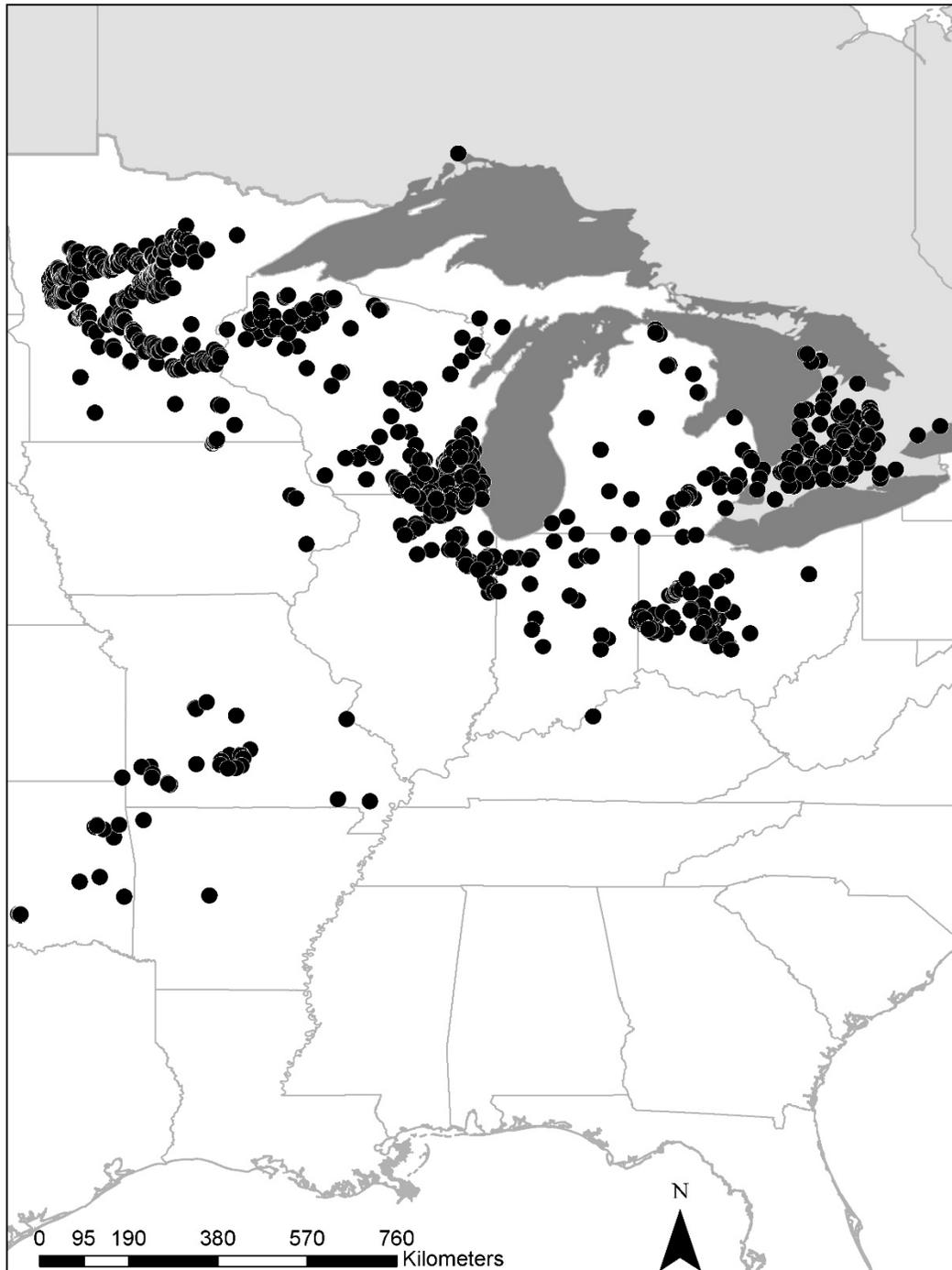


Figure 1. Least Darter collection records for the United States and Canada. Data were obtained through literature review, online databases, and professional correspondence in 2017. See Appendix 1 for references.

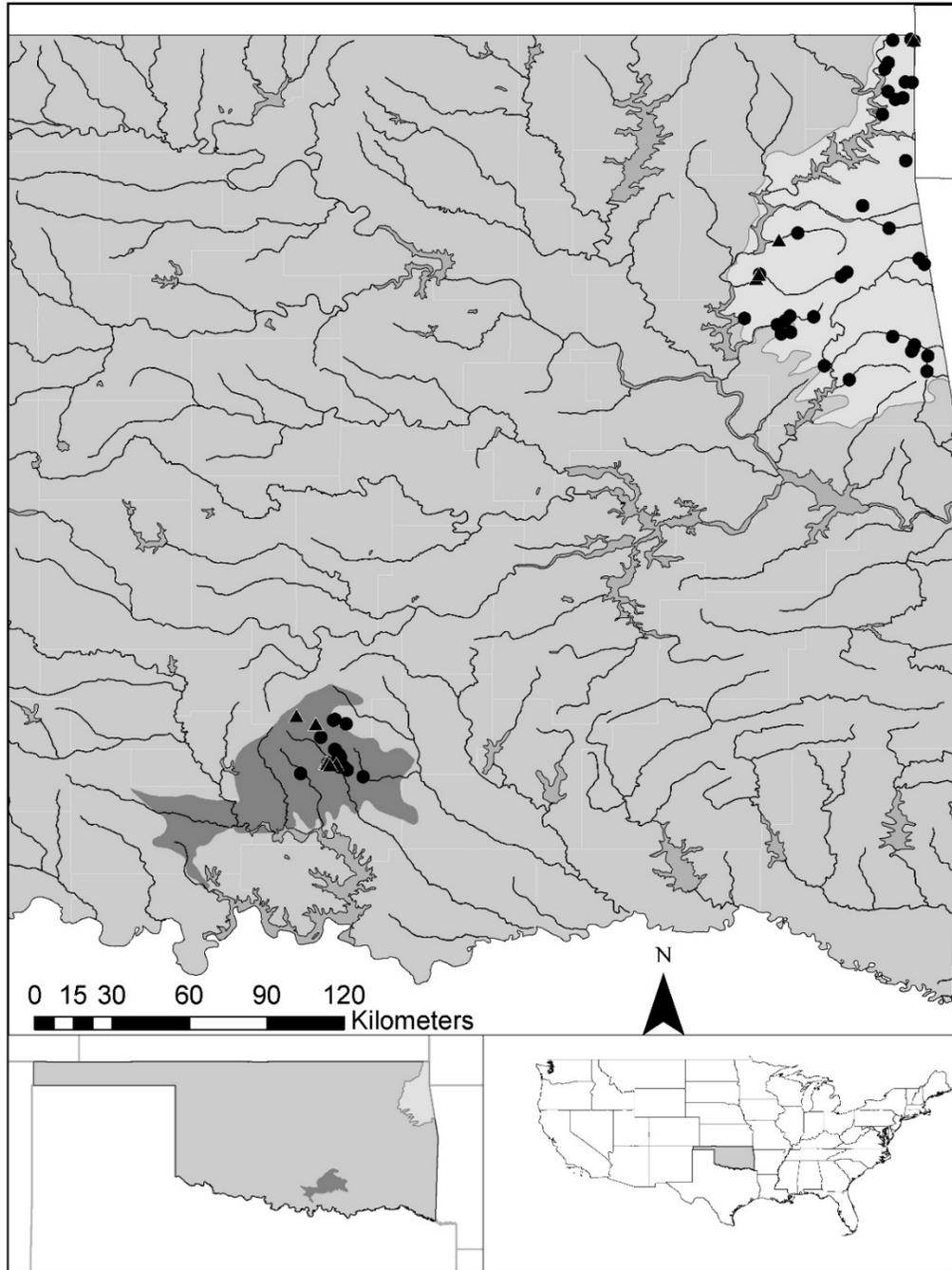


Figure 2. Reaches sampled (black circles) in summer 2018 (30 reaches) and 2019 (31 reaches) and Least Darter detections (black triangles) in the Arbuckle Uplift ecoregion (dark grey, Woods et al. 2005) and Ozark Highland ecoregion (light grey, Woods et al. 2005) of Oklahoma.

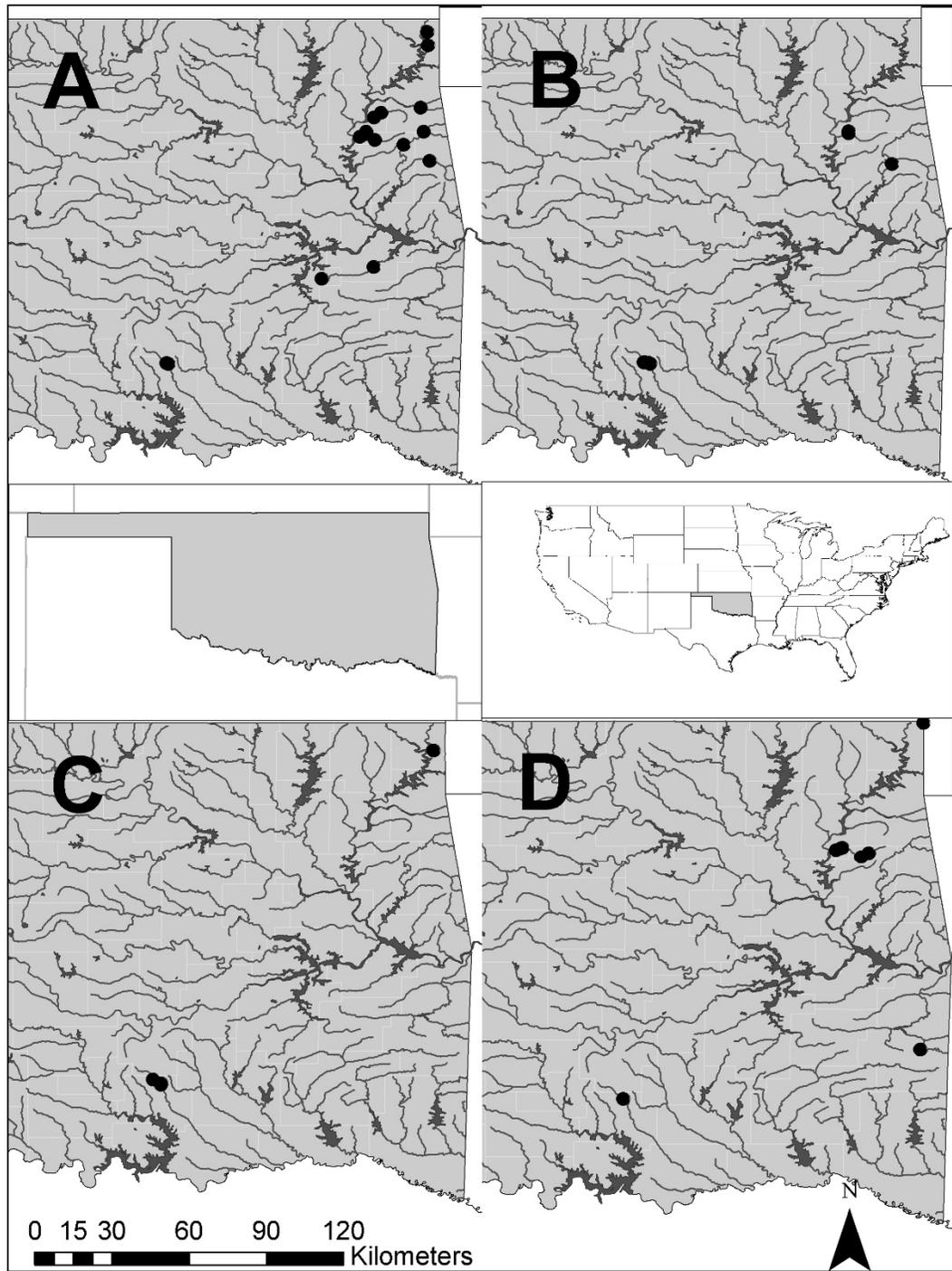


Figure 3. Historic Least Darter collection in Oklahoma during four time periods: (A) Pre 1970, (B)1970 to 1990, (C) 1990 to 2000, and (D) 2000 to current. See Appendix 1 for sources.

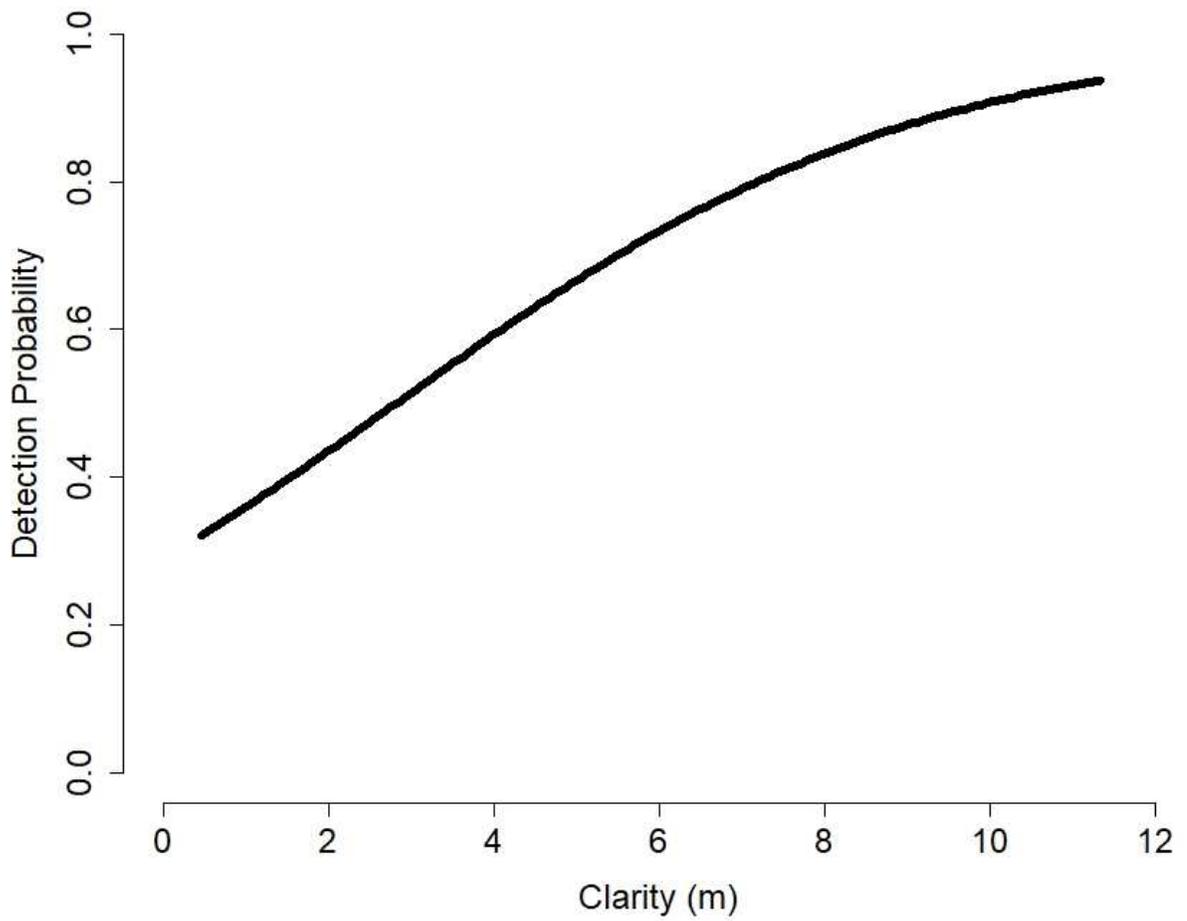


Figure 4. Relationship between detection probability and water clarity for all sites when sampling fishes via snorkeling (i.e., group detection). The relationship shown is in reference to seining.

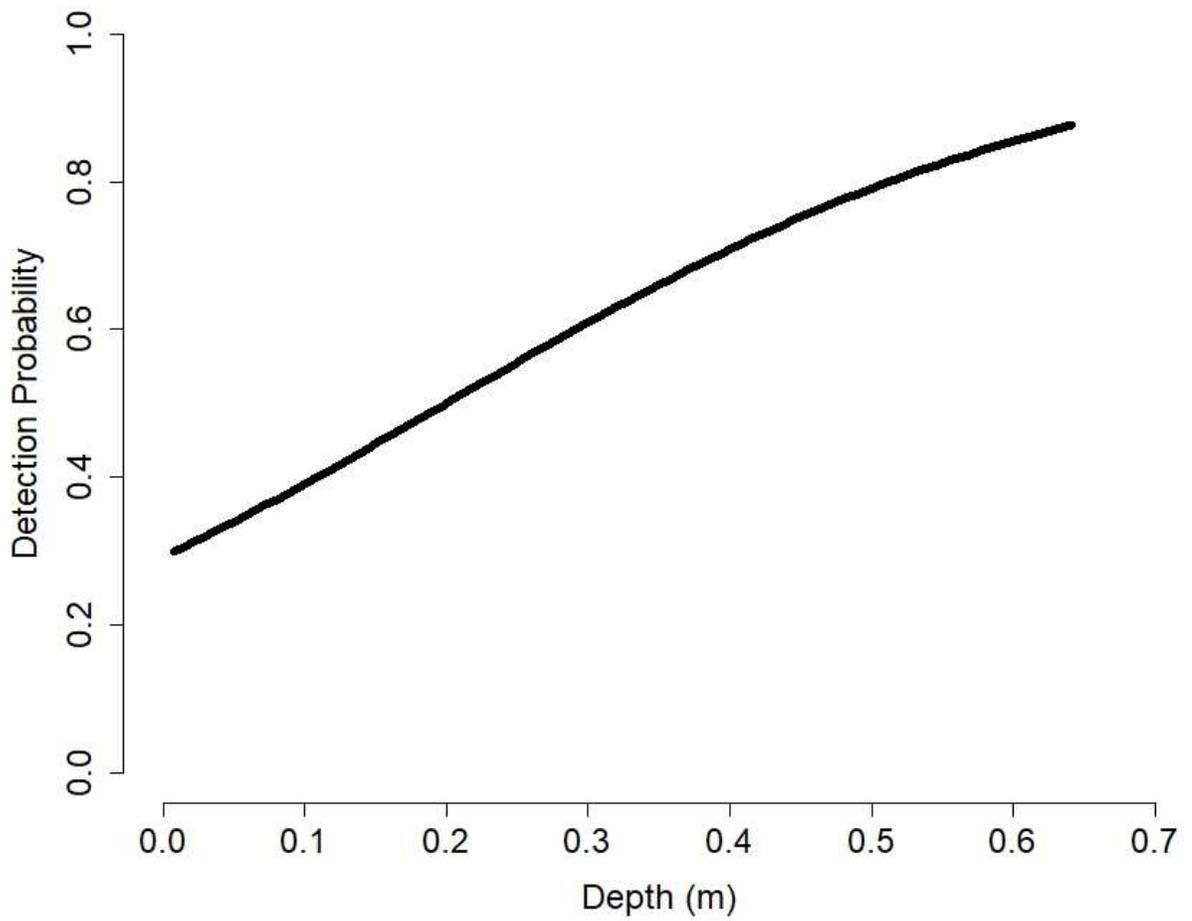


Figure 5. Relationship between detection probability and water depth (depth) for all sites when sampling fishes via snorkeling (i.e., group detection). The relationship shown is in reference to seining.

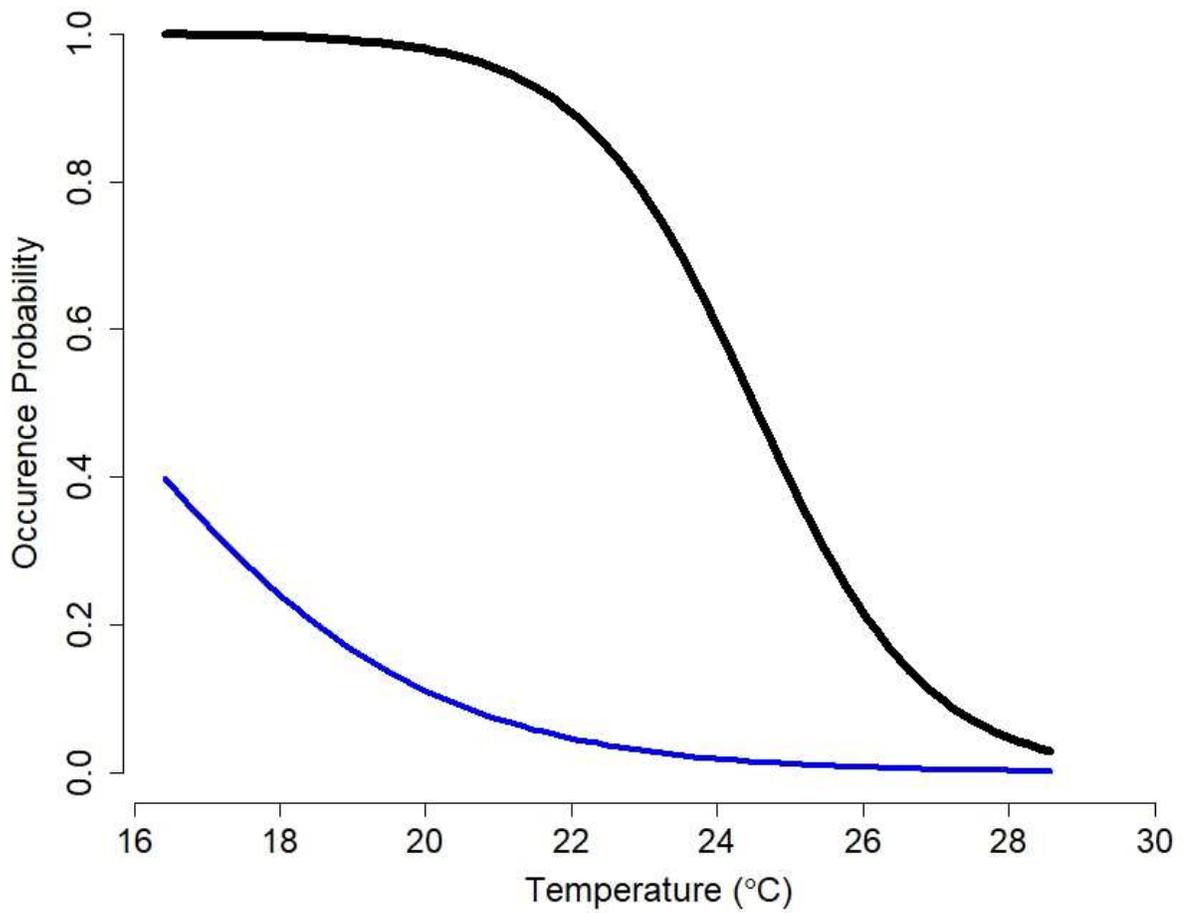


Figure 6. Relationships between occurrence probability of Southern Redbelly Dace (black line) and Least Darter (blue line) and 2-week average stream water temperature (Temperature) as a deflection from the group mean for all sites.

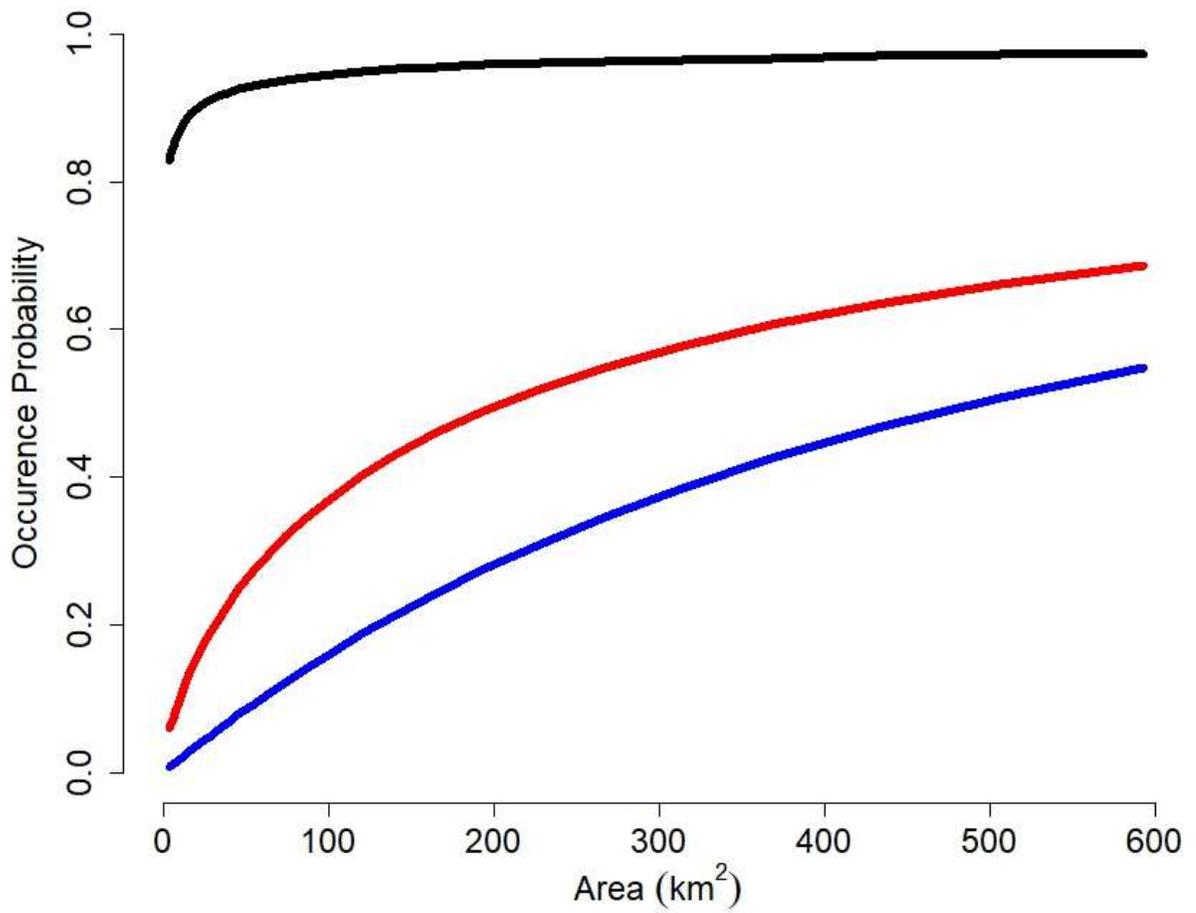


Figure 7. Relationships between drainage area (Area) and occurrence probability of Redspot Chub (black line), Smallmouth Bass sub-adult (blue line), and Smallmouth Bass adult (red line) as a deflection from the group mean.

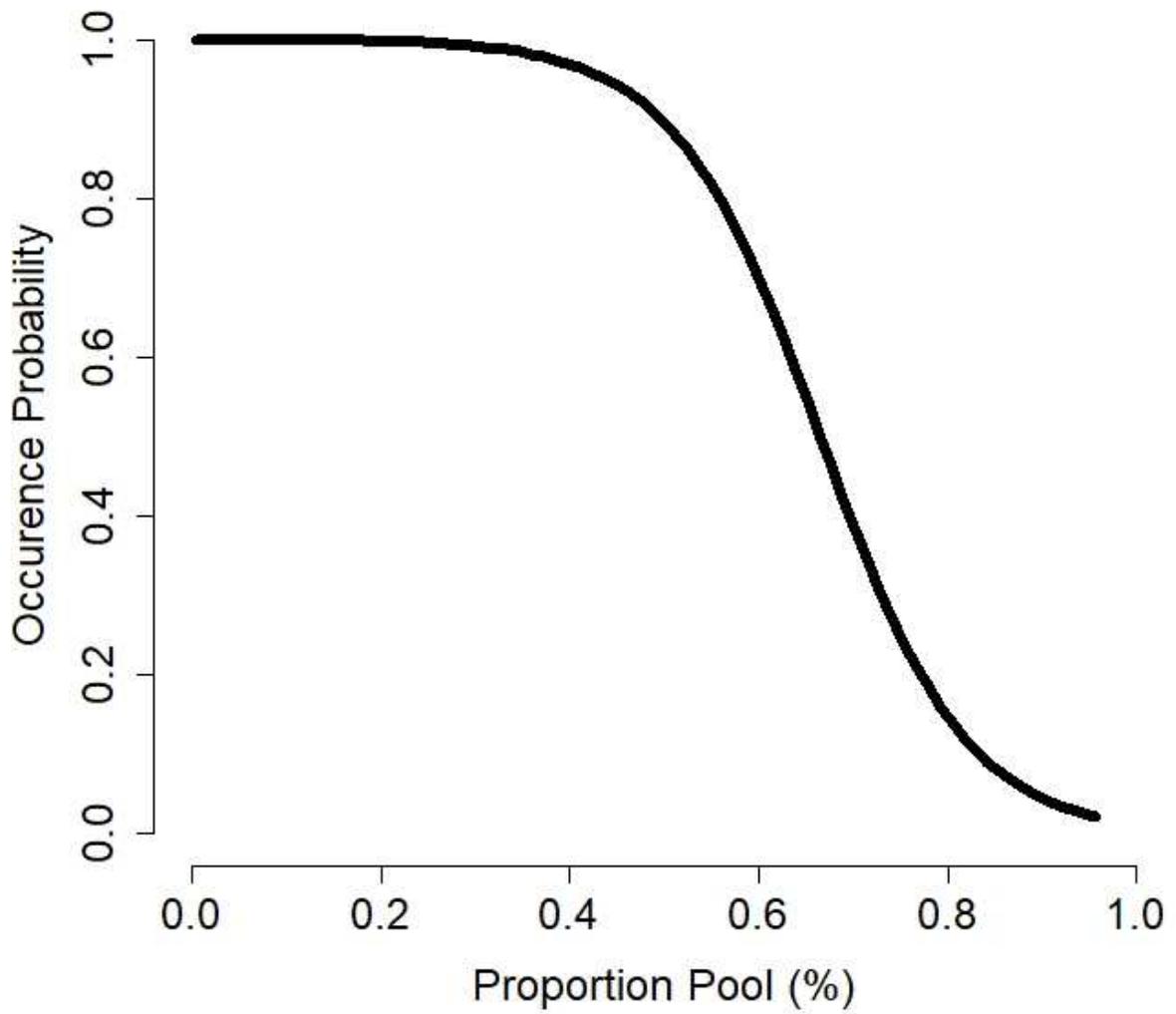


Figure 8. Relationships between occurrence probability of Southern Redbelly Dace (black line), and proportion of pool area at a site (Proportion Pool) as a deflection from the group mean.

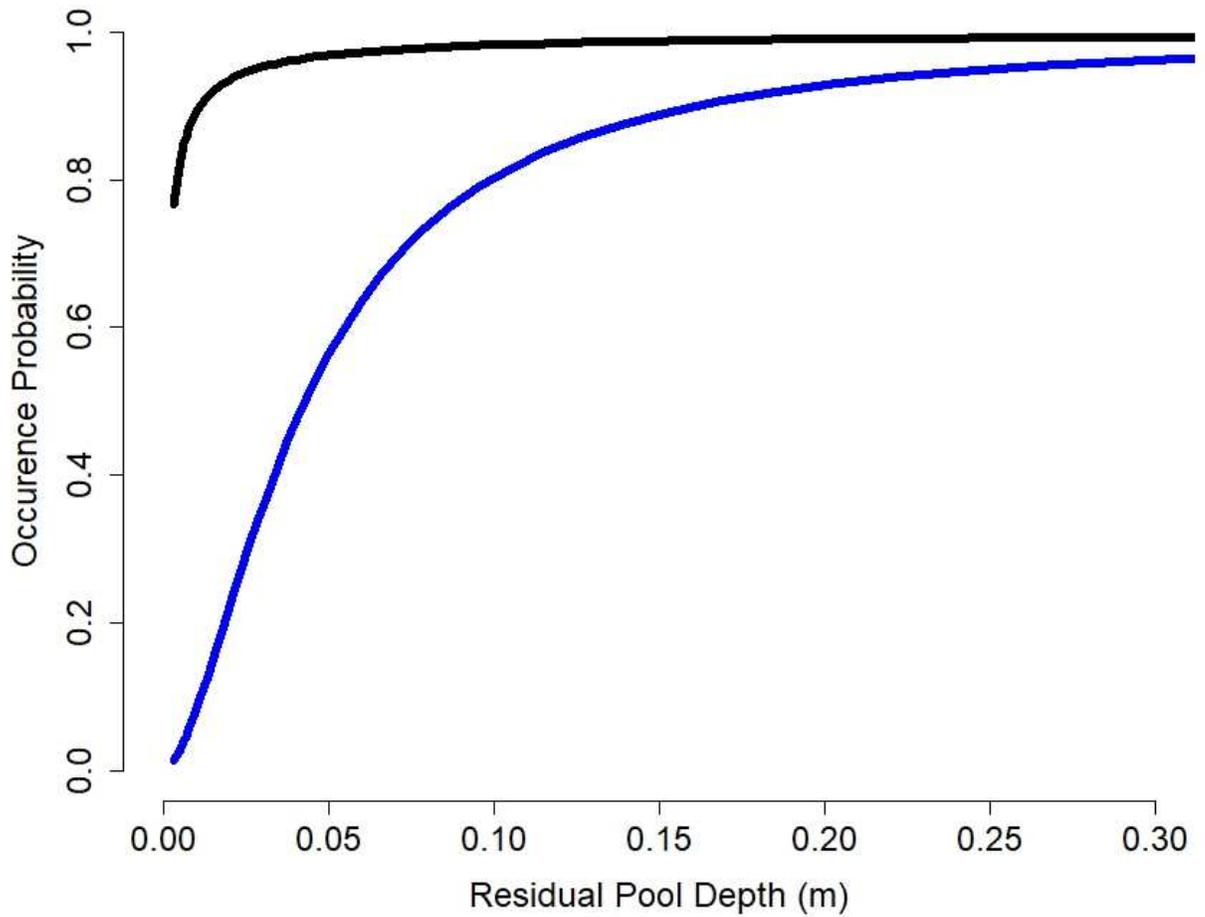


Figure 9. Relationships between occurrence probability of Redspot Chub (black line) and Southern Redbelly Dace (blue line) and residual pool depth as a deflection from the group mean. X-axis is cutoff at 0.30 meters because occurrence probability from that point remains constant.

CHAPTER III

MICROHABITAT USE OF LEAST DARTER AT THE SOUTHERN EXTENT OF THEIR RANGE IN OKLAHOMA

ABSTRACT

At fine spatial scales (e.g., within a reach), heterogeneity within streams supports the habitat needs of fishes. Understanding seasonal habitat-selection patterns is important when developing conservation and restoration plans intended to improve conditions for stream fishes throughout the year. Without a basic understanding of habitat associations, species are often considered ‘data deficient’ limiting conservation and management options. The Least Darter is an isolated spring-obligate species with patchy southern populations in the Ozark Highlands and Arbuckle Uplift ecoregions and a species of conservation concern in Oklahoma. Little information is available regarding habitat use for these disjunct southern populations. Therefore, my objective was to assess how Least Darter orient themselves in response to fine-scale environmental features (temperature, depth, velocity) during relatively harsh seasonal periods (summer and winter). To do this I sampled two stream reaches, in each ecoregion during the winter and summer of 2019. I

divided each reach into microhabitat patches and measured several physicochemical parameters that were hypothesized to effect Least Darter use over 5 to 6 days. Least Darter patch use was recorded and habitat information from these patches were used to determine relationships. Least Darter patch use varied by season. During winter Least Darter used slightly higher water velocities, less vegetation, and shallower water depths relative to summer. However, Least Darter selected fine substrates over coarse substrates regardless of season. These results will allow us to understand how Least Darter use habitat seasonally across the southern extent of their range and increase our ability to develop conservation strategies for this species.

INTRODUCTION

Groundwater associated fishes are of concern to scientists due to the overwhelming conservation issues affecting both warmwater and coldwater species and the important role of groundwater in stream ecosystems (Poff 1996; Power et al. 1999; Mcmanamay et al. 2014). The importance of groundwater has been relatively well studied for salmonids (Meisner et al. 1988; McCullough 1999; Boulton and Hancock 2006; Chu et al. 2008), but less emphasis has been paid to warmwater fishes (but see Power et al. 1999; Perkin et al. 2017; Mollenhauer et al. 2019). Groundwater is also an important component in warmwater streams via relationships with fish survival (Labbe and Fausch 2000; Whitley et al. 2006; Westhoff and Paukert 2014) and occurrences (Brewer 2013; Perkin et al. 2017; Mollenhauer et al. 2019). Additionally, groundwater contributions in warmwater streams provide relatively stable temperatures and high productivity (Hynes 1983). Under current anthropogenic pressures, groundwater habitats

in warmwater streams are increasingly degraded by poor water quality (Whitehead et al. 2009) and reduced water quantity (Xenopoulos et al. 2005).

As the effects of climate change and other human perturbations intensifies, there is a need to understand responses by fishes (Lynch et al. 2016). In lotic habitats, climate change relates to distributional shifts by some species (Buisson et al. 2008, 2010; Comte and Grenouillet 2013; Snyder et al. 2015), affects demographic processes shaping fish population structure via disruption of life-history characteristics (Walther et al. 2002; Letcher et al. 2015), and alters assemblage structure, leading to changes in stream function (Carey and Wahl 2011). Altered flow regimes (Pringle 2001) and land-use changes (Mantyka-Pringle et al. 2014; Guse et al. 2015) act in concert with climate change to intensify stress on stream systems. The overall effect is loss of fish assemblage diversity (Allan and Flecker 1993). However, stream and catchment heterogeneity can increase the availability of suitable stream habitats providing opportunities for fish to occupy the more well suited of the remaining habitats (Capell et al. 2014; Westhoff and Paukert 2014).

Stream habitat heterogeneity is affected by abiotic and biotic processes operating across a range of spatial and temporal scales (Palmer and Poff 1997; Labbe and Fausch 2000). Course-scale phenomena, such as geology and climate, determine or limit species ranges over a long period of time (Hynes 1975; Frissell et al. 1986; Wiens 1989). However, at fine spatial scales, we can observe behavioral responses by fishes to rapidly occurring perturbations (Frissell et al. 1986; Grossman and Freeman 1987). At fine spatial scales (e.g., within a reach), heterogeneity within streams supports the essential habitat needs of fishes at given points in time. These include specific water velocities

aiding bioenergetic demands (Rinóon and Lobón-Cerviá 1993) macrophyte patches providing cover (Gantes and Caro 2001), substrate affecting foraging opportunities (Angermeier 1985), depth helping mitigate predation risk (Lonzarich and Quinn 1995), wood providing cover and foraging areas (Wondzell and Bisson 2003), and temperature benefiting growth (Brewer 2013). Because of a long history sport fish management, we understand the fine-scale habitat associations for many game species but this is often lacking for rare or non-commercially valuable fish (Donaldson et al. 2011).

Water temperature is a fundamental factor for many species and can lead to a species being rare or having a patchy distribution. Temperature can affect fish in a variety of ways; controlling, masking, limiting, stressing, and directing effects (see Coutant 1976). For example, Ultsch et al. (1978) found darters (*Etheostoma spp.*) could lower their summertime metabolic rate to reduce oxygen consumption. Temperature can also interact with other physicochemical factors thereby causing changes in fish behavior (Taniguchi et al. 1998; Sloat and Osterback 2013), movement (Bjornn 1971; Albanese et al. 2004), and feeding habits (Fraser et al. 1993; Taniguchi et al. 1998). Therefore, temperature can be a crucial component of fish habitat selection and survival (Coutant 1976). Moreover, temperature refugia over a 24-h period can have some relationship with the overall thermal tolerances of stream fishes (Farless and Brewer 2017). The importance of temperature can manifest at different scales where large springs, certain lithologies, and dam releases of water can result in relatively cold and homogenous water temperatures over large spatial extents (Poff and Zimmerman 2010; Cheng et al. 2016). However, many warmwater streams have patchy environments where local groundwater contributions via seeps and small springs result in a thermally heterogeneous habitat

(Zhou et al. 2018), often leading to patchy distributions because of thermal tolerances or bioenergetics (Whitledge et al. 2006 e.g., Smallmouth Bass growth, and Strange et al. 2002 e.g., Rainbow Darter *Etheostoma spectabile* growth). Combined with other physiochemical factors, temperature is an important factor affecting habitat selection by fishes.

Understanding habitat-selection patterns is useful for developing conservation and restoration actions intended to improve conditions for stream fishes. Without a basic understanding of habitat associations, species are often considered ‘data deficient’ limiting conservation and management options (Jelks et al. 2008) or leading to haphazard efforts with little if any positive outcome (Dodrill et al. 2015). For groundwater-reliant organisms, minimizing groundwater pumping can improve vegetation persistence (Shaw and Cooper 2008), limit erosion and downcutting (Kondolf and Curry 1986) and increase stream productivity (Hynes 1983). Groundwater-based microhabitat provides thermal refugia for stream fishes (Torgersen et al. 1999; Ebersole et al. 2001) and maintain or improve base flows during droughts (Poff et al. 1997). Groundwater is also crucial for maintaining hydrologic connectivity for streams and fish persistence in the southern United States (Ross et al. 1985; Labbe and Fausch 2000; Gido et al. 2006; Jaeger et al. 2014). It is also feasible to alter or restore groundwater flow (Kasahara and Hill 2006; Boulton 2007; Suthersan et al. 2013) to achieve desired population sizes (Fleckenstein et al. 2004), assist habitat recovery efforts (Kasahara et al. 2009), or achieve other objectives (Arthington and Pusey 2003). Habitat selection studies have been used to monitor efforts to improve the habitat and abundance of salmonids with the use of wood structure and large substrates (Louhi et al. 2016). Additionally, habitat selection studies

have been used to improve stream fish dispersal and maintain water velocities by removal of barriers affecting fish distribution (Mattingly and Galat 2002; Reid et al. 2005). Flow variation (i.e., stream connectivity), pool scour, and deposition was an important component in the conservation and management for the Arkansas Darter by identifying the stream processes important to seasonal habitat creation and use (Labbe and Fausch 2000). An understanding of the instream environment related to temperature patterns and associated biota is essential for the development of meaningful conservation and management strategies.

My study objective was to examine fine-scale habitat selection (where proportionate habitat use exceeds proportionate availability, Johnson 1980) by Least Darter during summer and winter. I hypothesized Least Darter would occupy cooler thermal patches with vegetation coverage and relatively calm water. Previous studies in the northern and southern portion of the species range indicate associations with cold water (Hargrave and Johnson 2003), relatively high percentages of vegetation (Johnson and Hatch 1991; Seilheimer and Fisher 2010), sand (Burr and Page 1979; Johnson and Hatch 1991) or silt substrates (Burr and Page 1979; Johnson and Hatch 1991), and low water velocities (Burr and Page 1979; Johnson and Hatch 1991; Seilheimer and Fisher 2010). I focus on the winter and summer seasons because they represent extremes of water temperatures and are especially important for Least Darter populations at the southern portion of its range as it provides a stable average annual temperature similar to what is found in its northern range.

STUDY AREA

My study area consisted of two stream reaches (~150-m long with shallow riffles or a waterfall on each end), one each in the Arbuckle Uplift and Ozark Highland ecoregions (Figure 10). Both ecoregions represent southernmost populations of Least Darter (see Chapter 1 Study Area for an overview). The climate of both ecoregions is relatively humid (Arbuckle Uplift 79-96 cm/year; Ozark Highland 104-122 cm/year) with forest vegetation and open fields in lowland areas (see Chapter 2 for a complete description). The lithology of the Ozark Highlands is primarily limestone whereas the Arbuckle Uplift ecoregion is a mix of dolostone, limestone and granite. The ecoregions have karst topography. Ozark Highland streams in Oklahoma tend to have spottily distributed groundwater patches and small springs (Vineyard and Feder 1982; Zhou et al. 2018), whereas streams of the Arbuckle Uplift have thermally rather constant springs beginning at artesian wells feeding small spring branches (Osborn 2009; Christenson et al. 2011). The stream reaches chosen for study were selected because they had relatively high abundances of Least Darter (based on Chapter 2 sampling), and the landowners granted access for the study. The reach in the Arbuckle Uplift was an unnamed headwater tributary of the Blue River (3rd order stream, Strahler 1957) containing numerous artesian springs and consisting of multiple pool-riffle complexes. The Ozark Highlands study reach was a riffle-pool complex located on Snake Creek (3rd order, Strahler 1957). The respective coordinates were 34°27'23.4"N 96°39'58.8"W and 36°09'02.1"N 95°10'11.6"W.

METHODS

Habitat availability

Relatively homogenous ($\sim 2 \text{ m}^2$) habitat patches (hereafter, sampling units) were mapped across the study reaches prior to each seasonal sampling (February 2019, August 2019, and December 2019). I established transects both perpendicular and parallel to streamflow to quantify habitat conditions (Figure 11). I measured water depth (to nearest 0.1 m) at the center of each sampling unit. Average water-column velocity (nearest 0.1 m/s) was measured at 60% of depth using a Marsh-McBirney Flo-Mate (Hach, Loveland Colorado) (Gordon et al. 2004). I visually estimated dominant substrate within each sampling unit using substrate sizes from a modified Wentworth scale (Wentworth 1922). I simplified dominant substrate into two classes: fine (i.e., bedrock, silt and sand, ≤ 2.0 mm), and coarse (i.e., gravel, pebble, cobble, >2.0 mm). The presence-absence of coarse wood (> 10 cm diameter, Dodd et al. 2008) and percent aquatic vegetation cover was also estimated in each sampling unit.

I quantified water temperature in each habitat patch by measuring temperature continuously over each sampling period. Temperature availability was quantified using a fiber-optic distributed temperature sensing (FO-DTS) cable (Lios, Cologne, Germany), which measures temperature by sending a laser pulse down the cable and measuring the return speed and backscatter of the signal (Selker et al. 2006). To calibrate the instrument, the cable was run through a series of two or three differing temperature baths (cold, ambient, and hot) equipped with temperature loggers. Temperature at each point along the cable was calibrated using signal backscatter based on differences between the uncalibrated temperatures and known temperature from the calibration baths (Selker et al. 2006). I used these data to determine an average temperature for each patch along the cable (e.g., Selker et al. 2006; Westhoff et al. 2010). For the study, I laid the cable on the

stream bottom parallel to streamflow, anchoring it with a rock or polyvinyl chloride (PVC) cylinder filled with cement in the center of each of my sampling units. The fiber optic cable had markings printed every meter so temperature measurements could be spatially referenced to each patch during each sampling event (see below).

Habitat use

I used snorkeling to determine habitat use by Least Darter during both winter (February 2019) and summer (August 2019) in the Arbuckle Uplift (Figure 10). The Ozark Highlands were only sampled during winter (December 2019) because a suitable stream reach was not identified until summer 2019 (Figure 10). I anticipated groundwater upwelling would have the most influence on water temperatures during summer and winter rather than spring or autumn (Hubbs 1995; Constantz 1998). I hypothesized Least Darter would use patches of water temperature cooler than the median temperature available during summer and warmer than the median temperature during winter.

Fish location and associated habitat use were quantified during summer and winter. During each season, I conducted one snorkel survey daily for five or six days in winter and summer, respectively. I alternated between morning (~9:00) and afternoon (~15:00) survey times on consecutive days. Snorkeling followed the approach described for Chapter 2 (see Fish Sampling). Briefly, snorkelers swam upstream in their designated lanes at approximately 2 m/min, spending more time in complex habitats. Observers carefully examined habitat patches to locate fish, including under coarse substrate material and within dense vegetation. Upon identification of Least Darter, a numbered, weighted fluorescent flag was placed on the substrate near the fish's location. Flag number and fish count were recorded on a PVC wrist cuff. If the fish's behavior appeared

to be altered by the snorkeler, that habitat-use observation was omitted. I determined which spatially referenced sampling unit was nearest each fish observation at each sampling event. I was then able to assign habitat use data to the fish use-point based on the habitat availability data (see previous section).

Analyses

To improve model interpretation and function, I transformed several predictor variables. Average water column velocity and vegetation were right-skewed, so they were log-transformed. Depth was still right-skewed following log transformation, so I had to square root transform these values. The deviation from the ecoregions median temperature was used in place of average temperature for each sample unit to normalize temperature across each ecoregion and season. I standardized all my covariates by subtracting the mean of the covariate from each value and dividing by the standard deviation to improve model interpretation (Table 9).

I determined my final variable set by examining correlations and considering factors affecting Least Darter detection. I checked correlations among continuous covariates using the Pearson coefficient correlation. Categorical covariates were checked for correlations by determining the frequency of co-occurrence in my data and none were correlated (Table 10). Correlations between my standardized continuous covariates were $|r| \leq 0.58$, so all covariates could be retained for model development (Table 10). I omitted water clarity from model development because it exceeded 5 m and was not likely to affect Least Darter detection (see also Chapter 2). My final model set contained the following variables: deviation from the site median-temperature, square root of depth, log of percent vegetation, log of average water column velocity, four binary variables

representing substrate (coarse or fine; fine was the reference), coarse wood (present or absent; absent = reference), season (winter or summer; summer = reference), and ecoregion (Arbuckle Uplift or Ozark Highlands; Ozark Highlands = reference).

I determined habitat selection (response variable) by Least Darter using a generalized linear mixed model. The use-nonuse approach uses data from both occupied and unoccupied patches to strengthen habitat-use relationships (Johnson 1980). First, I built my most complex microhabitat model. In addition to the main effects, I considered reasonable interaction terms: deviation from median temperature \times depth, vegetation \times depth, and vegetation \times deviation from median temperature. Patch use of Least Darter would be higher in shallow areas with more temperature deviation because larger-bodied predators tend to use moderate depths (Peck et al. 2013). I predicted patch use of Least Darter would be independent of residual pool depth at lower temperature deviations (Hetrick et al. 1998). Next, I hypothesize patch use for Least Darter in areas of high vegetation coverage would remain relatively constant across pool depths because it represent refuge from a variety of predators, whereas low vegetation coverage in shallow water could reduce patch use due exposure to avian predation. Deeper water, however, even with less vegetation reduces the risk of avian predation (Savino and Stein 1982; Rozas and Odum 1988). Finally, I predicted patch use in sample units with little vegetation would be higher in areas of constant temperature as this provides the thermal refuge patches thought to be important for Least Darter (Seilheimer and Fisher 2010). In areas of high vegetation coverage, I predict Least Darter patch use would be independent of temperature deviation. To account for variation between ecoregions, I included ecoregion as a nuisance factor to improve model fit and convergence. I also included a

sampling-day grouping factor to account for unexplained temporal variation due to concurrent sampling days in each season. Lastly, I also included a grouping factor for patches at each site because of anticipated spatial autocorrelation (Gelman and Hill 2006; Wagner et al. 2006). My most complex microhabitat model can be written as:

$$\begin{aligned} \text{logit}(occ_i) = & \sum_{k=1}^1 \alpha_{0k} + \sum_{k=1}^1 \alpha_{Reach[i]} + \sum_{k=1}^1 \alpha_{Season[i]} + \sum_{k=1}^1 \alpha_{Coarse\ Wood[i]} + \\ & \sum_{k=1}^1 \alpha_{Substrate[i]} + \sum_{m=1}^4 \sum_{n=1}^4 \beta_m X_n[i] + \sum_{m=5}^5 \sum_{c=1}^1 \beta_m X_c[i] + \sum_{m=9}^9 \sum_{n=1}^4 \beta_m X_f[i] * \\ & Season[i] + \sum_{k=1}^1 \alpha_{Coarse\ Wood[i]} * Season + \sum_{k=1}^1 \alpha_{Substrate[i]} * \\ & Season + \sum_{k=1}^1 \gamma_t[i] + \sum_{k=1}^1 \delta_t[i], \text{ for } i = 1, 2..N \end{aligned}$$

$$\alpha_{0k}, \alpha_{Season[i]} \text{ and } \alpha_{Reach[i]} \sim t(\mu, \sigma^2, \nu),$$

$$\beta_m \sim t(\mu, \sigma^2, \nu),$$

$$\gamma_t \sim t(0, \sigma^2, \nu), \text{ for } t = 1, 2..16,$$

$$\delta_t \sim t(0, \sigma^2, \nu), \text{ for } t = 1, 2..420,$$

where occ_i is Least Darter occurrence probability for site i , α_{0k} is the Least Darter accumulative use intercept, α_{Reach} is the ecoregion factor for Least Darter with Arbuckle Uplift as the reference, α_{Season} is the season factor for Least Darter with summer as the reference, β_m is the Least Darter patch use for slope m , X_n is an occurrence environmental covariate (see above). $\alpha_{Coarse\ Wood}$ is a categorical covariate reflecting the presence or absence of coarse wood (absence as the reference), whereas $\alpha_{Substrate}$ is a categorical covariate for the presence of coarse or fine substrate (coarse as the reference). Additionally, X_f is an occurrence covariate \times season interaction: water depth \times season, deviation from median temperature \times season, vegetation \times season, and velocity \times season. X_c represents all other covariate interactions: percent vegetation \times depth, median

temperature \times depth, and percent vegetation \times deviation from median temperature. γ_t is the grouping factor for pass t and δ_t is the grouping factor for patch t .

The final overall model was selected using the same backward selection approach used in Chapter 2. First, I fit a model containing interactions and removed any two-way interactions where the 95% HDI overlapped zero (i.e., not considered significant). The model was then refitted with main effects and only significant main effects were retained. The final model included only significant main effects and interactions (including associated main effects).

Models were fit using the program JAGS (Plummer 2003) called from the statistical software R (version 3.5.3; R Developments Core Team 2019) using the package jagsUI (Kellner 2019). I used broad uniform priors for species coefficients and main effects and vague gamma priors for associated standard deviations (Kery and Royle 2015). Posterior distributions for coefficients were estimated using Markov chain Monte Carlo methods with 100,000 iterations after a 50,000 iteration burn-in phase. Posterior predictive distributions were in the range of my data and were used to assess model fit. Convergence was determined by applying the Brooks-Gelman-Rubin statistic (\hat{R}). Values of the Brooks-Gelman-Rubin statistic <1.1 indicate adequate mixing of chains for all parameters (Gelman and Rubin 1992).

RESULTS

Fish sampling

Occupied patches by Least Darter varied by site and season. Least Darter was present in more microhabitat patches in the Arbuckle Uplift during winter (28%, 157 of 570 patches) when compared to the Ozark Highlands (6%, 52 of 870 patches). Only my

site in the Arbuckle Uplift was sampled during both winter and summer. In the Arbuckle Uplift site, patch occupancy by Least Darter during summer was higher (36%, 281 of 786 patches) than during the winter (28%, 157 of 570 patches).

Habitat availability

There were some seasonal differences in habitat availability at my sites. In the Arbuckle Uplift, water temperatures were cooler during the winter compared to summer, though deviation from the median water temperature was similar between the two seasons. Fine substrates were common during both seasons and both ecoregions. Habitat patches of the Ozark Highlands tended to be less homogenous than patches of the Arbuckle Uplift (Table 9). Average temperatures during winter were cooler in the Ozark Highlands than the Arbuckle Uplift. There was also less variation from median water temperature at my site in the Ozark Highlands compared to the Arbuckle Uplift. Habitat patches were deeper with slower water velocities in the Ozark Highlands. Vegetation (% coverage) was higher at the Arbuckle Uplift site during winter and there was a greater presence of coarse wood in habitat patches of the Ozark Highlands.

Habitat use

My final microhabitat model had appropriate model fit and adequate mixing of chains. The final model consisted of 10 significant terms (HDIs did not overlap zero). All model parameters successfully converged at \hat{R} of 1.0.

Least Darter was more common in habitat sample-units of the Arbuckle Uplift ecoregion, and habitat use tended to vary between winter and summer (significant two-way interaction habitat use and season, Table 11). During winter, Least Darter used higher water column velocities (0.12 m/s versus 0.06 m/s in the summer) and shallower

habitat patches with less aquatic vegetation (Figure 12). Average water depth used was 19.67 cm during winter and 20.80 cm during summer. Vegetation was consistently used in both seasons, but usage was higher during winter at low levels compared to summer. Lastly, sample-unit usage was negatively associated with coarse substrates regardless of season.

DISCUSSION

Least Darter used habitat patches differently during winter and summer. Least Darter relationship with habitat use of water depth, water velocity, and vegetation all shifted from summer to winter. Similar seasonal shifts in habitat use have been documented for other darter species often in response to reproduction cues or food resources (Wynes and Wissing 1982; Hubbs 1985; Harding et al. 1998). Least Darter at my Arbuckle Uplift site shifted to slightly higher water velocities and shallower water during winter when compared to the summer. The wintertime shift to shallower water is contrary to the observation that, in Minnesota, the species moved to deeper pools during the winter (Johnson and Hatch, 1991). This discrepancy might reflect the warmer winter temperature in the southern portion of the range. Further, ice coverage in the northern portion of the range may force the species into deeper water during winter. Johnson and Hatch (1991), recorded that Least Darter moved to vegetated run margins after spawning in July and August. Given generally warmer stream temperatures in my study area, Least Darter may be occupying run margins throughout the winter. The slight decrease in vegetation use by Least Darter in the winter is interesting because all studies have documented strong relationships with vegetation for the species, for example Illinois (Burr and Page 1979), Minnesota (Johnson and Hatch 1991), and Arkansas (Hargrave and Johnson 2003).

However, these studies have not documented Least Darter habitat use during the winter. The decrease in vegetation use in winter could reflect lower vegetation availability in the winter causing shifts to other cover types, such as detrital material. Finally, seasonal shifts could be a function of spawning activity, Winn (1958) observed seasonal movement in response to reproduction for Least Darter. Previous records of Least Darter in Oklahoma suggest they enter breeding condition in February (Burr and Page 1979). Accordingly, I found Least Darters in breeding condition during my February sampling.

Least Darter uses patches characterized by fine sediments (silt or sand) regardless of season (Burr and Page 1979; Johnson and Hatch 1991; Hargrave and Johnson 2003; Seilheimer and Fisher 2010; my results). Although the functional reasons are unknown, fine substrates may be related to spawning habitat (Winn 1958) or foraging. Fine substrates are used for foraging by prey species consumed by small bodied fishes like Least Darter (Angermeier 1985; Gilliam et al. 1989). Some degree of increase in fines has been shown to increase fish densities in other studies (e.g., Smallmouth *Bass* *Micropterus dolomieu*, Brewer and Rabeni 2011), although a threshold response is hypothesized for excessive fines due to land uses or other human effects may have undesirable consequences (Quinn and Hickey 1990). Moreover, fine substrates can represent areas of suitable spawning due to the high amount of vegetation often located in high silty areas (Burr and Page 1979; Johnson and Hatch 1991). I found no correlation between fine sediments and vegetation in my study suggesting that vegetation and fine substrate act independently regarding Least Darter patch use.

I found temperature at a fine scale was not a significant factor related to habitat use by Least Darter. This result is interesting because at the reach scale temperature was

the only factor I found to be associated with occupancy by Least Darter (See Chapter 2). It is common for habitat relationships to manifest themselves or become indiscernible at different spatial scales (Frissell et al. 1986; Wiens 1989; Levin 1992). Temperature is an environmental factor affecting fish distributions (see Chapter 2), but might not be important at fine spatial scales (Coutant 1976; Baltz et al. 1987; Buisson et al. 2008; Comte et al. 2013). Limited variation in temperature has been observed in other spring systems (Hubbs 1995). Likewise, my data also suggested little variation in temperature among patches at my sites (deviation from the median ranged -1.15 to 2.68 °C). However, even small changes could be important for patch use across seasons (Kollaus and Bonner 2012); this relationship may be more important in streams with less spring or hyporheic influence though it is questionable whether the Least Darter would occupy those reaches (see Chapter 2).

My findings support existing habitat-use patterns reported for Least Darter, but with some important winter habitat use differences. Least Darter in the Arbuckle Uplift of Oklahoma selected habitat patches with finer substrates and lower water velocities during summer (Seilheimer and Fisher 2010). However, to my knowledge, my study is unique for the southern United States in noting a seasonal shift in habitat from summer to winter. Preparation for spawning by Least Darter is expected by early spring (Burr and Page 1979; Johnson and Hatch 1991). I did find slight differences in depth use in my December (22.5 cm) and February (19.5 cm) sampling and, in February but not December, I found individuals in breeding condition, suggesting that spawning begins in February. Though noticeable shifts between seasons do occur, the shifts seem to be minimal suggesting that winter habitat selection might be more general. Summer to winter shifts in darter

(*Etheostoma spp.*) habitat use are not uncommon. Fantail Darter (*Etheostoma flabellare*) and Rainbow Darter (*Etheostoma caeruleum*) in Ozark Highland streams used riffle, run, or pool habitats more indiscriminately in winter than in summer (Rettig and Brewer 2011). This might reflect seasonal temperature, thus metabolic differences, making summer selection of habitats more important (Gillette et al. 2006). An alternate hypothesis could be that deeper habitat are being used as refugia during midday, but during morning and afternoon (when my sampling occurred) Least Darter could be moving to the shallower habitats to feed. Additionally, it is common for groundwater associated species to exhibit seasonal shifts in habitat use in response to spawning, rearing, and sometimes overwintering needs (Wynes and Wissing 1982; Hubbs 1985; Harding et al. 1998; Wolf et al. 2019). Many studies focus on spring and summer habitat use, but relatively few have focused on winter habitat. Such studies may be important in light of climate change, increasing water demands, and other human perturbations.

My study is one of the first to examine habitat use by Least Darter in different ecoregions. Similar analyses of species-habitat relationships were developed for other nongame species, including the Arkansas Darter (Labbe and Fausch 2000; Groce et al. 2012). Unfortunately, I did not have enough data to test ecoregion-habitat interactions that would be important for developing context-dependent conservation actions.

Although important, we first need to understand seasonal habitat shifts by rare species and then build future efforts on understanding differences among ecoregions. One of the difficulties in examining ecoregional interactions is the fact that the species appears to be incredibly rare in many Ozark Highland streams that I sampled (see Chapter 2). The site that I sampled in the Ozark Highlands was located during my second field season seemed

to have lower Least Darter abundances as than was present at Blue River sites in the Arbuckle Mountains. A better understanding of gene flow in the Ozark Highlands streams may be an important consideration for examining metapopulations and abundances.

My results for Least Darter might be also useful for conservation of other rare spring-associated species. For instance, Hargrave and Johnson (2003) found Arkansas Darter occupied similar habitat types as Least Darter in Arkansas, whereas Bergey et al. (2008) found similar results in Oklahoma. Focusing on conserving habitat used by multiple species could lead to a better management of resources (Joseph et al. 2009). Similar relationships for spring-associated species have been noted at coarse scales, with distributions of spring associated species restricted to areas of noticeable spring influence (Matthews et al. 1985; Hubbs 1995; Bergey et al. 2008). Future research on spring-associated species would benefit from consideration of scale when developing habitat-model parameters and sampling protocol. My results suggest examination of reach-scale attributes would be more fruitful for relatively rare species. Protecting shared habitats may be an important conservation strategy but recognizing differences among these species is also important given cautionary tales associated with inferences based on surrogate species (Andelman and Fagan 2000; Hitt and Frissell 2004).

Seasonal shifts in habitat use are important considerations for stream fish conservation even in groundwater-dominated streams where minimal seasonal habitat variability is common. Maintaining microhabitat habitat heterogeneity could benefit Least Darter in the Interior Highlands. For instance, minimizing land use disturbance to decrease summer temperature and increase seasonal stream connectivity has been useful

in management of the groundwater-associated Arkansas Darter in Colorado (Groce et al. 2012). Additionally, my study indicates that management objectives based solely on winter or summer habitat use may not protect all Least Darter habitats necessary for the species to persist. Least Darter seem to begin spawning in February in the southern portion of its range, however, concrete spawning movement and spawning habitat use is still not completely known for this area. Protecting stream heterogeneity by watershed management and reducing anthropogenic process within a watershed would benefit Least Darter across all season as it would provide habitats during all seasons (Palmer et al. 2010). Future studies encompassing the full range of seasons and a greater range of habitats (i.e., greater spatial extent) would help increase our understanding of how this species will be affected by future changes to its environment.

Table 9. Summary statistics (sample size [N], mean, standard deviation [SD], minimum [min] and maximum [max]) of habitat patch covariates considered in the Least Darter microhabitat model. Temperature (temp) was not included in any of my models but summarized here for reference. Deviation from median is the difference between patch water temperature and the median reach water temperature in each season (i.e., all patches combined).

	N	Mean	SD	Min	Max
Arbuckle Uplift summer					
Water temperature (°C)	786	18.52	0.85	16.54	24.29
Deviation from median temp (°C)	786	0.11	0.44	-2.53	2.09
Depth (cm)	786	17.32	7.54	4	41
Aquatic vegetation (%)	786	24.12	24.24	0	100
Average water column velocity (m/s)	786	0.15	0.16	0	0.65
Arbuckle Uplift winter					
Water temperature (°C)	570	16.88	0.62	13.57	17.91
Deviation from median (°C)	570	0.10	0.52	-1.15	2.68
Depth (cm)	570	18.03	7.94	3	39
Aquatic vegetation (%)	570	7.53	12.86	0	75
Average water column velocity (m/s)	570	0.18	0.20	0	0.79
Ozark Highlands winter					
Water temperature (°C)	870	12.46	1.98	9.52	17.44
Deviation from median (°C)	870	-0.02	0.46	-1.34	2.05
Depth (cm)	870	31.96	13.44	5	60
Aquatic vegetation (%)	870	35.86	30.31	0	100
Average water column velocity (m/s)	870	0	0.020	0	0.20

Table 10. Pearson's correlation matrix for habitat use covariates for all sites. Deviation from the median water temperature (Median), water depth (Depth), coarse wood (Wood), percent vegetation (Veg), and average water column velocity (Velocity), were all measured at each patch.

	Median	Depth	Wood	Veg
Depth	-0.19			
Wood	-0.07	0.24		
Veg	-0.03	0.14	-0.03	
Velocity	0.15	-0.58	-0.14	-0.36

Table 11. Final Least Darter microhabitat model results containing all coefficients.

Substrate was a binary variable (coarse or fine where fine was the reference). Ecoregion was a binary variable (Ozark Highlands or Arbuckle Uplift where Ozark Highlands was the reference). All covariates contain lower (Low) and upper (High) 95% credibility intervals where no overlap indicated significance. References for binary variables are in parentheses: substrate (fine), reach/ecoregion (Ozark Highlands ecoregion), and season (summer).

Parameter	Mean	Low	High
Intercept	-4.16	-5.57	-2.84
Substrate	-0.67	-1.16	-0.19
Depth	1.13	0.59	1.75
Vegetation	0.68	0.29	1.09
Water velocity	-0.64	-0.88	-0.43
Season	-0.26	-1.18	0.62
Ecoregion	3.10	1.97	4.33
Season \times depth	-1.29	-1.98	-0.65
Season \times vegetation	-0.71	-1.24	-0.18
Season \times velocity	0.42	0.14	0.70

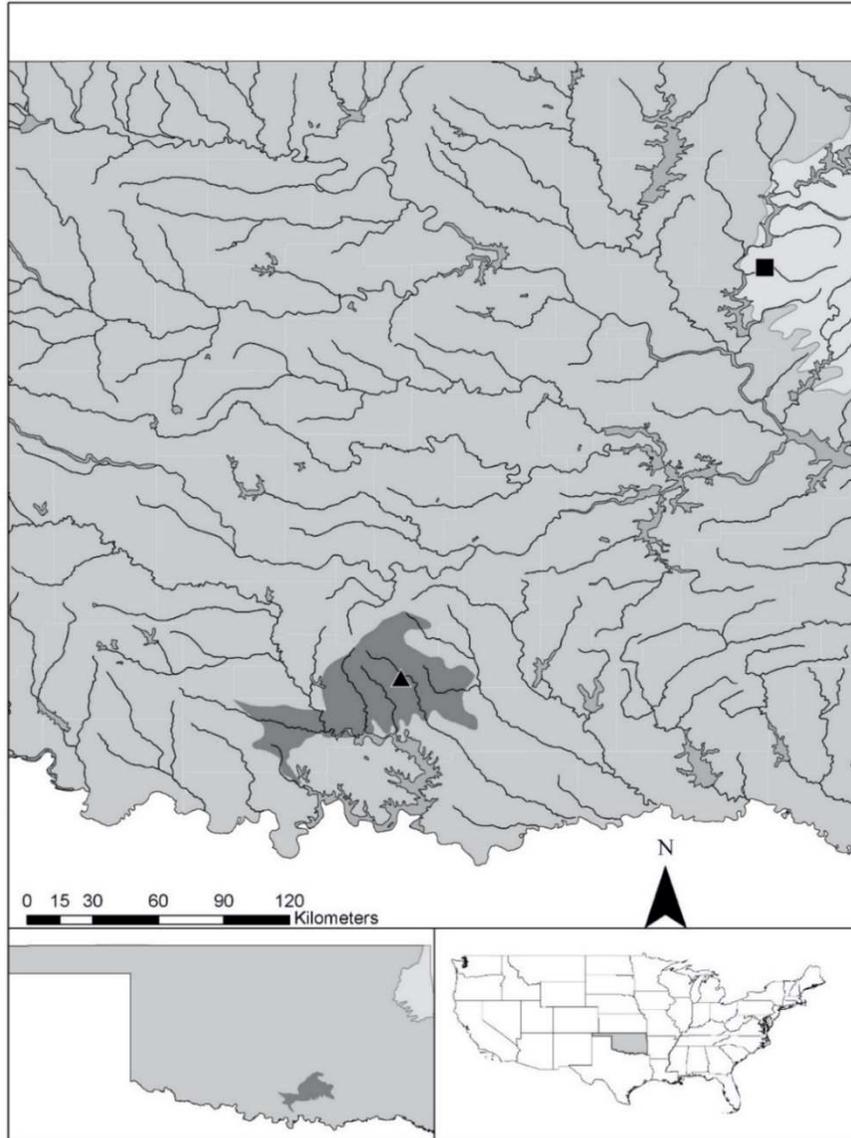


Figure 10. Sample location within the Ozark Highlands ecoregion (black square) and Arbuckle Uplift ecoregion (black triangle). The ecoregions within Oklahoma are shaded gray: Arbuckle Uplift ecoregion (dark gray, Woods et al. 2005) and Ozark Highland ecoregion (light gray, Woods et al. 2005). The site within the Arbuckle Uplift was sampled using snorkeling during both summer and winter 2019, whereas the Ozark Highland site was only sampled during winter 2019.



Figure 11. Image shows microhabitat grid used for Least Darter microhabitat sampling. Snorkelers start at the downstream end and work upstream underneath marking string that represent the longitudinal transects. The fiber optic cable was placed parallel to flow beneath the water's surface to complete the grid network.

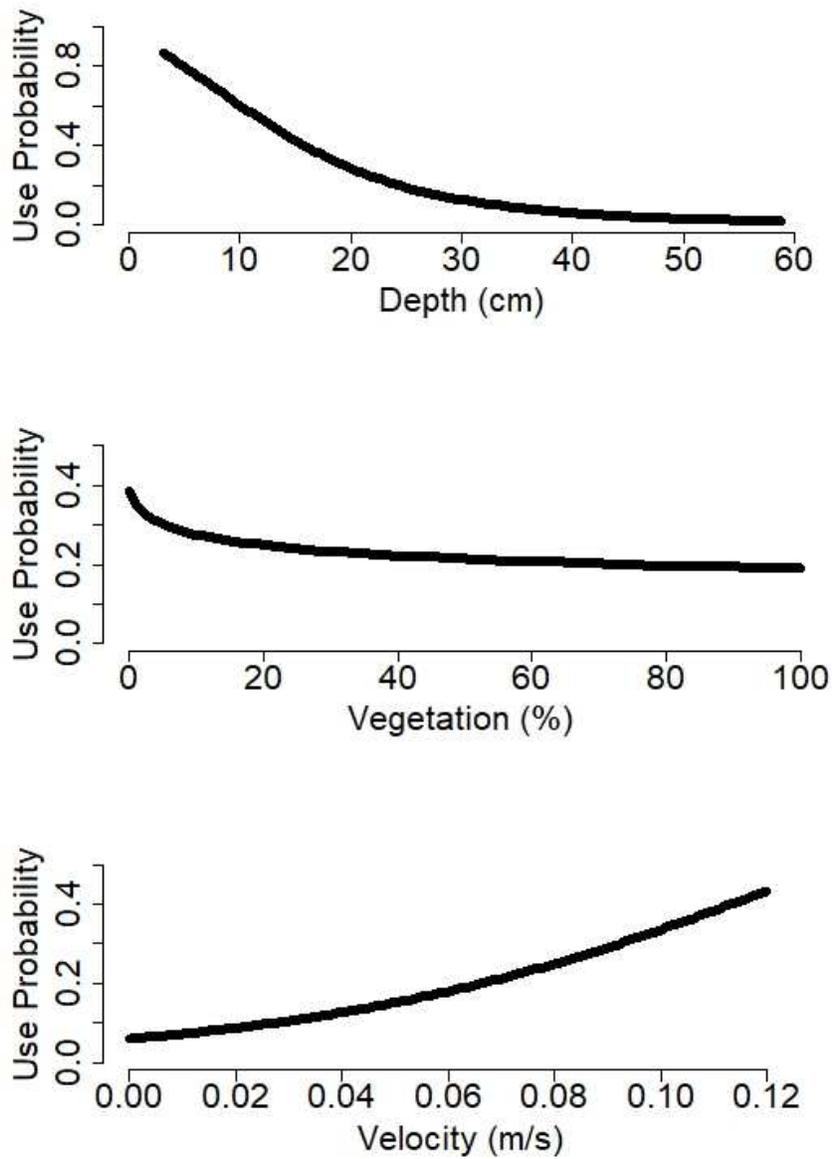


Figure 12. Use probabilities (Y-axis) for the three significant covariate interactions with season, where summer was the reference: velocity, vegetation, and depth. Relationships are shown with other significant covariates constant at median levels. The Y-axis of the bottom two relations (vegetation and velocity) are truncated at a use probability of 0.5 because the probability never exceeded 0.4.

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APPENDICES

National collection information for states within Least Darter Range. State agencies and occasional museums were contacted prior to research in Fall of 2017 and provided Least Darter information if available. GBIF and BISON are online resources and were accessed in October 2017.

State	Agency
Oklahoma	Oklahoma Water Resource Board
Oklahoma	Sam Noble Museum of Natural History
Oklahoma	Oklahoma Department of Wildlife Conservation
Missouri	Missouri Department of Conservation
Illinois	Illinois Natural History Survey
Iowa	Iowa Department of Natural Resources
Michigan	Michigan Department of Natural Resources
Arkansas	Arkansas Game and Fish Commission
Minnesota	Minnesota Department of Natural Resources
Indiana	Indiana Department of Natural Resources
Wisconsin	Wisconsin Department of Natural Resources
Ohio	Ohio State Museum of Biodiversity
Michigan	Michigan Department of Natural Resources
United States	Biodiversity Information Serving Our Nation (BISON) USGS
United States	Global Biodiversity Information Facility

VITA

Dusty Allen Swedberg

Candidate for the Degree of

Master of Science

Thesis: ASSESSING THE DISTRIBUTION AND HABITAT NEEDS OF THE
LEAST DARTER AND SYMPATRIC SPECIES OF THE OZARK
HIGHLANDS AND ARBUCKLE MOUNTAIN ECOREGIONS

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