Assessing the distribution and habitat needs of the Least Darter and sympatric species of the Ozark and Arbuckle Mountain ecoregions

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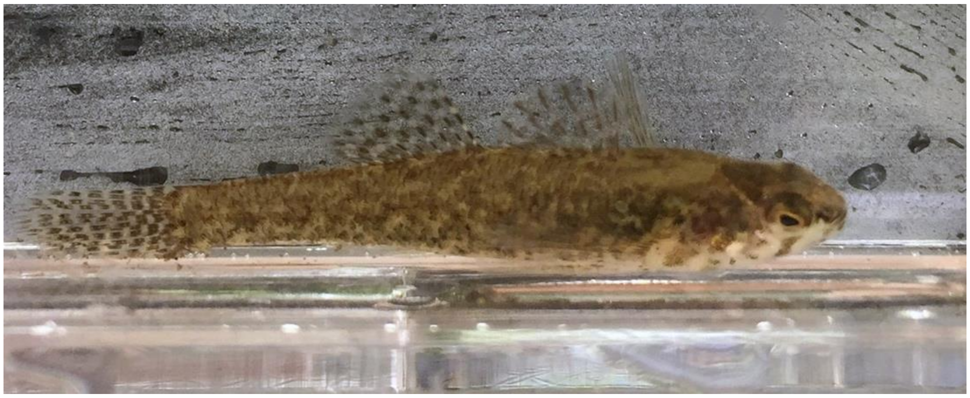

* Image by Dusty Swedberg (July 2018)

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Executive Summary

Limited information is known about factors driving the distribution of Least Darter in Oklahaoma. The Least Darter occurs in the Ozark Highland and Arbuckle Uplift ecoregions of Oklahoma which represent the southern extent of its range. Least Darter was historically recorded in Oklahoma from groundwater-fed streams. Our study objectives were to determine the distribution of Least Darter and a subset of congeners across the two ecoregions of Oklahoma and assess factors driving patch occupancy of Least Darter at a fine spatial scale. We used temporally replicated snorkel surveys conducted in July through October 2018-2019 to determine occupany by Least Darter. We snorkeled and seined for four species in each reach including two life stages of Smallmouth Bass (subadult and adult). We sampled 153 sites (i.e., riffle-pool complexes) nested within 61 stream reaches (i.e., 200-500-m long) in the Arbuckle Uplift and Ozark Highland ecoregions. Detection probability was similar between ecoregions. Least Darter was detected at more sites when snorkeling compared to seining (24 versus 18). Smallmouth Bass, Redspot Chub and Southern Redbelly Dace were typically 2-3 times more likely to be detected by snorkeling than by seining. We found relationships between occupancy and habitat parameters that were both shared among species but also species-specific. Least Darter occurrence probability in the Ozark Highlands was lower than in the Arbuckle Uplift. Occurrence probability was higher for subadult Smallmouth Bass and Southern Redbelly Dace in 2018 compared to 2019. Occurrence probabilities of both Least Darter and Southern Redbelly Dace were higher in cooler habitat patches. Southern Redbelly Dace was negatively associated with a higher proportion of pool habitat across a reach. Lastly, subadult Smallmouth Bass and Redspot Chub were more likely to occur in deeper pools and in larger streams (i.e., drainage area). We sampled one study reach (~150-m long with shallow riffles or a waterfall on each end) in the Arbuckle Uplift (winter and summer sampling) and Ozark Highland (winter sampling) ecoregions to determine fine-scale habitat selection during the thermally harsh seasons. We developed transects across the reaches to quantify depth, velocity, substrate, cover and water temperature. We found Least Darter used higher water column velocities and shallower water depths with little vegetation during the winter. The average water depth used was similar during summer and winter (~ 20 cm deep). Least Darter used denser vegetation during the summer and tended to avoid coarse substrates in both seasons. If the conservation of Least Darter is a management goal, actions to mitigate increasing stream water temperatures (e.g., protection of springs and riparian corridors) and protecting stream morphologies that facilitate species separations (i.e., allow for a wide range of water depth and velocities) may be beneficial (e.g., fencing cattle from streams, promoting natural bankful flows during spring).

Background

The Least Darter (*Etheostoma microperca*) is an isolated spring-obligate species with patchy southern populations in the Ozark Highlands and Arbuckle Uplift ecoregions (Burr 1977; Pflieger et al. 1997; Wagner et al. 2012). Least Darter populations also occur in the stream and lakes of the northern United States (Figure 1), but southern and northern populations are genetically divergent and isolated (Echelle et al. 2015). Thus, the two populations may benefit from different conservation and management strategies. In the southern extent of the range, historic collections of Least Darter suggest the species has an affinity for smaller, calm headwater streams and springs, but also occupies the vegetated margins of larger stream runs and pools (Burr 1977; Burr and Page 1979; Pflieger et al. 1997; Bergey et al. 2008; Hargrave and Johnson 2003). However, historic sampling efforts were conducted without consideration of sampling detection which could bias our understanding of both habitat relationships and distributions (Mackenzie et al. 2002). Though Least Darter is considered a spring-obligate species, landscape and other stream-level factors could be important drivers of occupancy, and management or monitoring plans could benefit from a more thorough evaluation of the species needs. The purpose of this project is to improve the conservation and management of Least Darter and other sympatric species by identifying drivers of the split distribution and habitat needs. Our objectives were to 1) model the factors related to the distribution of Least Darter and other sympatric fishes in the Arbuckle Mountain and Ozark Mountain ecoregions; and 2) identify the fine-scale habitat factors related to species occupancy, emphasizing temperature.

Study area

Our study took place in both the Ozark Highlands and Arbuckle Mountain ecoregions. Both ecoregions are characterized by karst topography and spring flow characteristics (Woods et al.

2005); however, the springs of the Arbuckle Mountain ecoregion are typically isothermic (Osborn 2009; Christenson et al. 2011) and often located on small spring branches. The Ozark Highlands region is humid (102-122 cm precipitation annually), limestone dominated, and comprises mixed deciduous forest with lowland areas converted to pasture in many areas (Woods et al. 2005). Likewise, the Arbuckle Mountain ecoregion is humid (96-109 cm precipitation annually), dominated by both limestone and granite, and comprises tall grass prairie and oak savannas, with lowland areas converted to both cropland and pasture (Woods et al. 2005). Small and large impoundments, and other human alterations (e.g., mining, (Christenson et al. 2011); poultry pollution (Olsen et al. 2012), and accelerated streambank erosion are common to both ecoregions (Woods et al. 2005).

Objective 1. Model the factors related to the distribution of Least Darter in the Arbuckle Mountain and Ozark Mountain ecoregions.

Study design

We sampled fish and habitat from streams of the Arbuckle Uplift and Ozark Highland ecoregions (Figure 2); all sampling was conducted from July through October in 2018 and 2019 under base-flow conditions (0.00-5.00 m^3/s) and relatively warm water temperatures (16.1-28.9 °C). Our 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 to sample locations where previous detections were not reported to avoid sampling bias.

At each site (riffle-pool complex), two temporally replicated surveys were conducted to account for imperfect sampling detection (Mackenzie et al. 2002; Tyre et al. 2003). Because Least Darter is patchily distributed but also considered locally abundant (Pflieger et al. 1997), we anticipated an average detection probability of 0.50 (i.e., the species was equally likely to be observed as not observed) when designing the study. Given our detection estimate, two surveys at each site would be adequate to account for average detection, thereby 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-Arroita et al. 2010).

Target species

Least Darter was the primary focus of this study, but we also documented conditions for a select group of sympatric species. We determined occurrence probabilities for Least Darter and Southern Redbelly Dace *Chrosomus erythrogaster*, Redspot Chub *Nocomis asper*, and Smallmouth Bass *Micropterus dolomieu*. Species were chosen based on 1) the hypothesized importance of spring habitats to species occurrences, and 2) the species ecological and economic importance. Southern Redbelly Dace and Redspot Chub were selected because they are considered spring associates (Seilheimer and Fisher 2010). We 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 our resulting ecological models.

Fish sampling

We used both snorkeling and seining to sample Least Darter and our other target fishes. Seining and snorkeling are commonly used to sample Least Darter (Burr and Page 1979; Bergey et al. 2008; Wagner et al. 2012) and snorkeling is successfully used to sample Smallmouth Bass (Brewer and Ellersieck 2011; Mollenhauer et al. 2018) and Redspot Chub (Mollenhauer et al. 2019) from clear, warmwater streams. Using two sampling 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 us 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 dimensions and complexity, 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 and shallow water). 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, we 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 seine hauls) through each site was completed because seining was intrusive (e.g., removal of vegetation); therefore, detection probability would be expected to change if we used a second pass on the same day.

Environmental data collection

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.

We 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 ≥ 90-mm diameter (Wentworth 1922). Percent coverage of coarse wood (1.0 m^2; i.e., circumference > 10 cm, Dodd et al. 2008) was visually estimated at each site. We 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), we 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 we did not expect or observe clarity varying between nested sites.

We 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, we 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 ºC) over the same 2-week period. The same water temperature value was applied to each site within the reach. Discharge (0.1 m^3/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 m^3/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 within the same reach (i.e., nested). We calculated drainage area for each reach as it is a primary factor structuring fish distributions (Schlosser 1995; Fausch et al. 2002). We calculated the drainage area (km^2) 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 our 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 (2005) 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 category values were averaged and assigned the same average value for each land category (see Mouser et al. 2019). We also designated all forested or wetland areas as being in a relatively "natural state." The final coefficients for a site could range 0-10 where a higher LDI coefficient reflected increased land cover disturbance; however, in our data, the values only ranged from 1-3.

Occupancy modeling and validation

We developed a single-season, multispecies occupancy model for our 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). We used data where fish were both detected and not detected, allowing us 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 our study season between July and October after spring floods and before water temperatures cooled during late autumn. 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).

We made several data transformations and checked correlations among our detection covariates. Coarse substrate, velocity and depth were log-transformed because they were right-skewed. We checked the continuous detection covariates for high correlations ($|r| > 0.50$) using the Pearson correlation coefficients (Table 2). If two covariates were correlated, we 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 across sites. Our most complex detection model contained a quadratic depth term and several continuous detection covariates: percent coarse substrate, average water column velocity, water clarity, water temperature, and depth.

First, we built a detection model accounting for some species-specific relationships, but also more general relationships expected to be shared among species. We fit species-specific relationships with gear and ecoregion to determine how each species differed between ecoregions and with gear. We assumed species would have similar detection relationships with continuous covariates to avoid an overly complex detection model (i.e., place the emphasis on occupancy). Our most complex model included several continuous covariates and a gear and ecoregion factor where seining and the Arbuckle Uplift ecoregion were references. We included interactions with each of the continuous covariates and gear to account for a gear effect with differing habitat conditions. Additionally, we 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).

After the most complex detection model was fitted, we simplified the model using an iterative process where we 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.

We made several data transformations and checked correlations among occurrence covariates (Table 3). 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). We chose drainage area over two other highly correlated variables (discharge and total area, Table 3) to minimize redundancy between variables.

Next, we fit the most complex occupancy model, while including the detection relationships in our model. Incorporating the detection portion of the model allowed us 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. We additionally included three interaction terms we hypothesized could be important: average water temperature and residual pool depth, total vegetation and residual pool depth, and a total vegetation-pool area interaction. We hypothesized 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). We predicted that occurrence probability of the smaller-bodied species would be independent of residual pool depth at cooler water temperatures. Next, we 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, we 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).

We 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 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 our 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).

We used a backward selection approach to simplify our overall model. First, we fit our most complex model including all three-way interactions. We 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. We again omitted any non-significant interactions by examining HDIs and removing non-significant interactions. Lastly, we fit a model that included significant three-way, and two-way interactions, and all main effects. In the last iteration, we 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 distributions 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 (Gelman and Rubin 1992), for which values <1.1 indicate adequate mixing of chains for all parameters.

We used MacKenzie and Bailey (2004) chi-squared goodness-of-fit test to assess the fit of our 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 that is 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.

Objective 2. Identify the fine-scale habitat factors related to species occupancy, emphasizing temperature.

Design

We chose two study reaches (~150-m long with shallow riffles or a waterfall on each end), one in the Arbuckle Uplift ecoregion and one in the Ozark Highland ecoregion (Figure 4). The two reaches were selected because they had relatively high abundances of Least Darter (based on Objective 1 sampling), and we had access to these privately-owned lands. 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.

Habitat availability

Relatively homogenous (~ 2 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). We established transects both perpendicular and parallel to streamflow to quantify habitat conditions (Figure 5). We measured water depth (0.1 m) at the center of each sampling unit. Average water-column velocity (0.1 m/s) was measured at 60% of depth using a Marsh-McBirney Flo-Mate (Hach, Loveland Colorado) (Gordon et al. 2004). We visually estimated dominant substrate within each sampling unit using a modified Wentworth scale (Wentworth 1922). We then 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.

We quantified water temperature in each habitat patch by measuring temperature continuously over each sampling period. Temperature 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). We used these data to determine an average temperature for each patch along the cable (e.g., Selker et al. 2006; Westhoff et al. 2010). We laid the cable on the stream bottom parallel to streamflow and anchored it with a rock or polyvinyl chloride (PVC) cylinder filled with cement in the center of each of our 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

We determined habitat use by Least Darter during both winter (February 2019) and summer (August 2019) in the Arbuckle Uplift (Figure 4). The Ozark Highlands reach was only sampled during winter (December 2019) because a suitable stream reach was not identified until summer 2019 (Figure 4). We anticipated groundwater upwelling would have the most influence on water temperatures during summer and winter rather than spring or autumn (Hubbs 1995; Constantz 1998). We 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, we conducted one snorkel survey daily for five or six days in winter and summer, respectively. We alternated between morning (~9:00) and afternoon (~15:00) survey times on consecutive days. Snorkeling followed the approach described for Objective 1 (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 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. We determined which spatially referenced sampling unit was nearest each fish observation at each sampling event. We were 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, we 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 we 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. We standardized all our covariates by subtracting the mean of the covariate from each value and dividing by the standard deviation to improve model interpretation.

We determined our final variable set by examining correlations and considering factors affecting Least Darter detection. We checked correlations among continuous covariates using the Pearson coefficient correlation. Categorical covariates were checked for correlations by determining the frequency of co-occurrence in our data and none were correlated (Table 4). Correlations between our standardized continuous covariates were $|r| \leq 0.58$, so all covariates could be used for model development (Table 4). We omitted water clarity because it was > 5 m and was not likely to affect Least Darter detection. Our 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).

We determined habitat selection 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, we built our most complex microhabitat model. In addition to the main effects, we considered reasonable interaction terms: deviation from median temperature × depth, vegetation × depth, and vegetation × 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). We predicted patch use by Least Darter would be independent of residual pool depth at lower temperature deviations (Hetrick et al. 1998). Next, we hypothesized Least Darter would use patches with high vegetation coverage consistently across water depths because it would offer refuge from fish piscivores; whereas, fish would be less likely to use patches with low vegetation coverage in shallow water due exposure to avian predation. Deeper water without vegetation, however, acts as cover and reduces the risk of avian predation (Savino and Stein 1982; Rozas and Odum 1988). Finally, we hypothesized Least Darter would be more likely to use sample units with little vegetation if the water temperature was constant (i.e., no major deviation in heating extremes) because thermal refugia is considered important for Least Darter (Seilheimer and Fisher 2010). In areas of high vegetation coverage, we hypothesized Least Darter patch use would be independent of temperature deviation. To account for variation between ecoregions, we included ecoregion as a nuisance factor to improve model fit and convergence. We also included a sampling-day grouping factor to account for unexplained temporal variation due to concurrent sampling days in each season. Lastly, we also included a grouping factor for patches at each site because of anticipated spatial autocorrelation (Gelman and Hill 2006; Wagner et al. 2006).

The final overall model was selected using the same backward selection approach used in Objective 1. First, we 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). We 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 our data and were used to assess model fit. Convergence was determined by applying the Brooks-Gelman-Rubin statistic. Values of the Brooks-Gelman-Rubin statistic <1.1 indicate adequate mixing of chains for all parameters (Gelman and Rubin 1992).

RESULTS

Objective 1. Model the factors related to the distribution of Least Darter in the Arbuckle Mountain and Ozark Mountain ecoregions.

Fish sampling

We sampled 153 sites nested within 61 stream reaches in the Arbuckle Uplift and Ozark Highland ecoregions (Table 5; 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 5). During the two summers of sampling, we conducted 284 seining surveys and 264 snorkel passes across all sites (Table 5). During summer 2018, 69 sites were sampled: 26 sites in the Arbuckle Uplift and 43 in the Ozark Highlands (Table 5). During summer 2019, we sampled 84 sites: 38 sites sampled in the Arbuckle Uplift and 46 sites sampled in the Ozark Highlands.

Commonness of our target species differed by ecoregion, and some species were easier to sample using one of the two gears (Table 6). Least Darter was the rarest of the four target species and two life stages of Smallmouth Bass. 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, adult Smallmouth Bass and sub-adult Smallmouth Bass occurred at more than twice as many sites in the Ozark Highlands compared to the Arbuckle Uplift. Least Darter was detected at a comparable number of sites when seining or snorkeling. 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 6). In the Arbuckle Uplift, Redspot Chub and subadult Smallmouth Bass were exceptions as detection was comparable when using either gear (Table 6).

Physicochemical Conditions

The physicochemical conditions associated with our surveys varied across sites but were similar between ecoregions and sample year (Table 7). 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 comparable 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 comparable among sample years (Table 8). Water temperature, seepage runs, and LDIs were, on average, comparable 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 our 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 comparable 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 with an effective sample size of at least 7,847 suggesting the model had appropriate mixing.

Relationships between our 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 8). 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 8). Detection increased with water clarity while snorkeling (i.e., seining as the reference) (Table 8, Figure 6). Similarly, detection probability was higher in deeper water when snorkeling (Table 8, Figure 7). Detection probability was not significantly different between ecoregions, but we retained an ecoregion factor in our model to account for unexplained spatial variation (Table 8).

Our occurrence model indicated both common (i.e., shared among species) and species-specific occurrence relationships with our predictor variables (Table 9). 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 9). Occurrence probability was higher for Smallmouth Bass sub-adult and Southern Redbelly Dace in 2018 than in 2019 (Table 9). Occurrence probabilities of both Least Darter and Southern Redbelly Dace increased with cooler water temperatures (Figure 8). Redspot Chub and both Smallmouth Bass life-stages were associated with larger drainage areas (Figure 9). Southern Redbelly Dace was negatively associated with sites having a higher proportion of pool habitat (Figure 10). Lastly, occurrence probabilities of Smallmouth Bass sub-adults and Redspot Chub were higher in deeper pools (Figure 11).

Objective 2. Identify the fine-scale habitat factors related to species occupancy, emphasizing temperature.

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). At 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 our 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. During the winter, habitat patches of the Ozark Highlands tended to be less homogenous than patches of the Arbuckle Uplift (Table 10). Average temperatures during winter were cooler in the Ozark Highlands than the Arbuckle Uplift. There was also less variation from median water temperature at our 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 our site in the Ozark Highlands compared to Arbuckle Uplift during the winter. Lastly, coarse wood was present in more habitat patches of the Ozark Highlands compared to Arbuckle Uplift (data not shown in Table 10 as these data were collected as presence or absence at each patch).

Habitat use

Our 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.

Least Darter was more common in habitat patches of the Arbuckle Uplift ecoregion, and habitat use varied between winter and summer (significant two-way interaction between use of depth, velocity, and vegetation 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 19.6 cm during winter and 20.8 cm during summer. Vegetation was consistently used in both seasons but use of low amounts of vegetation was higher during winter compared to summer. Lastly, patch use was negatively associated with coarse substrates regardless of season (Table 11).

DISCUSSION & MANAGEMENT IMPLICATIONS

Objective 1

The historical distribution of Least Darter differed between the two ecoregions, and the arrangement of springs may be related to those observations. 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 Least Darter was historically broadly distributed (Figure 3). The western Ozark Highlands boasts karst topography but tends to have patchy cool water upwelling rather than the isothermic springs visible in the main channel of the Arbuckle Uplift. The arrangement of springs and the spatial and temporal influence of the associated cooler water temperatures may be key to current distribution of Least Darter where a certain length of stream with cooler water temperatures may be necessary for population persistence.

We detected Least Darter at three new locations in the Arbuckle Uplift and two new locations in the Ozark Highlands during the summers of 2018 and 2019. Two of the locations in the Arbuckle Uplift were further upstream in the Blue River than previously documented (see 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 temperatures were cooler but were not detected on the following visit at the end of July. We found no noticeable spring during our site visits. The third 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 our knowledge, this is the first documentation of the species from that section of Blue River. 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 (Falke and Fausch 2010). However, locating these small, isolated populations is difficult due to low sampling detection (MacKenzie et al. 2006). The two new localities within the Ozark Highlands both occurred adjacent to reaches with previous documented use by 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 (Echelle et al. 2015) upstream of the confluence with Rock Creek. However, no records of Least Darter have been documented for Rock Creek in Oklahoma or Missouri. We also detected Least Darter in a backwater approximately 70 m from the mainstem of Snake Creek downstream of a previous location at the Highway 82 bridge south of Locust Grove, Oklahoma. At the time of sampling, the backwater was completely disconnected from the mainstem river, but hyporheic flow was 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 could be a reliable monitoring location. Future research could 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 is likely related 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 was likely more widespread in the Ozarks as suggested by historical data. Populations of Least Darter may have become more isolated and rarer after human landscape changes (Tejerina-Garro et al. 2005) that affected spring-flow volume and stream morphologies (i.e., channel depth). Sand mines have become common in the Arbuckle Uplift area, disrupting baseflows including disconnecting surface water and groundwater of 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) likely due to the importance of water temperature. Future efforts focused on understanding the spatial distribution of springs, and the relationships between springs and spatial thermal dynamics could be beneficial to developing detailed management actions. Best management practices associated with land-uses that affect groundwater-surface water are available in several states though the focus is often placed on groundwater contamination rather than flow volume or connections (see https://www.pca.state.mn.us/sites/default/files/wq-gw1-08.pdf).

Habitat alterations due to landscape changes not captured by our 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 our 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 could benefit from improvement for applications in the Great Plains. Mouser et al. (2019) used a similar method and found occurrence probability of *Faxonious* spp. 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 our 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 might benefit from 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.

Our 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 (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. Our results support snorkeling 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 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). Human pressures are changing stream function and structure that is affecting the unique thermal regimes of groundwater habitats and their associated fish assemblages (Hynes 1975; Ward 1989; Fausch et al. 2002; Caissie 2006). Longitudinal stream management is important for groundwater-associated species because headwater streams 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). Catchment 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 could benefit from regional efforts to protect critical aquifers by regulating groundwater withdrawals (Labbe and Fausch 2000; Seilheimer and Fisher 2010). Protecting base flows could also protect against stream channels drying and reducing hyporheic exchange resulting in increased stream temperatures (Cardenas 2009). The consistent water temperatures associated with springs 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).

Objective 2

Least Darter relationship with habitat use of water depth, water velocity, and vegetation 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 the 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 (i.e., air and groundwater temperature) in the southern portion of the range or the effects of springs moderating temperature extremes. 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 our 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 in 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 that they enter breeding condition in February (Burr and Page 1979), which matches our observations during 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; our results). Although the functional reasons are unknown, fine substrates may be related to spawning habitat (Winn 1958) or foraging. Fine substrates are often 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, Brewer and Rabeni 2011), although a threshold response is hypothesized for excessive fines due to land uses or other human effects that 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). We found no correlation between fine sediments and vegetation in our study, suggesting that vegetation and fine substrate act independently regarding Least Darter patch use.

We 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 that we found associated with Least Darter occupancy (See Objective 1). It is common for habitat relationships to manifest themselves or become indiscernible at different spatial scales (Frissell et al. 1986; Wiens 1989; Levin 1992). For example, temperature is an environmental factor affecting fish distributions 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, our data also suggested little variation in temperature among patches at our sites (deviation from the median ranged -1.15 to 2.68 °C). However, 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 Objective 1), particularly given the high summer air temperatures at this latitude. Our finding emphasizes the importance of springs in determining occupancy of stream reaches. It is unlikely that smaller seeps at finer patches are sufficient for maintaining populations. Management actions directed at maintaining cool stream temperatures (e.g., protecting spring and riparian buffers) could be worth considering if maintaining these populations is a conservation goal.

Our 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 our knowledge, our 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). We did find slight differences in depth use in our December (22.5 cm) and February (19.5 cm) sampling. Further, we found individuals in breeding condition during our February sampling (not December sampling), suggesting this is likely when spawning activity begins. Though seasonal habitat shifts did occur, the shifts seem to be rather minimal. Summer to winter shifts in darter 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). Additionally, it is common for groundwater-associated species to exhibit seasonal habitat shifts in response to spawning, rearing, and overwintering

(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.

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Table 1. The detection and occupancy covariates and associated spatial scale (Scale) of each variable. Hypothesized effects on Least Darter: negative (−), positive (+), or null (∅) indicating no expected effect. The rationale for inclusion of each variable in the modeling process is provided under the justification column. RPD = residual pool depth

Detection			
Scale	Covariate	Hypothesized effect	Justification
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 water temperatures 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			
Scale	Covariate	Hypothesized effect	Justification
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	−	Lack of riparian and the presence of 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/s^3)	−	Least Darter documented from smaller streams (i.e. lower discharge streams).[10,13,14]
Site	Seepage Run (m/s^3)	+	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]

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. The correlation matrix (Pearson's correlation coefficients) for the continuous detection variables included in the detection model. Percent coarse wood, percent coarse substrate, percent vegetation, average water column velocity, average water depth, and water temperature were all measure at the site level (i.e., riffle-pool complex). Water clarity (clarity) was measured at the reach where multiple riffle-pool complexes were assumed to share similar conditions.

	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 3. The correlation matrix (Pearson's correlation coefficients) for the continuous variables that were considered in the occupancy model. The variables that were measured at the reach scale were 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) were expressed as percent coverage for each site. Pool area (Pool) was the proportion of total area (Total) represented by pool habitat. Discharge (Q) was quantified at the reach scale. The residual pool depth (RPD) was quantified for each site (i.e., riffle-pool complex).

	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 4. The correlation matrix (Pearson's correlation coefficients) for the continuous variables that were considered in the habitat use model. Deviation from the median water temperature (temp), water depth (depth), coarse wood (wood), percent vegetation (vegetation), and average water column velocity (velocity) were measure at each patch (~ 2 m^2).

	Temp	Depth	Wood	Vegetation
Depth	-0.19			
Wood	-0.07	0.24		
Vegetation	-0.03	0.14	-0.03	
Velocity	0.15	-0.58	-0.14	-0.36

Table 5. The number of sites (i.e., riffle-pool complexes) and reaches (200-500-m long) sampled in 2018 and 2019 in the Arbuckle Uplift (Arbuckles) and Ozark Highlands (Ozarks) ecoregions. The total is the combined number of reaches and sites from the two sampling years.

Ecoregion	2018 reaches	2018 sites	2019 reaches	2019 sites	Total reaches	Total sites
Arbuckles	12	26	13	38	25	64
Ozarks	18	43	18	46	36	89
Total	30	69	31	84	61	153

Table 6. Species detections by sampling method (i.e., snorkeling or seining surveys) in the Arbuckle Uplift (Arbuckle) and Ozark Highlands (Ozarks) ecoregions. The numbers associated with each species and ecoregion reflect the frequency of surveys at each site where the species was detected, whereas occupied sites refers to the number of stream reaches where each species was detected (i.e., there were multiple gear surveys within each site). Smallmouth bass is referenced as SMB.

Species	Ecoregion	Seine surveys	Snorkel surveys	Occupied sites
Least Darter	Ozarks	3	2	3
Least Darter	Arbuckles	15	22	15
Redspot Chub	Ozarks	35	130	72
Redspot Chub	Arbuckles	32	30	20
Adult SMB	Ozarks	4	96	55
Adult SMB	Arbuckles	0	13	8
Subadult SMB	Ozarks	29	97	59
Subadult SMB	Arbuckles	8	8	10
Dace	Ozarks	37	57	36
Dace	Arbuckles	15	26	18

Table 7. The summary statistics of covariates included in the detection or occupancy models for A) Ozark Highlands ecoregion, detection model; B) Ozark Highlands ecoregion, occupancy model; C) Arbuckle Uplift ecoregion, detection model; and D) Arbuckle Uplift, occupancy model. Abbreviations used for summary statistics are: N is sample size, SD is standard deviation, min is minimum, and max is the maximum value. Covariate abbreviations are: LDI, the land disturbance index; average temperature (occupancy covariate) refers to the 2-week average temperature; and temperature (detection covariate) was quantified as a point measurement at the time of sampling.

	N	Mean	SD	Min	Max
A)					
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
B)					
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
C)					
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
D)					
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 8. The significant coefficients (i.e., those with HDIs not overlapping zero) retained in the final detection model. The 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 common relationships among all species and are reported as the mean with the lower (Low) and upper (High) 95% credibility intervals.

	Mean	Low	High
Species by gear			
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
Species by ecoregion			
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
Detection intercept by gear			
Depth	0.61	0.28	0.95
Clarity	0.65	0.37	0.93

Table 9. The significant coefficients (i.e., those with HDIs not overlapping zero) retained in the final occupancy model (deflections from the group mean). Ecoregion and year are categorical covariates using Arbuckle Uplift and 2018 as references. The two-week average water temperature, drainage area, proportion pool, and residual pool depth are covariates that had 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. Values are reported on the logit scale.

	Mean	Low	High
Ecoregion			
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
Year			
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
2-week average temperature			
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
Drainage area			
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
Proportion pool area			
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
Residual pool depth			
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	-0.44	1.01

Table 10. The 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 our models but summarized here for reference. Deviation from median was the difference between patch water temperature and the median reach water temperature in each season (i.e., all patches combined). The Ozark Highlands reach was only sampled during winter (December 2019) because a suitable stream reach was not identified until summer 2019 (see methods).

	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	0.0001	0.020	0	0.20

Table 11. The 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 indicates 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 (fine)	-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 (summer)	-0.26	-1.18	0.62
Ecoregion (Ozarks)	3.10	1.97	4.33
Season × depth	-1.29	-1.98	-0.65
Season × vegetation	-0.71	-1.24	-0.18
Season × velocity	0.42	0.14	0.70

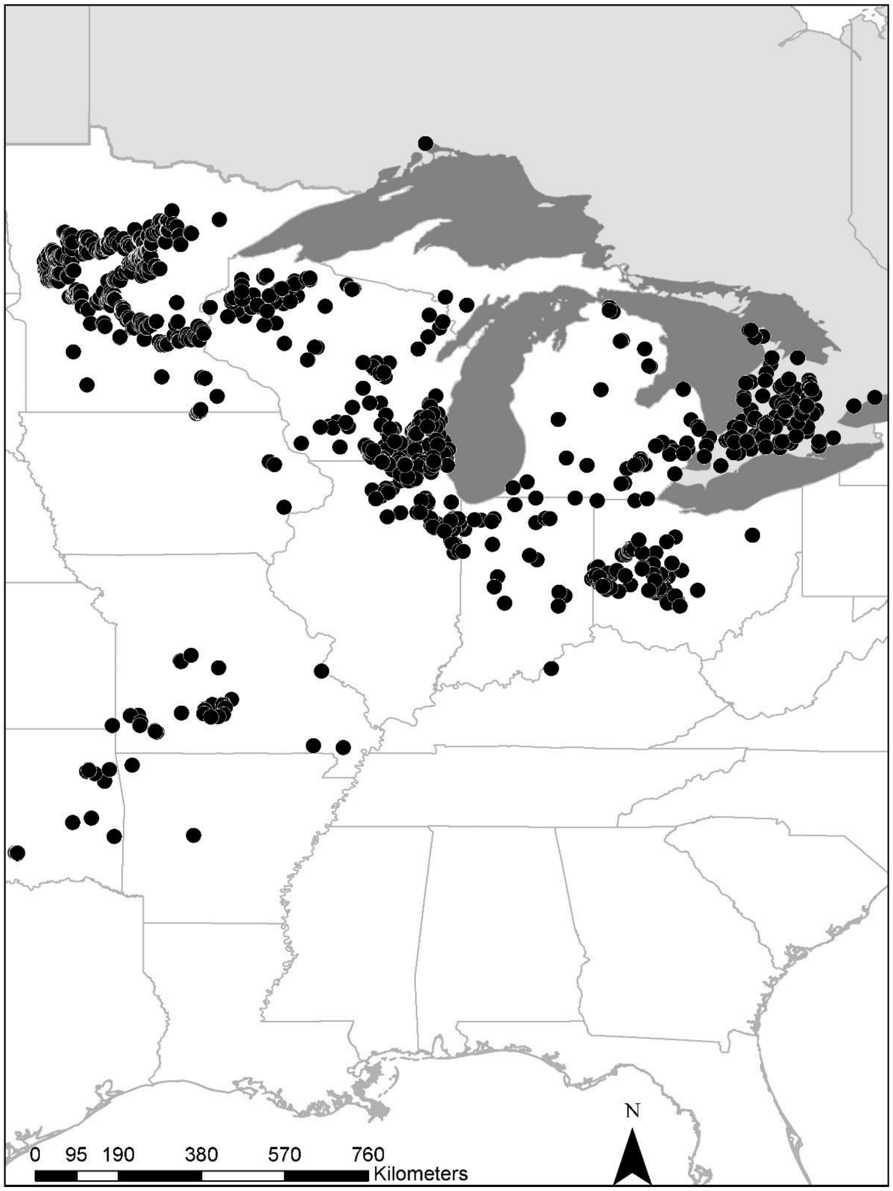

Figure 1. Least Darter collection records for the United States and Canada. Data were obtained through literature review, online databases, and professional correspondence in 2017. See Appendix A for references. The state and U.S. border data were obtained by the authors from the USDA, NRCS geospatial data gateway (https://datagateway.nrcs.usda.gov/GDGHome.aspx). River layers were obtained from the USGS NHDPlus (https://www.usgs.gov/core-science-systems/ngp/national-hydrography/access-national-hydrography-products).

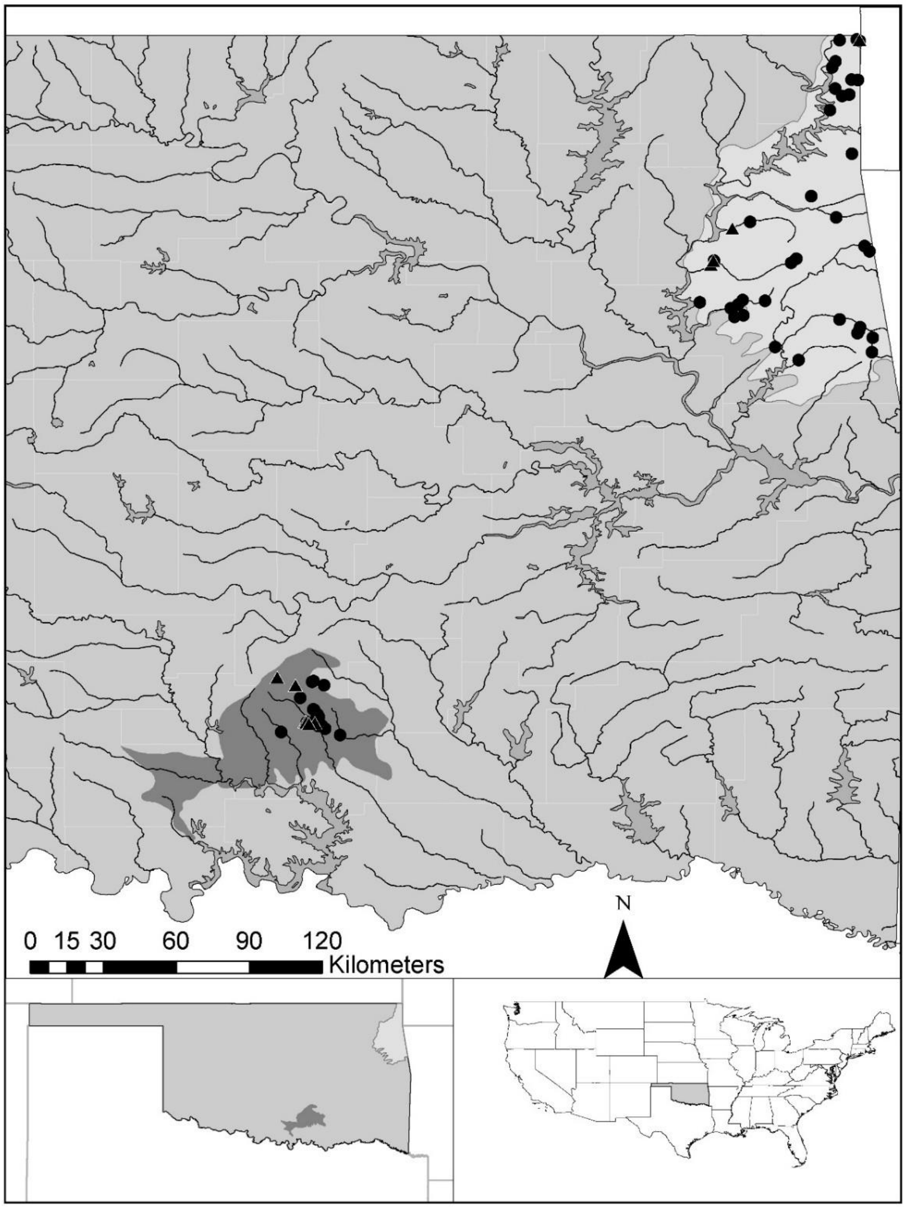

Figure 2. Reaches sampled (black circles) in summer 2018 (30 reaches) and 2019 (31 reaches) and Least Darter detections (black triangles) in the Arbuckle Uplift ecoregion (dark grey, Woods et al. 2005) and Ozark Highland ecoregion (light grey, Woods et al. 2005) of Oklahoma. The state and U.S. border data were obtained by the authors from the USDA, NRCS geospatial data gateway (https://datagateway.nrcs.usda.gov/GDGHome.aspx). River layers were obtained from the USGS NHDPlus (https://www.usgs.gov/core-science-systems/ngp/national-hydrography/access-national-hydrography-products).

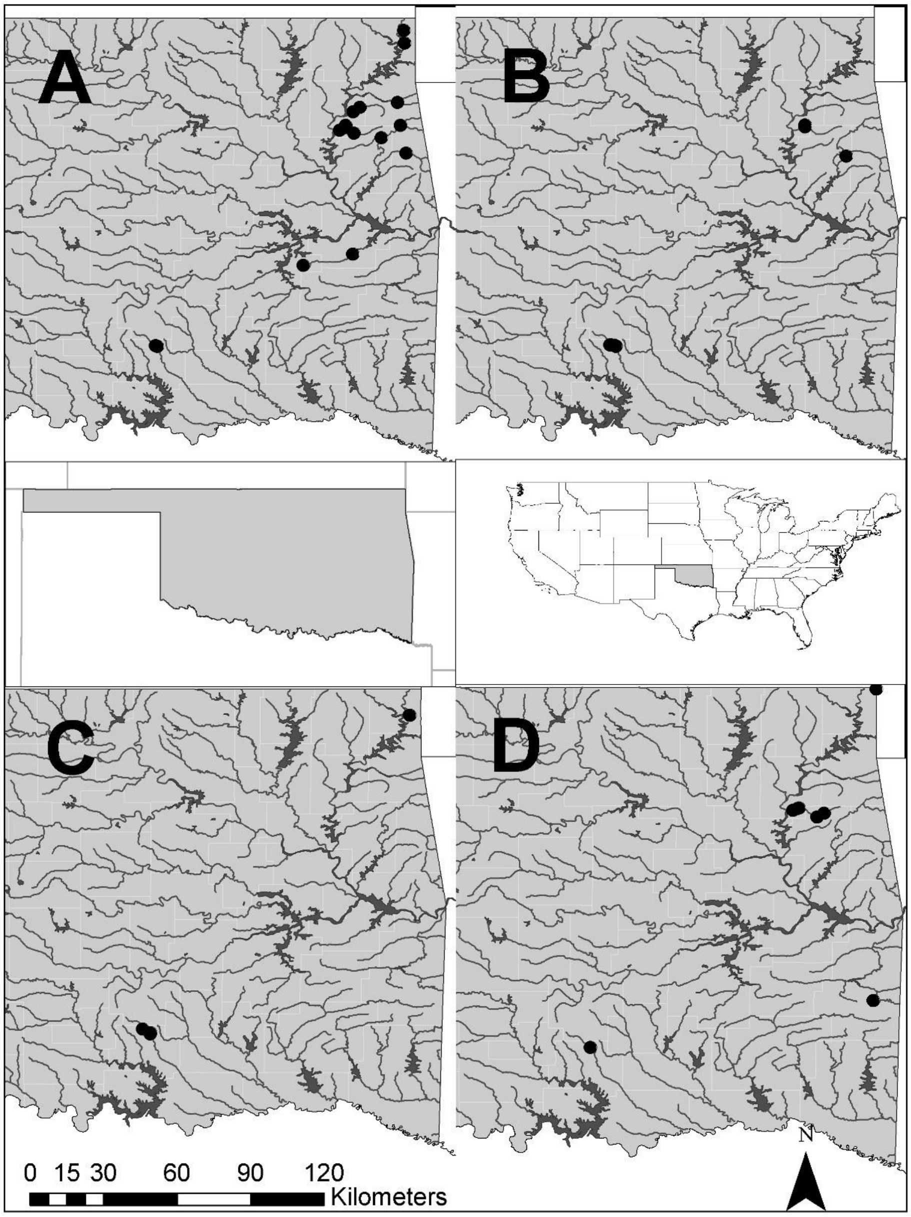

Figure 3. Historic Least Darter collection in Oklahoma during four time periods: (A) Pre 1970, (B)1970 to 1990, (C) 1990 to 2000, and (D) 2000 to current. See Appendix A for fish data sources. The state and U.S. border data were obtained by the authors from the USDA, NRCS geospatial data gateway (https://datagateway.nrcs.usda.gov/GDGHome.aspx). River layers were obtained from the USGS NHDPlus (https://www.usgs.gov/core-science-systems/ngp/national-hydrography/access-national-hydrography-products).

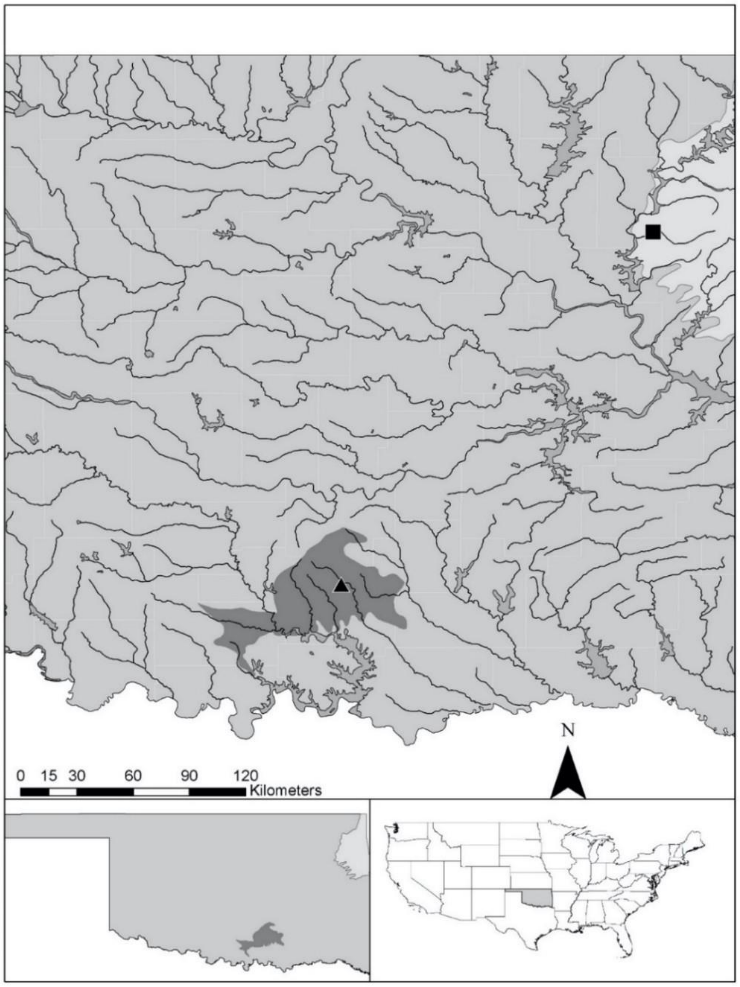

Figure 4. Sample location within the Ozark Highlands ecoregion (black square) and Arbuckle Uplift ecoregion (black triangle). The ecoregions within Oklahoma are shaded gray: Arbuckle Uplift ecoregion (dark gray, Woods et al. 2005) and Ozark Highland ecoregion (light gray, Woods et al. 2005). The site 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. The state and U.S. border data were obtained by the authors from the USDA, NRCS geospatial data gateway (https://datagateway.nrcs.usda.gov/GDGHome.aspx). River layers were obtained from the USGS NHDPlus (https://www.usgs.gov/core-science-systems/ngp/national-hydrography/access-national-hydrography-products).

Figure 5. 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. Photo credit: Dusty Swedberg (February 2019).

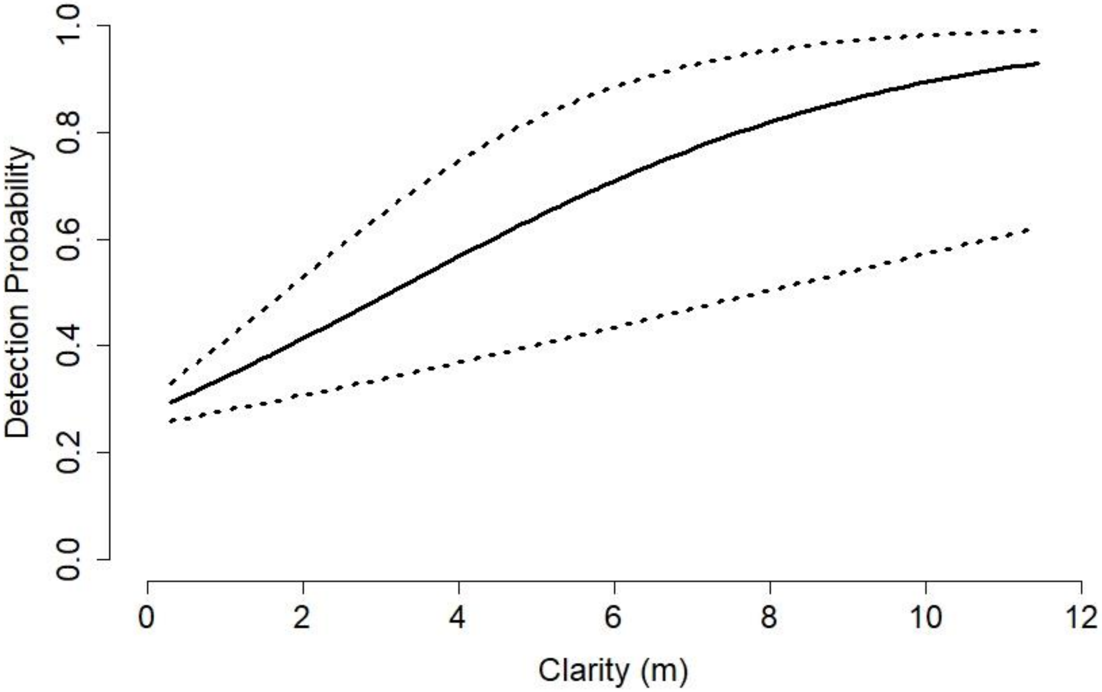

Figure 6. The relationship between mean detection probability (dashed lines are 95% credibility intervals) among target fishes (i.e., group detection) and water clarity when sampling via snorkeling (i.e., group detection) The relationship shown is in reference to seining.

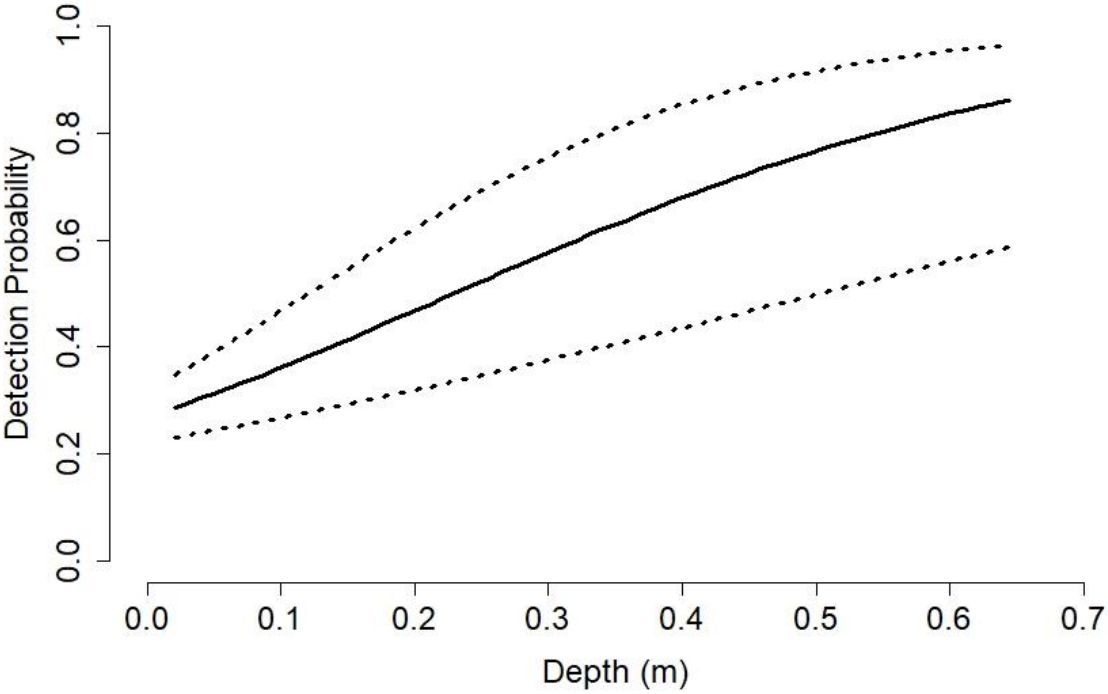

Figure 7. The relationship between mean detection probability (dashed lines are 95% credibility intervals) among target fishes (i.e., group detection) and water depth when sampling via snorkeling (i.e., group detection) The relationship shown is in reference to seining.

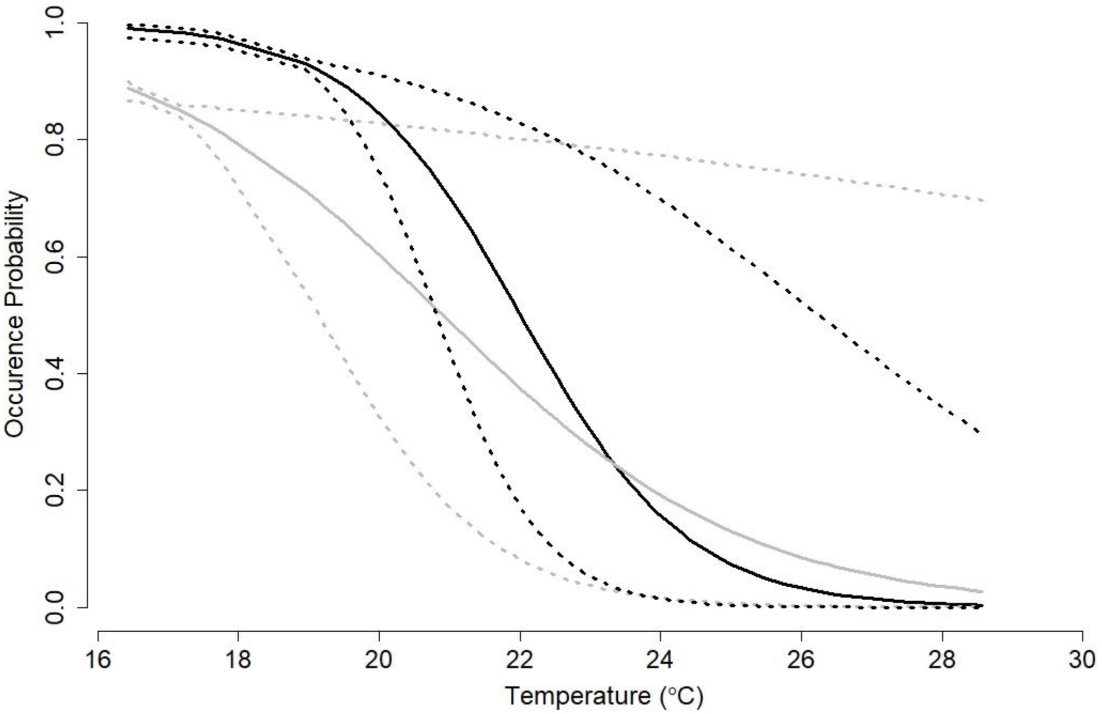

Figure 8. The relationships between mean occurrence probability (deflection from the group mean with 95% credibility intervals) of Southern Redbelly Dace (black line) and Least Darter (gray line) and 2-week average stream water temperature (Temperature).

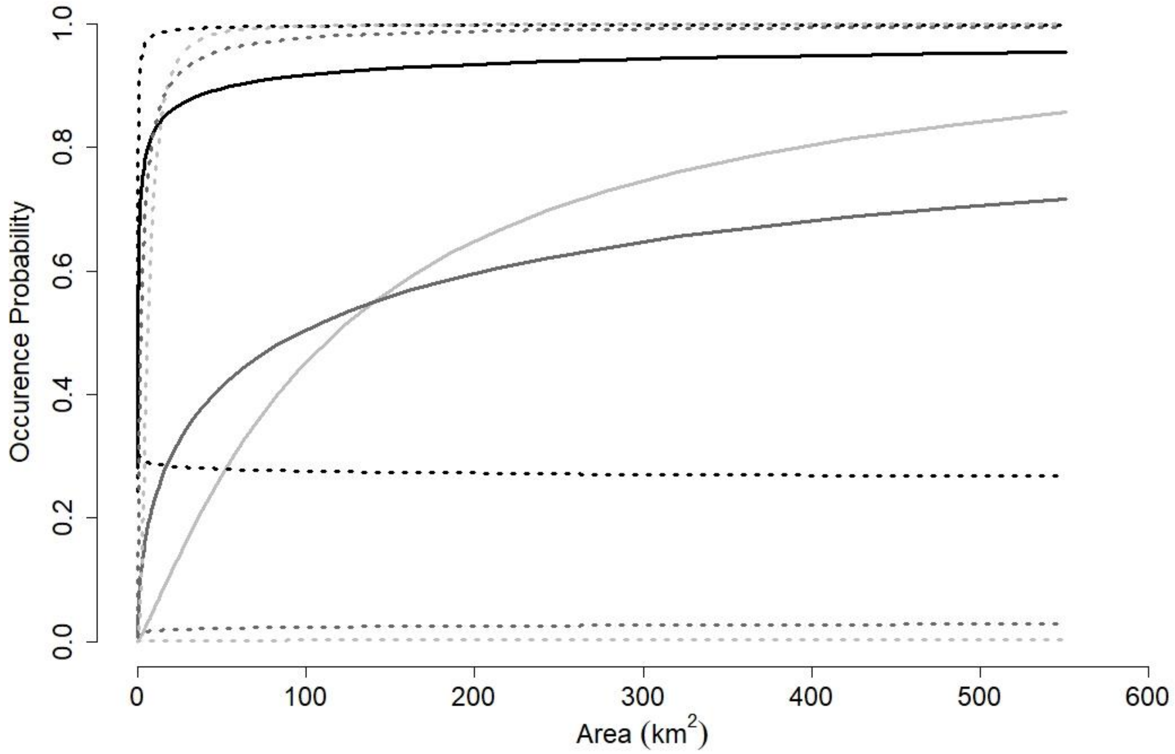

Figure 9. The relationships between drainage area (Area) and mean occurrence probability (deflections from the group mean with 95% credibility intervals) of Redspot Chub (black line), sub-adult Smallmouth Bass (light gray line), and adult Smallmouth Bass (dark gray line)

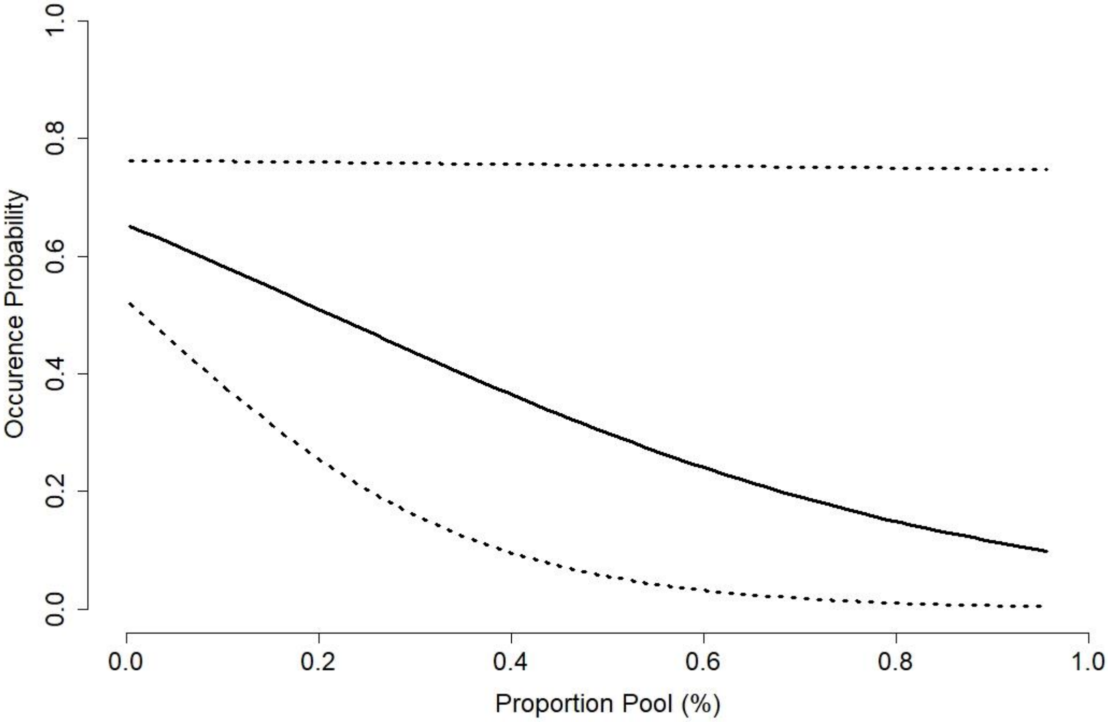

Figure 10. The relationships between mean occurrence probability (deflections from the group mean with 95% credibility intervals) of Southern Redbelly Dace (black line), and proportion of pool area at a site (Proportion Pool).

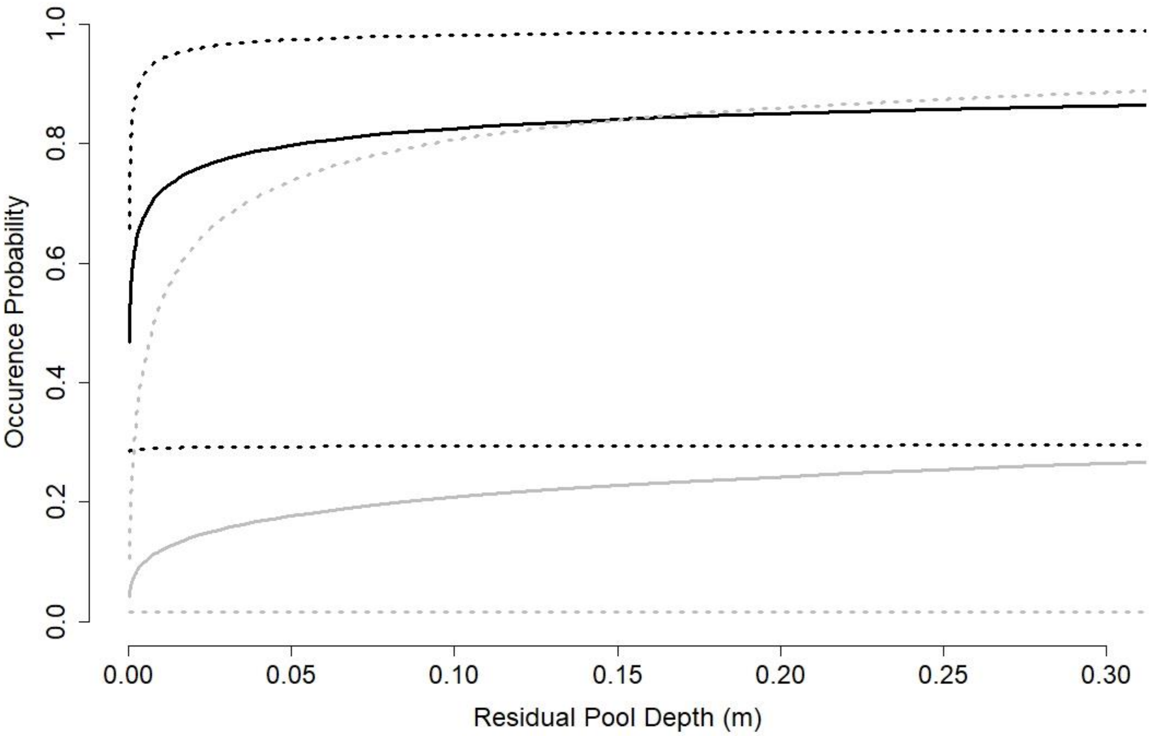

Figure 11**.** The relationships between mean occurrence probability (deflections from the group mean with 95% credibility intervals) of Redspot Chub (black line) and Southern Redbelly Dace (gray line) and residual pool depth. The x-axis is cutoff at 0.30 m because occurrence probability remained high thereafter.

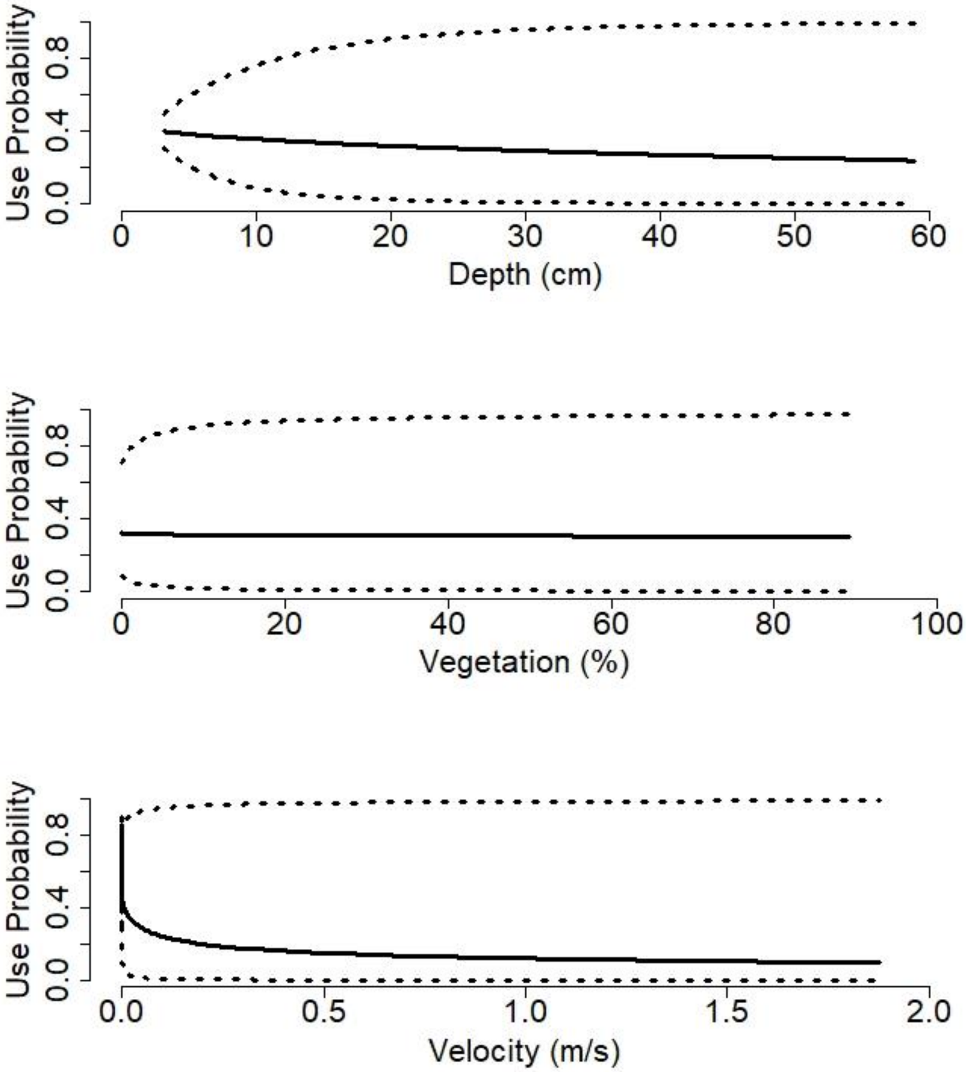

Figure 12. The mean probability of Least Darter use (with 95% credibility intervals) for the three significant covariate interactions with season, where summer was the reference: depth (top panel), vegetation (middle panel), and velocity (bottom panel). Relationships are shown with other significant covariates held constant at mean levels.

Appendix A. Sources of historical collection data obtained from agencies or databases (in parentheses). State agencies and museums were contacted in autumn 2017. The two databases, GBIF (Global Biodiversity Information Facility) and BISON (Biodiversity Information Serving Our Nation), were accessed in October 2017.

Scope	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	U.S. Geological Survey; BISON
*International	GBIF

* GBIF is an international data infrastructure funded by multiple governments