REGULAR PAPER

Movement and habitat use by smallmouth bass *Micropterus dolomieu velox* in a dynamic Ozark Highlands riverscape

Andrew D. Miller[1] 🔘 | Shannon K. Brewer[2] 🔘

[1]Oklahoma Cooperative Fish and Wildlife Research Unit, 007 Agriculture Hall, Oklahoma State University, Stillwater, Oklahoma, USA

[2]U.S. Geological Survey, Oklahoma Cooperative Fish and Wildlife Research Unit, 007 Agriculture Hall, Oklahoma State University, Stillwater, Oklahoma, USA

Correspondence
Shannon K. Brewer, U.S. Geological Survey, Oklahoma Cooperative Fish and Wildlife Research Unit, 007 Agriculture Hall, Oklahoma State University, Stillwater, Oklahoma, USA; U.S. Geological Survey, Alabama Cooperative Fish and Wildlife Research Unit, 203 Swingle Hall, Auburn University, Auburn, Alabama, USA.
Email: skb0064@auburn.edu

Present address
Andrew D. Miller, School for Environment and Sustainability, University of Michigan, Ann Arbor, Michigan, USA

Shannon K. Brewer, U.S. Geological Survey, Alabama Cooperative Fish and Wildlife Research Unit, 203 Swingle Hall, Auburn University, Auburn, Alabama, USA

Funding information
This project was funded by the Oklahoma Department of Wildlife Conservation (F15AF00102).

Abstract

Stream fish movement in response to changing resource availability and habitat needs is important for fish growth, survival and reproduction. The authors used radio telemetry to evaluate individual movements, daily movement rates, home ranges and habitat-use characteristics of adult (278–464 mm L_T) Neosho smallmouth bass *Micropterus dolomieu velox* in three Ozark Highlands streams from June 2016 to February 2018. The authors quantified variation in movement and habitat use among seasons and streams and examined relations with select environmental cues (*i.e.*, temperature and discharge), fish size and sex. Maximum movement distances were an order of magnitude greater in the larger Elk River (17.0 km) and Buffalo Creek (12.9 km) than in the smaller Sycamore Creek (1.71 km), were similar in both upstream and downstream directions and typically occurred during the spring. Most movement rates were ≤10 m day^{-1} in all streams and seasons, except for Elk River during spring. Ranking of linear mixed-effects models using AIC_c supported that movement rates were much greater in spring and increased with stream size. Spring movement rate increased with discharge and water temperature; only weak relationships were apparent during other seasons. Increased variation in water temperature had a small negative effect on movement rate. Home range size was highly variable among individuals, ranging 45–15,061 m (median: 773 m), and was not related to fish size, sex, season or stream. Although some fish moved between rivers, this study's tagged fish did not use reservoir or associated interface habitat. Water temperatures used by this study's tagged fish followed seasonal patterns but indicated the use of thermal refugia during summer and winter. Deeper-water habitats were used in Buffalo Creek and in winter across all study streams, whereas greater velocities used in the Elk River likely reflect the increased use of run habitats. Use of pool habitats predominated among tagged fish, particularly in smaller streams. The results of this study indicate considerable heterogeneity in movement and habitat use within and among lotic populations of Neosho smallmouth bass. These findings suggest that population-specific management may be appropriate and highlight the importance of natural flow conditions (*i.e.*, spring high flows) and connected habitats for this endemic sport fish, particularly in smaller streams.

KEYWORDS
habitat, home range, movement, Neosho smallmouth bass, Ozark Highlands, radio telemetry

1 | INTRODUCTION

Riverine fish movements reflect changing resources and habitat needs throughout their life cycle. Resources such as prey availability and critical habitats (*e.g.*, spawning, rearing and refuge) are often life-stage dependent and dynamic in space and time, thereby necessitating movement by many stream fishes (Schlosser, 1991; Thurow, 2016). For example, many stream fishes migrate to thermal environments beneficial for overwinter growth and survival, but the timing of these movements can vary widely (Peterson & Rabeni, 1996; Westhoff *et al.*, 2016). Movements associated with the reproductive period are often pronounced, with many species showing potamodromy (*i.e.*, migration within freshwater environments) to reach distinct spawning habitats (Lucas & Baras, 2001; Thurow, 2016). Typical movement cues include water temperature, discharge and combinations thereof, and often correspond to shifts in resource availability (Taylor & Cooke, 2012). These cues may vary within and among catchments, and failure to support these habitat needs can cause declines in stream fish populations (Benitez & Ovidio, 2018; Nagrodski *et al.*, 2012; Pelicice & Agostinho, 2008). Thus, understanding movement patterns and cues is crucial for the effective conservation and management of stream fishes (*e.g.*, defining critical habitats, movement corridors, management units and threats; Cooke *et al.*, 2016; Schlosser, 1991; Thurow, 2016).

Generalizing movement and habitat-use patterns of stream fishes is difficult due to differences in the timing and availability of resources and variation within and among populations. Stream habitats reflect processes operating at multiple spatial and temporal scales resulting in substantial heterogeneity in resources across the riverscape (Fausch *et al.*, 2002; Frissell *et al.*, 1986). The resulting patchy habitat conditions may cause changes in movement behaviours and habitat use by fishes (Lucas & Baras, 2001; Warren Jr., 2009). Higher movement rates may be more common among isolated populations or those occurring on range boundaries because of increased vulnerability to disturbances (*e.g.*, climate change; Radinger *et al.*, 2017; Rubenson & Olden, 2017). Within- and among-population differences often reflect mobile and non-mobile individuals and divergent life-history strategies (*e.g.*, lacustrine *vs.* riverine spawning, Barthel *et al.*, 2008; Chapman *et al.*, 2012; Radinger & Wolter, 2014). Variation in habitat use among stream populations may lead to conflicting conclusions about a species' designation as a "generalist" *vs.* "specialist" (*e.g.*, Pert *et al.*, 2002); in reality, movement among habitat patches often relates to specific resource needs that are not continuously available in space or time (Schlosser, 1991).

Black bass (genus *Micropterus*) are both recreationally and ecologically important, but our ecological knowledge of the narrow-range endemics is lacking relative to quickly evolving species designations (Birdsong *et al.*, 2015; Taylor *et al.*, 2019). Black basses are among the most highly sought game species in North American freshwater ecosystems, including streams (US Fish and Wildlife Service, 2018), and play a critical role as top predators in aquatic food webs (MacRae & Jackson, 2001; Power *et al.*, 1985). The authors of this study know little about the ecological needs of endemic basses such as the Neosho sub-species of smallmouth bass *Micropterus dolomieu velox* Hubbs & Bailey, 1940 (hereafter Neosho smallmouth bass) even though management agencies acknowledge a conservation need (Boxrucker *et al.*, 2004; Quinn *et al.*, 2004). This sub-species is found on the edge of the smallmouth bass native range (*i.e.*, southwestern Ozark Highlands, Brewer & Long, 2015; Stark & Echelle, 1998) and occupies a landscape that is highly dynamic with respect to physical habitat such as hydrology and water temperature (Hafs *et al.*, 2010; Leasure *et al.*, 2016; The Nature Conservancy, Ozarks Ecoregional Assessment Team, 2003), making it ideal for examining the importance of different ecosystems (*e.g.*, streams, large rivers and reservoirs) to the ecology of this sub-species. Understanding how this sub-species uses resources across the riverscape can inform conservation and management strategies. These approaches could be relevant to other endemic black basses as environmental conditions continue to change because of factors including development and climate change (Birdsong *et al.*, 2015; Taylor *et al.*, 2019).

Existing knowledge of smallmouth bass movements suggests strong seasonal patterns, long-distance movement potential and considerable variability within and among populations, but derives primarily from northern populations in large, connected river-tributary or river–lake systems. In these ecosystems, smallmouth bass are typically most mobile before and after spawning and before the overwinter period (Barthel *et al.*, 2008; Langhurst & Schoenike, 1990; Webster, 1954). Individuals can move >100 km, even within populations where a subset of fish is non-mobile (*i.e.*, moving <0.5 km; Rubenson & Olden, 2017; Schall *et al.*, 2019). At the population level, movement extents and patterns of mobility among individuals vary considerably, thereby complicating the designation of "mobile" and "non-mobile" sub-groups (Lyons & Kanehl, 2002; Rubenson & Olden, 2017). In streams of the Ozark Highlands ecoregion, many smallmouth bass use springs as overwinter thermal refugia and follow similar movement patterns as northern populations around the spawning period, albeit with smaller movement extents (Peterson & Rabeni, 1996; Todd & Rabeni, 1989; Westhoff *et al.*, 2016).

Movement and habitat use by smallmouth bass in fragmented, highly modified riverscapes (*i.e.*, river-reservoir systems) are not well studied. Impoundments often create barriers to movement by native fishes (Herbert & Gelwick, 2003; Pelicice *et al.*, 2015). Smallmouth bass can move throughout connected river–lake systems (Barthel *et al.*, 2008; Gerber & Haynes, 1988; Webster, 1954), whereas the use of connected habitats in human-modified systems, where native populations have had less time to adapt to lacustrine habitats, is less clear (but see Schall *et al.*, 2019). The goal of this study was to quantify patterns of Neosho smallmouth bass movement in streams within a river-reservoir landscape of the Ozark Highlands ecoregion. The objectives of this study were to (a) describe seasonal movement extents, rates and habitat-use patterns of Neosho smallmouth bass in three streams with varying physicochemical conditions and (b) identify relationships between movement and temperature and discharge within these ecosystems. These findings will contribute to improved conservation and management of this narrow-range endemic that occupies a complex river-reservoir landscape.

2 | MATERIALS AND METHODS

2.1 | Study area

The streams used in this study were in the Ozark Highlands ecoregion, specifically the portions of south-west Missouri, north-east Oklahoma, north-west Arkansas and south-east Kansas that comprise the Neosho smallmouth bass range (Brewer & Long, 2015). Average annual precipitation is 108 cm, and annual hydrology is characterized by spring floods and lower baseflows during other seasons (Nigh & Schroeder, 2002). Land cover is primarily forest or pasture, with the latter more common in valleys, and lithology is largely cherty limestone (Nigh & Schroeder, 2002). The streams used in this study are emblematic of the Ozark Highlands ecoregion and contain distinct riffle-pool sequences with some off-channel habitats (Rabeni & Jacobson, 1993) and are clear under baseflow conditions (i.e., clarity of 3 m is common). Substrates are predominately gravel, pebble and cobble with some exposed bedrock and groundwater inputs are common but spatially variable (Brewer, 2013; Zhou et al., 2018).

The authors tracked radio-tagged adult Neosho smallmouth bass from three populations occupying different streams with varying connectivity to larger ecosystems: (a) Sycamore Creek, a third-order stream (Strahler, 1952) that flows directly into the impounded Grand Lake O' the Cherokees (hereafter Grand Lake); (b) Buffalo Creek, a third-order tributary that terminates at the confluence of a river-reservoir interface and (c) Elk River, a fifth-order river situated between a low-head dam and Grand Lake (Figure 1). Sycamore Creek flows 18 km, draining a 133 km^2 catchment, before reaching Grand Lake, Oklahoma. A road crossing 4 km upstream of the reservoir on Sycamore Creek creates a barrier to fish movement at baseflow conditions. A small tributary, Brush Creek (drainage area: 62 km^2), joins Sycamore Creek just downstream of the road crossing and is itself blocked by such a crossing 0.2 km upstream of the confluence (Figure 1). Buffalo Creek flows 42 km south-west from Missouri to Oklahoma, draining a 293 km^2 catchment before terminating in the transient river-reservoir interface of Grand Lake and the Elk River. The main stem Elk River flows west for 41 km from Pineville, Missouri, to Grand Lake, draining a 2524 km^2 catchment. A low-head dam in Noel, Missouri, disconnects the lower 23 km of the Elk River except during higher flows (i.e., c. 2 year return interval discharge; R. Horton, Missouri Department of Conservation, oral comm., 2016).

2.2 | Environmental measurements

The authors collected water temperature and discharge data for each stream throughout the study period to determine their influence on movement and habitat-use patterns. They placed temperature loggers (HOBO Pro v2, Onset Corp., Bourne, MA, USA) in two or three equally spaced, well-mixed locations (c. 0.75 m deep) along the thalweg in each stream and recorded temperature every 30 min. The authors averaged temperature data across loggers within streams to calculate mean daily temperatures for comparison with fish movements. Mean daily discharge data were compiled from U.S. Geological Survey (USGS) stream gages on Buffalo Creek (gage 07189100) and Elk River (gage 07189000) near Tiff City, Missouri. The authors characterized Sycamore Creek discharge patterns by developing a rating curve. Briefly, the authors deployed a water level logger (HOBO U20, Onset Corp.) to continuously record stream stage, and compared stage values to measured cross-sectional discharge (Gordon et al., 2004):

$$Q = aS^b,$$

where Q is the discharge (m^3 s^{-1}), S is the stage height (m) and a and b are system-specific coefficients. The rating curve coefficients for Sycamore Creek were $a = 5.11$ and $b = 6.66$, and the relationship had an $R^2 = 0.63$. Gaps in discharge data were estimated using least-squares regression with discharge values from the USGS gage on nearby Honey Creek (gage 07189542; $R^2 = 0.94$).

2.3 | Fish tagging

The authors conducted initial capture and tagging of Neosho smallmouth bass in May 2016. All collection and tagging procedures were conducted under the auspices of Oklahoma State University Animal Care and Use Protocol AG-16-8. The authors used boat (Smith-Root 5.0 GPP, Vancouver, WA, USA) and tow-barge (Stealth Mini-Boat, Midwest Lake Management, Polo, MO, USA) electrofishing and angling to sample $n = 99$ individuals across streams studied ($n = 40$ in Buffalo Creek, $n = 30$ in Elk River, $n = 29$ in Sycamore Creek). For each stream, tagging occurred in four to six locations of varying distance from major confluences and the reservoir interface (Figure 1). The authors anaesthetised fish by immersing them in a 30 mg l^{-1} bath of Aqui-S 20E (Aqui-S, Lower Hutt, New Zealand) until they lost equilibrium (typically 2–5 min); the authors then recorded total length (L_T, ±1 mm) and weight (±1 g). Anaesthetised fish were placed ventral side up on a V-shaped surgical table with a low dose (15 mg l^{-1}) of Aqui-S 20E continuously flushed across the gills. The authors made a c. 15 mm incision slightly lateral to the ventral midline and inserted MCFT2 radio transmitters (Model 3BM: 11 × 43 mm, 8 g in air, 723 days expected battery life, and Model 3EM: 12 × 53 mm, 10 g in air, 860 days expected battery life; Lotek Wireless, Newmarket, ON, Canada) into the coelom (Cooke & Bunt, 2001). The authors moved the inserted transmitter away from the incision site and trailed the antenna out of a secondary incision to reduce risk of tag loss (Ross & Kleiner, 1982), and they trimmed the antenna to the posterior of the caudal fin to reduce the potential for biofouling (Thorstad et al., 2001). The authors closed the incision using absorbable material (Unify PGA, AD Surgical, Sunnyvale, CA, USA) and a pair of simple interrupted sutures (Cooke & Bunt, 2001). Following surgeries, fish were placed in shaded, flow-through containers in the stream and allowed to recover for a minimum of 30 min before release near the site of capture.
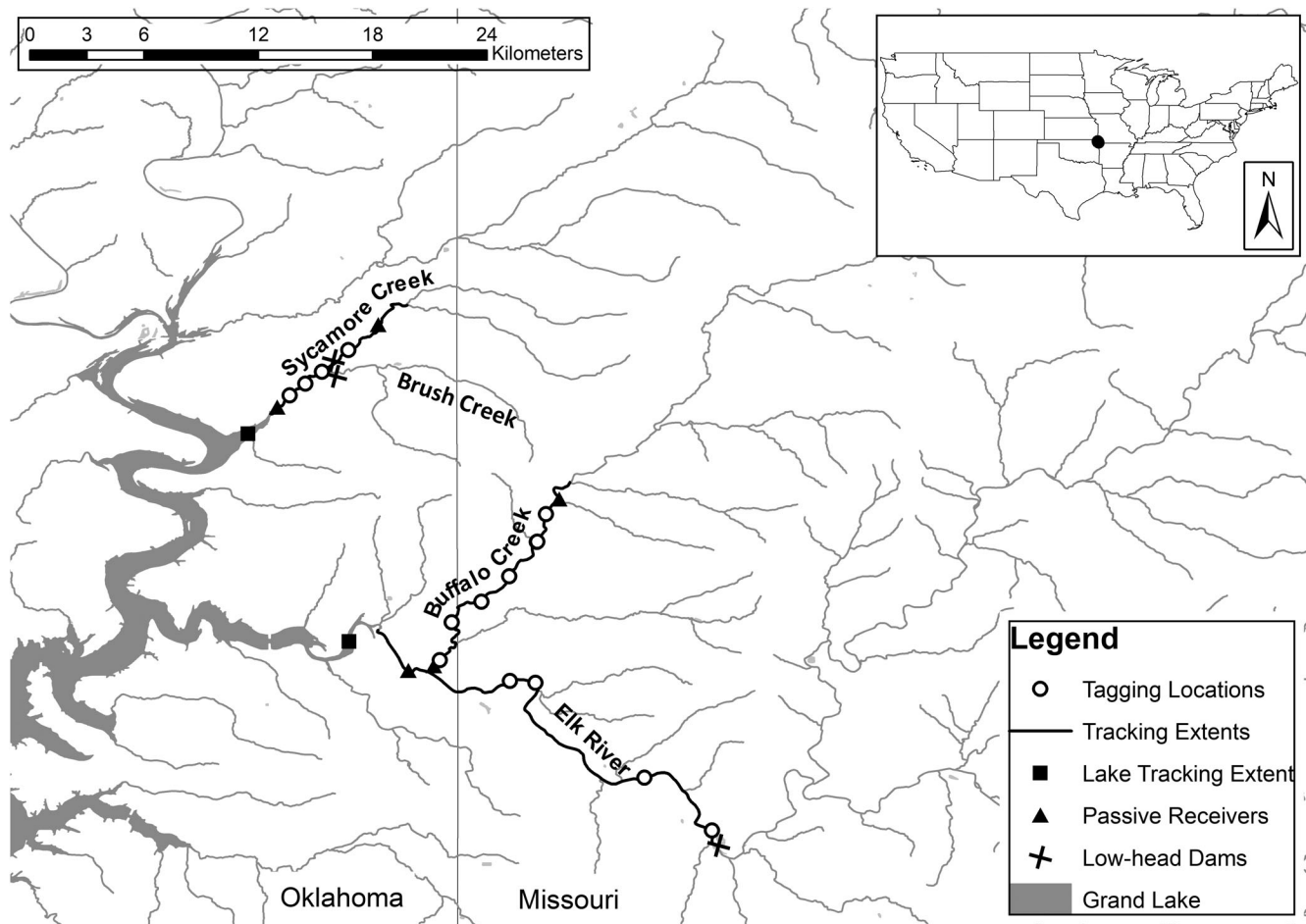
FIGURE 1   Tagging locations, tracking extents and passive receiver sites for three Ozark Highland streams used to examine movement and habitat use by adult Neosho smallmouth bass. Low-head dam locations are also indicated for (from north to south) Sycamore Creek, Brush Creek and the Elk River

The authors conducted additional tagging of Neosho smallmouth bass in October 2016 and March–April 2017 using transmitters recovered during earlier tracking efforts. If recovered transmitters were in good condition, they were cleaned and sterilized before implantation into new fish. They performed tagging in autumn and spring to avoid warmer water temperatures associated with greater handling stress, mortality and transmitter loss (Bunnell & Isely, 1999; Walsh et al., 2000). These efforts combined with initial tagging brought the total number of tagged fish to $n = 152$ for the study ($n = 62$ in Buffalo Creek, $n = 50$ in Elk River, $n = 40$ in Sycamore Creek).

2.4 | Fish movement and habitat use

Fish tagged with coded radio transmitters can be individually identified and located either actively (as described later) or with passive receivers (Kuechle & Kuechle, 2012). Both methods of tracking were used in this study, with the passive receivers used to determine if tagged fish left the active tracking area and moved into the reservoir or upstream. Five receiver stations with fixed-position antennas were

used to help monitor tagged fish in the study area. The stations were placed near downstream confluences or reservoir interfaces – to detect fish leaving the rivers or crossing the reservoir interface with Buffalo Creek during the spring when the reservoir backed up – and at upstream tracking extents to capture any fish moving out of the study area (Figure 1). Each receiver station consisted of two, three-element Yagi antennas (i.e., one facing upstream and one downstream) positioned 3–4 m high on the bank (i.e., in a nearby tree) and angled towards the river. The three stations continuously scanned the radio frequencies used and recorded the frequency, identification number and time stamp of each detection. Each receiver was powered by a marine battery connected to a solar panel. Data collected by the receivers were downloaded approximately every 7–10 days. All fish detected via the passive stations were also detected during active tracking efforts, and thus, passive locations were not used in the analyses but only to monitor fish movement out of the study area.

The authors actively tracked radio-tagged smallmouth bass from June 2016 to February 2018. The initial locations of tagged fish were determined a minimum of 48 h after surgery and release. All tracking was conducted during the day (c. 07.00–19.00 hours), and each

stream was surveyed approximately weekly from March to October and monthly from November to February. The authors conducted manual tracking from a kayak or on foot using an SRX800 VHF receiver (Lotek Wireless) and a three-element Yagi antenna. They moved in a downstream direction covering the lower 9.3 km of Sycamore Creek, the lower 14.3 km of Buffalo Creek and the lower 23.4 km of Elk River (Figure 1). In addition to tracking this study's regularly designated stream reaches, the authors actively tracked fish into the reservoir on multiple occasions. From Sycamore Creek, the authors tracked to a location near Council Hollow, whereas they tracked to S 678 Road from the Buffalo Creek-Elk River confluence (Figure 1). Following the initial detection of a tagged fish, they slowly approached the area of strongest signal and gradually reduced receiver gain to improve directionality (i.e., homing; Heim et al., 2018; Koehn et al., 2012; Westhoff et al., 2016). Location accuracy was within c. 1.5 m based on dummy tag relocations, and they visually confirmed tagged fish presence for 21% (506/2362) of relocations.

The authors obtained GPS coordinates and recorded several habitat characteristics at each fish location. Channel unit type was classified as riffle, run, pool or slackwater (i.e., low-velocity, off-channel habitats) based on current velocity, depth, gradient and substrate (simplified from Rabeni & Jacobson, 1993). They measured focal depth (±0.01 m), water-column velocity (i.e., at $0.6 \times$ depth, ±0.1 m s^{-1}; FP111 Flow Probe, Global Water, Sacramento, CA, USA), and water temperature (i.e., at $0.5 \times$ depth, ±0.1°C; Ultrapen PT1, Myron L, Carlsbad, CA, USA). They identified the nearest cover type: woody debris, boulders, rootwads, undercut banks/bedrock, vegetation, man-made cover or combinations of these types. Man-made cover included miscellaneous structures in the stream (e.g., bridge pilings, broken concrete and fencing). The authors also quantified the distance to cover (±0.5 m); fish were classified as using cover if it occurred within 1 m of their location (Probst et al., 1984). They visually estimated dominant substrate class within a 1 m^2 area surrounding each fish location using a modified Wentworth scale: silt (<0.06 mm), sand (>0.06–2 mm), gravel (>2–16 mm), pebble (>16–64 mm), cobble (>64–256 mm), boulder (>256 mm) and bedrock (Bain, 1999; Brewer, 2011). If a fish showed a fright response to tracking efforts made by the authors (indicated by a sudden, drastic decrease in received signal strength), they recorded a waypoint at the initial fish location but did not collect microhabitat information. In addition, sampling conditions (e.g., high flows and turbidity) and equipment malfunctions occasionally prevented the identification of habitat attributes at fish locations.

After evaluating location data, the authors summarized fish movement in two ways and estimated home range. They plotted fish locations in ArcMap 10.3.1 (ESRI, Redlands, CA, USA) and used field-collected information (i.e., recovered transmitters and visual confirmation of tagged fish) to evaluate the validity of each fish location (Schwarz & Arnason, 1990). For example, if a transmitter was recovered or detected in the same location over multiple consecutive tracking events, they evaluated prior and subsequent locations and visual confirmations for that fish to identify and remove spurious "fish" locations (e.g., shed tags). The authors combined these updated fish

location waypoints and manually digitized stream polylines in ArcMap and used the Locate Features Along Routes tool to measure the distance (±1 m) along the stream between relocations. The authors quantified movement distances and directionality (i.e., upstream and downstream) and calculated daily movement rate as the distance moved between consecutive locations divided by the number of days between locations. This scaled metric was particularly useful for evaluating the role of daily changes in environmental conditions (i.e., water temperature and stream discharge) on fish movements (see "Analyses" section). The authors also calculated home ranges for each fish as the distance between their maximum upstream and downstream locations (Hill & Grossman, 1987; Young, 1994).

2.5 | Analyses

Several variable calculations, transformations and standardizations were necessary before modelling to meet assumptions and improve interpretation. The response variable, movement rate, was natural-log transformed to account for skewness; the authors added a constant (i.e., y + 0.1) to all values to facilitate the transformation in cases of zero movement. They included categorical predictors for stream (three levels) and season (four levels). They defined the following seasons using time of year and water temperature: spring (rising between 12 and 20°C; c. March–May), summer (>20°C; c. June–September), autumn (decreasing between 20 and 12°C; c. October–November) and winter (<12°C; c. December–February). These cut-offs reflect warmer winter water temperatures in these streams relative to northern systems with spring and autumn encompassing the thermal conditions associated with spawning and over-wintering movements (Dauwalter & Fisher, 2007; Graham & Orth, 1986; Langhurst & Schoenike, 1990). The authors calculated mean water temperature and the coefficient of variation (CV $= \frac{\sigma}{\mu} \times 100$) of water temperature over the period between consecutive fish locations. To account for differences in stream size, discharge data were scaled by the median streamflow values for each stream during the study (McCune & Grace, 2002) using the following values: Buffalo Creek (0.43 m^3 s^{-1}), Elk River (6.68 m^3 s^{-1}) and Sycamore Creek (0.38 m^3 s^{-1}). They then calculated both mean discharge and the CV of discharge for the period between successive fish locations. Lastly, they included fish L_T as a predictor. All continuous predictors were natural-log transformed to account for skewness and standardized (mean = 0; s.d. = 1) to improve model interpretation (McCune & Grace, 2002).

The authors combined linear mixed models (LMMs) with a model selection approach to determine the relationship between smallmouth bass daily movement rate, stream, season, environmental conditions and fish size. They compared all sub-sets of the model containing terms for stream, season, mean water temperature, CV of water temperature, mean discharge, CV of discharge and fish L_T. Pair-wise correlations between predictor variables $|r|$ were <0.7, so all predictor combinations were included in the candidate model set (Dormann et al., 2013). They also considered the following interactions: stream × mean temperature, stream × mean discharge, season × mean

temperature and season × mean discharge. All models included a random effect for individual fish to account for unequal sampling and the lack of independence among measurements (Otis & White, 1999; Wagner et al., 2006). The authors assumed a normal distribution N (0, τ^2) for random effects, where τ^2 represents the population variance among random effect levels (i.e., among individual fish). They used AIC adjusted for small sample size (AIC$_c$, Sugiura, 1978) to rank the models of this study. For this and all subsequent model-selection efforts, the authors only considered models within two AIC$_c$ of the top model to have support if they contained the same number of or fewer parameters than the top model; this approach avoids unnecessary model complexity and reduces the inclusion of uninformative predictors (Arnold, 2010). They evaluated residual and normal Q-Q plots for the top model to ensure homogeneity of variance and the normal distribution of residuals and random effects. To assess the relative amount of variation explained by fixed and random effects in the top model, they calculated marginal and conditional R^2 (Nakagawa et al., 2017). Marginal R^2 (R^2_m) describes the variance explained by fixed effects, whereas conditional R^2 (R^2_c) reflects the variance explained by fixed and random effects (Vonesh et al., 1996). These and subsequent models were evaluated using the lme4 (Bates et al., 2015) and MuMIn (Bartoń, 2018) packages in R 3.5.1 (R Core Team, 2018).

The authors used model selection on a set of linear models to evaluate the influence of stream, fish sex and fish L_T on home range size. They compared home range size with the number of observations for each fish to determine an appropriate cut-off for estimating home range (Todd & Rabeni, 1989). With $n \geq 12$ observations for an individual fish, home range estimates showed no correlation with the number of observations ($r = 0.03$); therefore, this cut-off was used to identify $n = 72$ home ranges for summary and subsequent analysis. Home range size was natural-log transformed to reduce skewness. Stream was a categorical predictor with levels for Sycamore Creek, Buffalo Creek and Elk River. Fish sex was determined for individual fish during radio transmitter implantation. Sex could not be determined for all fish, including all autumn-tagged individuals, necessitating a third category for unknown sex. Fish L_T was natural-log transformed and standardized (mean = 0; s.d. = 1). All interactive and additive combinations of predictors were included in a candidate model set ($n = 15$ models), and AIC$_c$ was used to compare models (Sugiura, 1978).

To identify spatiotemporal patterns in habitat use, the authors calculated summary statistics of habitat variables at observed fish locations across seasons and streams. They computed means, standard deviations and ranges of depth, velocity and water temperature use by tagged fish. For categorical variables (i.e., channel unit, cover and substrate), the authors summarized proportional habitat use for all combinations of season and stream.

3 | RESULTS

The size of tagged fish varied within and among study systems, with fish size generally greater in larger streams. Fish that were tagged following capture from the Elk River had a mean L_T of 349 mm (range: 290–464 mm) and a mean weight of 600 g (range: 368–1603 g). Comparatively, fish sampled and tagged in Buffalo Creek were shorter (mean L_T: 327 mm; range: 278–408 mm) and lighter (mean weight: 518 g; range: 370–1010 g). Bass sampled and tagged from Sycamore Creek were the smallest fish by both L_T (mean: 322 mm; range: 290–370 mm) and weight (mean: 481 g; range: 376–765 g). Over the duration of the study, the authors tagged $n = 152$ fish and recovered 71 transmitters. Of these, 53 individuals were re-implanted with recovered transmitters ($n = 22$ in Buffalo Creek, $n = 20$ in Elk River, and $n = 11$ in Sycamore Creek). Tracking efforts from the 21 month study period resulted in $n = 2362$ individual locations ($n = 891$ in Buffalo Creek, $n = 463$ in Elk River, $n = 878$ in Sycamore Creek) from $n = 130$ fish. Of the $n = 152$ fish tagged, $n = 22$ were never relocated.

Discharge conditions and water temperature during the study followed typical seasonal patterns and reflected groundwater variability of these Ozark Highland streams (Figure 2). High flows typically occurred during the spring in all three streams. There was one major flood event in late April 2017 representing an extreme relative to flows during the remainder of the study period. In late summer and autumn 2016–2017, low flow conditions led to riffle drying and pool isolation in many reaches of both Buffalo Creek and Sycamore Creek. During the study period, discharge was much greater in Elk River (median: 6.68 m^3 s^{-1}) compared to Buffalo Creek (median: 0.43 m^3 s^{-1}) and Sycamore Creek (median: 0.38 m^3 s^{-1}). Mean water temperatures during the study period were warmest in Elk River (19.0 °C), followed by Sycamore Creek (17.0°C) and Buffalo Creek (16.9°C). Thermal variability was greatest in Sycamore Creek (CV: 38.2) and Buffalo Creek (CV: 38.0) and lowest in Elk River (CV: 30.2).

Movements of tagged smallmouth bass were highly variable among seasons, streams and individuals (Table 1). Most fish movements were localized (i.e., ≤10 m day^{-1}) in all streams and seasons, except for spring in Elk River (48.1% localized). Movement rates indicating relatively high mobility (i.e., >10 m day^{-1}) were most common in the spring across all three study systems and were more frequent in Elk River in all seasons; such movement rates were particularly rare (i.e., <10%) in Sycamore Creek outside of spring and in Buffalo Creek during autumn and winter. Among fish that moved, the percentage moving upstream and downstream for a given stream and season were generally similar in small streams, with some seasonal asymmetries in the Elk River (Table 1). Of the 73 individual movements >1.0 km, 43 (59%) occurred during the spring. The greatest individual movements were an order of magnitude larger in Elk River (17.0 km) and Buffalo Creek (12.9 km) compared to movements of tagged fish in Sycamore Creek (1.7 km). Across all streams, movement rates were greatest (median: 3.8 m day^{-1}) and most variable (CV: 450.7) during spring, lowest (median: 0.3 m day^{-1}) in winter and least variable (CV: 184.0) in autumn. Movement rates >1000 m day^{-1} were observed on nine occasions in Elk River (56%) and Buffalo Creek (44%) and were concentrated during the spring season (89%). Across seasons, movement rates were greatest in the Elk River (median: 5.2 m day^{-1}), followed by Buffalo Creek (median: 2.3 m day^{-1}) and
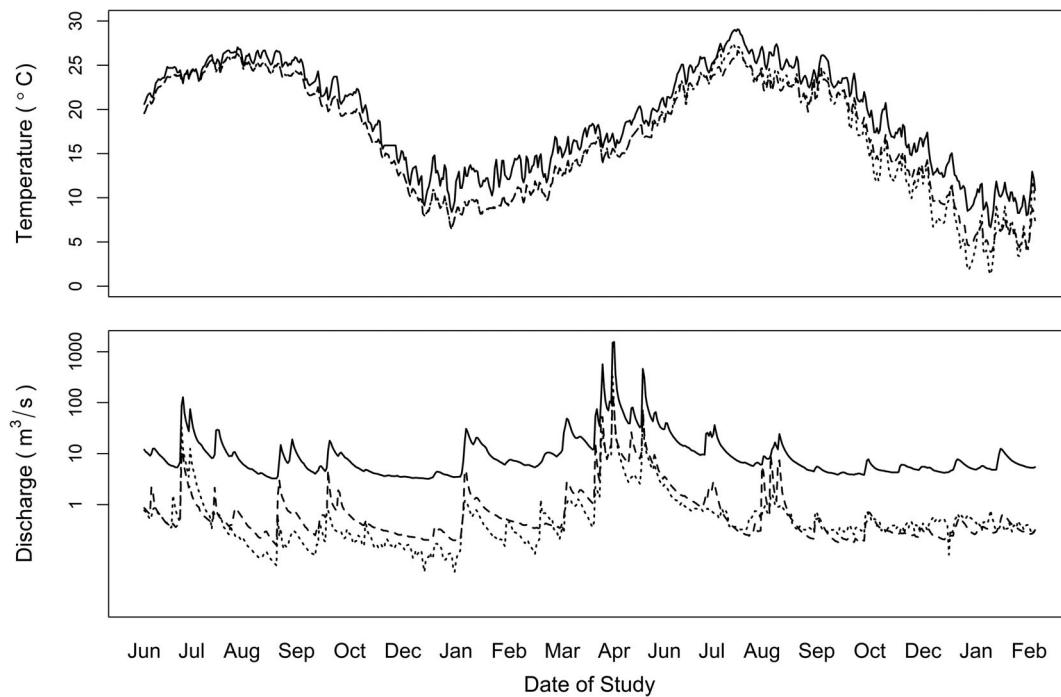
FIGURE 2 Daily mean water temperature (top) and discharge (bottom) conditions for Elk River (solid line), Buffalo Creek (dashed) and Sycamore Creek (dotted) during the June 2016 to February 2018 study of adult Neosho smallmouth bass movement and habitat use. For reference, 1.0 m^3 s^{-1} equals 35.3 ft^3 s^{-1}. Note that discharge is plotted using a log_{10} scale and that the y-axis is scaled to the maximum discharge during the study period (1557 m^3 s^{-1} on 30 April 2017 in Elk River)

TABLE 1 Summary statistics of $n = 2232$ radio-tagged smallmouth bass movements across seasons in three Ozark streams

	Max US (m)	Max DS (m)	n	% US	% DS	% NM	Mean ± s.d. (m day^{-1})	Max (m day^{-1})
Buffalo Creek								
Spring	12,710*	12,871*	178	20.8	17.4	61.8	64.7 ± 225.3	2145.1
Summer	5563*	9930*	641	10.1	10.3	79.6	13.5 ± 64.6	1418.5
Autumn	1346*	1287*	41	2.4	4.9	92.7	4.9 ± 10.0	47.7
Winter	360	4127[a]	31	0.0	9.7	90.3	5.7 ± 16.7	91.3
Elk River								
Spring	16,715*	16,958*	129	31.0	20.9	48.1	163.4 ± 583.5	5652.7
Summer	1632*	3243*	284	16.5	22.2	61.3	23.2 ± 72.2	816.0
Autumn	418	270	22	22.7	9.1	68.2	7.2 ± 8.6	29.9
Winter	1051[a]	2402	28	7.1	17.9	75.0	8.3 ± 18.1	77.3
Sycamore Creek								
Spring	1608*	1709*	176	16.5	15.3	68.2	19.4 ± 39.4	281.3
Summer	924	747	603	5.8	3.6	90.5	4.7 ± 11.5	106.7
Autumn	784	1060	61	4.9	3.3	91.8	4.1 ± 8.4	46.1
Winter	138	1067	38	0.0	2.6	97.4	1.3 ± 4.2	26.0

Note. Metrics include maximum (Max) upstream (US) and downstream (DS) movements (m) of individual fish, where distance was measured between consecutive relocations. Additional information is provided for the number of individual relocations (n) and the percentage of these movements classified as upstream (>10 m US day^{-1}), downstream (>10 m DS day^{-1}) and non-mobile (NM; ≤10 m day^{-1}). Movement rate (m day^{-1}) was calculated by dividing distance moved (regardless of direction) by the number of days between relocations; the authors provide means, standard deviations (s.d.) and maxima. * indicates the same individual fish was responsible for maximum movements in both directions within the indicated season.
[a]The same fish moved 4127 m DS in Buffalo Creek and 1051 m US in Elk River between relocations during winter 2016–2017.

TABLE 2 Rankings of models within 2 AIC_c of the top model from the candidate set of linear mixed models of movement rate (after adding 0.1 and natural-log transformation) by adult smallmouth bass in Ozark streams

Model	K	LL	AIC_c	ΔAIC_c	w_i	R^2_m	R^2_c
$Y_{ij} = \beta_0 + \gamma_j + \beta_1 Seas \cdot Flow + \beta_2 Seas \cdot Temp + \beta_3 Strm + \beta_4 Temp\_CV + \beta_5 TL$	18	−4376.8	8789.9	0.00	0.21	0.14	0.25
$Y_{ij} = \beta_0 + \gamma_j + \beta_1 Seas \cdot Flow + \beta_2 Seas \cdot Temp + \beta_4 Temp\_CV + \beta_5 TL + \beta_6 Strm \cdot Temp$	20	−4375.3	8791.0	1.15	0.12	0.15	0.25
$Y_{ij} = \beta_0 + \gamma_j + \beta_1 Seas \cdot Flow + \beta_2 Seas \cdot Temp + \beta_3 Strm + \beta_4 Temp\_CV$	17	−4378.5	8791.3	1.49	0.10	0.14	0.25
$Y_{ij} = \beta_0 + \gamma_j + \beta_1 Seas \cdot Flow + \beta_2 Seas \cdot Temp + \beta_3 Strm + \beta_4 Temp\_CV + \beta_5 TL + \beta_7 Flow\_CV$	19	−4376.6	8791.5	1.63	0.09	0.14	0.25
$Y_{ij} = \beta_0 + \gamma_j$	3	−4504.4	9014.7	224.8	<0.01	0.00	0.20

Note. Y_{ij} is the daily movement rate at relocation *i* for fish *j*, β_0 is the grand intercept, γ_j is the random fish intercept, Seas is season, Strm is stream, and L_T is fish total length (mm). Metrics quantified between relocations include mean discharge (Flow; $m^3 s^{-1}$), mean water temperature (Temp; °C) and their respective coefficients of variation (Flow_CV; Temp_CV). Main effects involved in interactions are included but not shown for each model. The null (random effect only) model is included for reference. *K* is the number of model parameters, LL is log-likelihood, AIC_c is Akaike's information criterion corrected for small sample size and ΔAIC_c is the difference in AIC_c score between a given model and the top model. Akaike weight (w_i) indicates the relative support for each model. Marginal R^2 (R^2_m) describes variance explained by fixed effects and conditional R^2 (R^2_c) describes variance explained by both fixed and random effects.
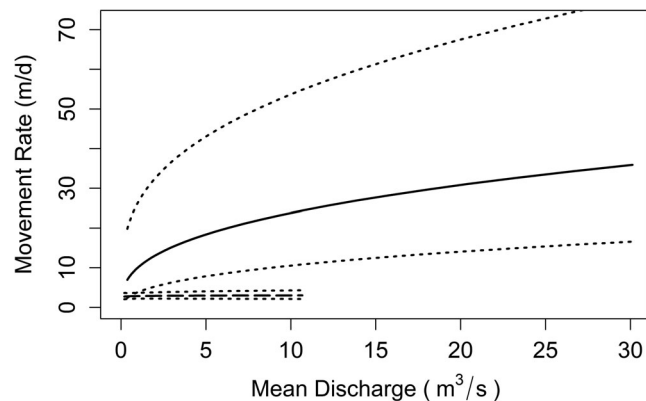

FIGURE 3 Predicted relationship between smallmouth bass movement rate (m day^{-1}) and mean discharge ($m^3 s^{-1}$) in spring (——) and summer (– – –). Dotted lines indicate 95% C.I. Predicted movement rates are not pictured for autumn (mean: 5.0 m day^{-1}) or winter (mean: 0.2 m day^{-1}), as these predictions do not vary over the small range of discharge values (0.28–0.91 $m^3 s^{-1}$) for which they are valid. Predicted values are made at mean values of all additional continuous predictors and with Buffalo Creek as the reference stream

Sycamore Creek (median: 1.3 m day^{-1}). The authors did not observe any tagged fish using Grand Lake or its associated river-reservoir interfaces during the study, either *via* passive receivers or active tracking. Three tagged fish moved between Elk River and Buffalo Creek when reservoir levels were low and there was flowing water at the confluence. In addition, one fish from Sycamore Creek used tributary habitat in Brush Creek from August to November 2017.

The top model for movement rate included two interaction terms (season × mean discharge, season × mean water temperature) and three main effects (stream, CV of water temperature and fish L_T; Table 2). Movement rate was positively associated with increasing discharge during spring, but no relationship was apparent over the

smaller range of flows that occurred during the summer (Figure 3). Predicted movement rates were consistent and comparatively low during relatively homogenous discharge conditions (range: 0.28–0.91 $m^3 s^{-1}$) associated with both autumn (mean: 5.0 m day^{-1}) and winter (mean: 0.2 m day^{-1}). The effect of mean water temperature on movement rate varied by season (Figure 4). This effect was most apparent in the spring when movement rate increased with water temperature. Movement rates were generally highest in the Elk River and lowest in Sycamore Creek, though this effect did not interact with the continuous predictors of this study (Table 1). Increasing temperature variability, as measured by the CV of water temperature, had a very weak, negative relationship with movement rate (Figure 5). Across all streams and seasons, larger fish had greater movement rates, though L_T was excluded from a more parsimonious competing model with similar fit (Table 2). The fixed effects in the top model explained 14% of the variation in movement rate ($R^2_m = 0.14$), and the addition of the random individual effect led to a total of 25% of the variation being explained ($R^2_c = 0.25$).

Linear home range sizes were highly variable and were not related to stream, fish sex or fish L_T (Table 3). Home range size differed substantially among individuals, ranging from 45 to 15,061 m. Each stream and sex included individuals with restricted home ranges and those that were relatively mobile. As with individual movements, the largest individual home range for each system reflected stream size, with maxima of 15,061 m in Elk River, 9933 m in Buffalo Creek and 2046 m in Sycamore Creek. Of the *n* = 72 home ranges calculated, *n* = 30 were >1000 m in size. Median linear home range size was 773 m and was similar across all streams and sexes. Home range size and fish L_T were not correlated (*r* = 0.03).

Several aspects of habitat use varied among seasons and streams (Table 4). Mean water temperatures used by tagged fish followed expected seasonal patterns and were similar among streams. Despite individual variability, average values reflect the use of more moderate
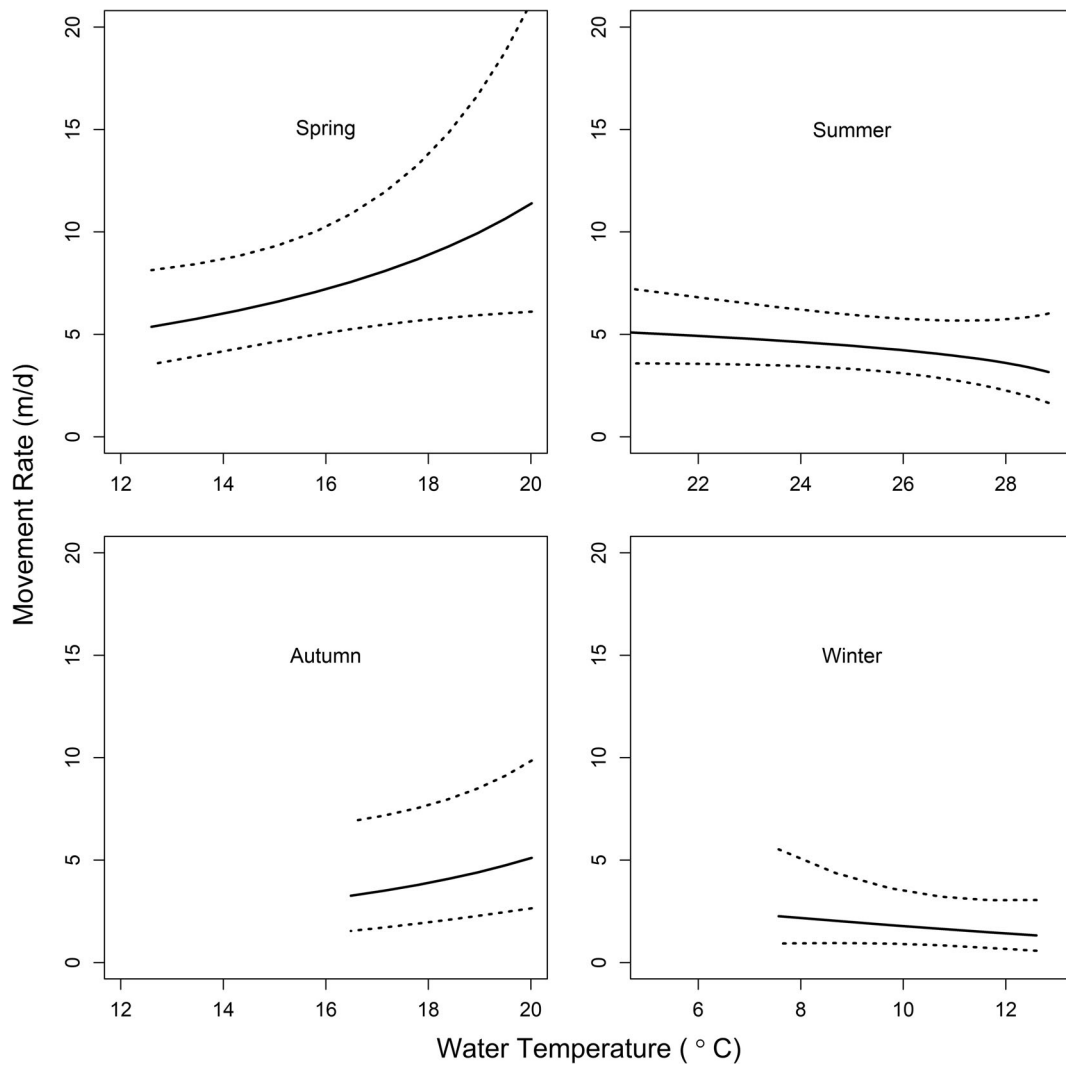
FIGURE 4 Modelled relationship between movement rate (m day^{-1}) of smallmouth bass and mean water temperature (°C) across four seasons. Confidence intervals (95%) are indicated by dotted lines. Predictions represent effects of water temperature with all other continuous predictors held at their mean values and with Elk River as the reference stream
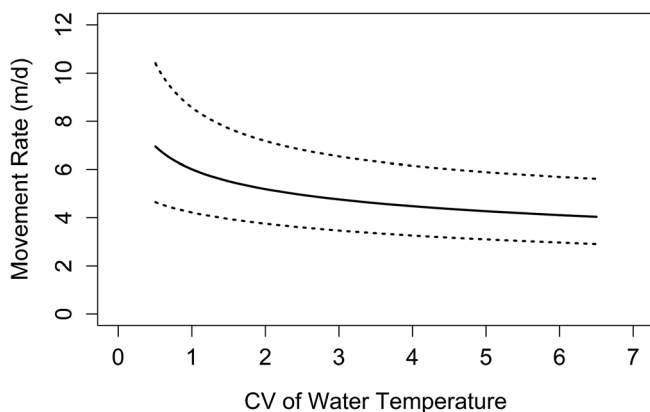
FIGURE 5 Relationship between movement rate (m day^{-1}) and water temperature variability (CV = σ/μ × 100) from the top-ranked model of movement rate. Dotted lines indicate 95% C.I. Predictions are made with all other continuous predictors at mean levels and with Elk River as the reference stream and summer as the reference season

thermal habitats when compared to ambient temperatures (*i.e.*, those averaged across loggers) during summer and winter. Velocity use was more variable and slightly greater in the spring, with some relatively higher velocity habitats also used in summer and the lowest values observed in autumn. Mean velocities used were typically low (≤0.3 m s^{-1}) in all streams and tended to be slightly higher in the Elk River. Water depth use was consistent across most seasons, with a wide range of depths used across systems (0.18–2.48 m) reflecting availability. Deeper habitats were used in Buffalo Creek and across all streams during winter, on average. Pools were the predominant channel unit used throughout the year in the smaller streams (90.9%), though their use was less frequent in Elk River (75.1%), owing partly to the greater use of run habitats (19.5%) when compared to smaller streams (5.4%). Use of riffle (3.1%) and run (11.3%) habitats was higher in the spring than the rest of the year across all streams (riffle: 0.2%, run: 7.5%). Proportional use of different substrate and cover types was slightly different among streams and seasons. Tagged

TABLE 3 Summary statistics of estimated linear home ranges of radio-tagged adult smallmouth bass in three Ozark streams by stream and fish sex

Predictor	n	Mean ± s.d. (m)	Median (m)	Range (m)
Elk River	20	2799 ± 4251	742	45–15,061
Buffalo Creek	32	1858 ± 2238	883	53–9933
Sycamore Creek	20	806 ± 573	503	167–2046
Female	14	1176 ± 1476	604	82–5220
Male	20	1974 ± 2392	1194	53–9933
Unknown	38	1990 ± 3289	714	45–15,061
Overall	72	1827 ± 2770	773	45–15,061

Note. The authors define linear home range as the distance between the farthest upstream and downstream points for each fish located at least 12 times.

TABLE 4 Summary statistics of depth, velocity and temperature conditions at $n = 2362$ observed smallmouth bass locations collected across four seasons in three lotic systems in the Ozark Highlands ecoregion

	Depth (m)		Velocity (m s^{-1})		Temperature (°C)	
	Mean ± s.d.	Range	Mean ± s.d.	Range	Mean ± s.d.	Range
Buffalo Creek						
Spring	1.13 ± 0.36	0.28–2.26	0.2 ± 0.3	0.0–1.4	16.4 ± 1.7	12.0–20.1
Summer	1.03 ± 0.36	0.18–2.30	0.1 ± 0.1	0.0–1.0	23.1 ± 2.3	16.0–28.4
Autumn	1.00 ± 0.30	0.38–1.66	0.0 ± 0.1	0.0–0.2	13.2 ± 3.7	5.6–18.3
Winter	1.13 ± 0.44	0.53–2.10	0.1 ± 0.2	0.0–0.7	11.7 ± 1.3	7.2–13.9
Elk River						
Spring	1.13 ± 0.44	0.41–2.48	0.3 ± 0.4	0.0–1.6	17.3 ± 2.6	10.8–22.1
Summer	0.79 ± 0.33	0.21–2.00	0.3 ± 0.2	0.0–1.2	26.5 ± 2.5	18.9–30.7
Autumn	0.82 ± 0.37	0.32–1.50	0.2 ± 0.2	0.0–0.6	12.4 ± 5.8	7.0–20.7
Winter	1.06 ± 0.34	0.46–1.70	0.2 ± 0.2	0.0–0.5	10.6 ± 1.8	8.9–14.5
Sycamore Creek						
Spring	0.88 ± 0.32	0.29–1.90	0.1 ± 0.2	0.0–0.9	17.4 ± 2.3	8.3–21.9
Summer	0.77 ± 0.28	0.28–1.80	0.1 ± 0.1	0.0–0.5	24.2 ± 2.4	16.5–29.7
Autumn	0.87 ± 0.38	0.22–1.70	0.0 ± 0.1	0.0–0.2	13.1 ± 5.1	4.9–20.1
Winter	1.05 ± 0.34	0.40–1.70	0.2 ± 0.3	0.0–0.7	13.0 ± 3.3	7.0–17.7

Note. s.d. refers to standard deviation. Stream conditions and equipment issues precluded measurements depth ($n = 87$), velocity ($n = 91$) and temperature ($n = 148$) at a small percentage of fish locations.

smallmouth bass used substrates in similar proportions across all streams and used gravel substrates to a greater degree during spring (40%) compared to other seasons (range: 3%–20%). Tagged bass used bedrock (22%) and pebble (30%) substrates less in spring than in other seasons (bedrock range: 31%–35%, pebble range: 37%–51%). Observations of fish not associated with any cover type were common across all study streams (37% overall), particularly Elk River (56%), and the use of woody debris was more frequent in Buffalo Creek (36%) than in other streams (8% in Sycamore Creek, 19% in Elk River). No seasonal differences were apparent regarding the use of different cover types.

4 | DISCUSSION

Neosho smallmouth bass exhibited considerable spatiotemporal heterogeneity in movement behaviour. The authors observed relatively mobile and sedentary individuals in each stream, as has been documented in other riverine smallmouth bass populations (Barthel *et al.*, 2008; Gerber & Haynes, 1988; Rubenson & Olden, 2017; VanArnum *et al.*, 2004) and stream fish in general (Lucas & Baras, 2001; Skalski & Gilliam, 2000). Tagged fish displayed greater mobility (both magnitude and rate) associated with spawning in the spring and reduced movement in other seasons (Lyons & Kanehl, 2002; Todd & Rabeni, 1989). The authors did not observe a concentration of movements to overwinter habitats, though these sometimes occur over a protracted period (*i.e.*, summer–late autumn, Robbins & MacCrimmon, 1977). Mobile fish typically moved between pool habitats, such that many pools throughout each study stream contained seasonal occupants along with year-round sedentary individuals. In this study, some spring movements were followed by a return to the original location just a few days later, whereas other fish remained through summer and autumn before moving. Maximum

movement distances, movement rates and home ranges increased with stream size, being greatest in Elk River and least in Sycamore Creek. This pattern likely reflects the restricted movement potential of fish in Buffalo Creek and Sycamore Creek because of seasonal drying of riffle habitats and the road crossing on Sycamore Creek. Intermittent streamflow is common in smaller Ozark Highland streams (Leasure et al., 2016) and limits smallmouth bass movement in dryer seasons (i.e., summer, Hafs et al., 2010; Martin, 2017). Movement magnitudes were not as large as those observed in some northern populations, which can exceed 100 km (Rubenson & Olden, 2017; Schall et al., 2019). This could reflect the fragmented nature of these systems, though this study was not designed to quantify such movements explicitly and thus these conclusions should be taken cautiously (Gowan et al., 1994; Rodríguez, 2002). The most mobile individuals in this study traversed most of the fluvial habitat available to them but were limited by upstream dams and intermittent flows and downstream impoundments. Those fish could only move greater distances by traversing the reservoir or crossing upstream barriers during extreme flow events, actions that were not apparent in the data of this study.

Movement rates of smallmouth bass reflected several seasonal environmental cues and system-specific conditions. Increased movement rates were observed during the spring and corresponded to increased discharge conditions. This seasonal effect likely reflects spawning movements, as n = 33 tagged individuals were documented guarding nests from mid-April through June in at least 1 year. Increased flows are known to be a movement cue for smallmouth bass in other riverine populations during spring (Langhurst & Schoenike, 1990; Westhoff et al., 2016). The authors observed lower discharge levels with little effect on fish movement in other seasons, suggesting that increased spring flows may alleviate connectivity issues that occur in other seasons, particularly for smaller streams (Bradford & Heinonen, 2008). They found the effect of water temperature on fish movement was small and positive in spring but appeared less important in the smaller streams. The effects of temperature on smallmouth bass movements are variable, but increasing spring temperatures are a common movement cue for smallmouth bass before spawning (Barthel et al., 2008; Lyons & Kanehl, 2002). In general, the authors found lower movement rates and dampened relationships with environmental cues in the two smaller streams studied (Buffalo Creek and Sycamore Creek), suggesting that movements are restricted by seasonal drying of riffle habitats and other barriers (e.g., road crossing on Sycamore Creek). A slightly negative effect of temperature variability on movement rate was included in the top model, but the biological effect appears minimal. This relationship may reflect the occurrence of greater thermal variability in colder months (i.e., November–January), when fish otherwise limit movement to preserve energy or use thermal refugia at a finer scale than measured by the temperature loggers used in this study (Peterson & Rabeni, 1996; Westhoff et al., 2016). The latter possibility is supported by the authors' observation of individuals using habitats warmer compared to those averaged across loggers, and the heterogeneous thermal conditions that result from contributions of groundwater in these systems

(Zhou et al., 2018). Although several movement cues were apparent, there was still considerable individual variability in movement behaviour within these populations.

Linear home ranges of tagged Neosho smallmouth bass were highly variable among individuals and not related to sex, stream or fish size. In an interior Ozark Highlands stream, Todd and Rabeni (1989) observed similar home range sizes and found no relationship between fish length and home range size. Individual variability in home range size has also been reported for smallmouth bass populations in Kentucky (VanArnum et al., 2004) and Ontario (Barthel et al., 2008). Individual variation is also the primary driver of home range size in other riverine fish species such as flathead catfish Pylodictis olivaris Rafinesque 1818 (Vokoun & Rabeni, 2005).

Individual variation and unexplained variability in movement patterns and cues were apparent among tagged smallmouth bass in this study. Individual differences may reflect variable condition, inherent movement propensity or reproductive status (Lucas & Baras, 2001; Rasmussen & Belk, 2017). As individual differences in movement ecology confer population-level resilience to environmental change (Pörtner & Peck, 2010; Waldman et al., 2016), their drivers merit further study. Additional individuality may reflect fidelity to specific seasonal habitats, which the authors observed for some individuals in this study. Two of the five individuals observed spawning in both years built nests within 40 m of the previous location (range: 7–785 m). This behaviour has been observed in some riverine smallmouth bass populations (Barthel et al., 2008; Langhurst & Schoenike, 1990) but not others (Gerber & Haynes, 1988; Lyons & Kanehl, 2002). Unexplained variability in movement rates remained after accounting for individual effects and may relate to unmeasured ecological factors (e.g., habitat, predation risk, food availability, territoriality, presence of mates; Lucas & Baras, 2001; Rasmussen & Belk, 2017).

The authors did not observe any evidence of tagged fish using Grand Lake or transient river-reservoir interfaces during the study, suggesting lentic habitats may act as a barrier to movement for the Neosho sub-species. In fact, when the pool level of Grand Lake rose 3.1 m in spring 2017 and flooded the lower 1.7 km of Buffalo Creek, all three tagged fish in the affected area moved just far enough upstream to remain in lotic habitat. The avoidance of lentic habitat by the sub-species is further supported by the high degree of genetic uniqueness within smaller stream populations, particularly those draining directly into impoundments (Gunn et al., 2020; Taylor et al., 2018). Some mixing of genetics with the Tennessee strain of northern smallmouth bass is evident in the Elk River catchment and thought to be related to angler movement of fish to Grand Lake (Gunn et al., 2020; Taylor et al., 2018). The Neosho sub-species is not known to have established fisheries in impoundments within their native range (Stark & Echelle, 1998), which has led to angler pressure to stock non-native smallmouth bass in reservoir habitats (Boxrucker et al., 2004). The reasons for this seeming avoidance of lentic habitat in Grand Lake are unclear, but other populations of fluvial-specialist basses have shown similar behaviours (e.g., Williams & Burgess, 1999). Interestingly, smallmouth bass use both lotic and lentic habitats in many natural river–lake systems (Barthel et al., 2008; Gerber &

Haynes, 1988; Webster, 1954). The authors did observe some movement between connected riverine systems, as three tagged fish moved between Elk River and Buffalo Creek when reservoir levels were low and there was flowing water at the confluence. In addition, one fish from Sycamore Creek used tributary habitat in Brush Creek from August to November 2017. Inter-tributary movements have been noted for smallmouth bass in several other studies (e.g., Langhurst & Schoenike, 1990; Lyons & Kanehl, 2002; VanArnum et al., 2004).

The authors observed seasonal and stream-specific patterns in habitat use by smallmouth bass that were largely consistent with known habitat preferences of the nominal species and intergrades, though a lack of quantitative availability data limits their interpretation of these findings. Temperature use followed expected seasonal patterns, though was often moderate relative to seasonal extremes in summer and winter. This could reflect fish movement, which often serves a thermoregulatory purpose in riverine smallmouth bass (Westhoff et al., 2016). The authors observed fish using deeper-water habitats during winter, regardless of stream size. Use of deeper water during winter is consistently reported for smallmouth bass populations (Ettinger-Dietzel et al., 2016; Lyons & Kanehl, 2002; Munther, 1970). Tagged fish in Buffalo Creek used deeper habitats compared to tagged fish in the other study streams. This pattern may relate to several factors: (a) the availability of deeper water, (b) the association of pools with thermal refugia at a patch scale that the authors did not measure and (c) the regular disconnection of surface flows during the summer and autumn seasons in small Ozark streams like Buffalo Creek (Hafs et al., 2010; Martin, 2017). In addition, depth and velocity often covary in streams (i.e., deeper water often reflects slower pool habitats; Rabeni & Jacobson, 1993). Use of low-velocity habitats in autumn is likely important for conserving energy before the overwinter period when fish subsist primarily on accumulated energy stores (Coble, 1975). Velocity use by tagged smallmouth bass was greatest in the largest river (Elk River), which is generally wider and faster than the smaller streams the authors studied. This result may reflect that smallmouth bass were more often associated with run habitats (19.5% of observations) in the Elk River than in the other streams. Although pool use predominated in all streams and seasons, this pattern was especially pronounced in the smaller streams during summer, autumn and winter. Pool use is frequently reported for riverine smallmouth bass, and the near-exclusive use of these habitats in summer and autumn may additionally be driven by the lack of other wetted habitat types in these seasons (Hafs et al., 2010; Martin, 2017). Use of gravel substrates increased in spring, consistent with the reproductive period and known spawning habitat preferences (Dauwalter & Fisher, 2007; Miller & Brewer, 2021). The authors also observed many tagged fish not associated with cover, which seems to be common among adult smallmouth bass (Lyons & Kanehl, 2002; Todd & Rabeni, 1989). Cover used by tagged fish in this study did not appear to differ among seasons, in contrast to previous studies (Ettinger-Dietzel et al., 2016; Todd & Rabeni, 1989).

One potential factor complicating this study was the high loss of transmitters by tagged fish. Transmitter loss may arise because of mortality of tagged individuals, stress-related expulsion or poor tagging practices (Jepsen et al., 2002). Natural mortality may explain some of the lost transmitters, as tag loss peaked when natural mortality was expected to be greatest (i.e., summer and winter; Dauwalter & Fisher, 2008; Hurst, 2007) and several recovered tags showed signs of predation (e.g., North American river otter Lontra canadensis Schreber 1777 and avian predators). Tagged fish were c. 4 years or older based on regional length-at-age curves, which, combined with a maximum observed age of 6 years in other small Ozark streams and 10 years in Elk River (Brewer & Long, 2015), may explain the high rate of transmitter loss. Angling can greatly reduce numbers of tagged fish (Westhoff et al., 2016), and several of fish were caught during the study, with at least one tagged fish harvested (the transmitter was returned). Several anglers encountered while tracking mentioned catching and releasing tagged bass, suggesting post-release mortality may have occurred because of angling throughout this study. On two occasions, the authors tracked fish to anglers' stringers and convinced the angler to release the fish; in both instances, the expelled transmitter was located during the following tracking period. As most tag loss occurred several months after tagging surgeries, the authors are confident that surgical technique was not the underlying cause of transmitter loss. Premature transmitter failure may have also played a role in the apparent loss of tagged fish, including those that were never relocated following initial tagging. The main complication of transmitter loss was the lower number of tagged smallmouth bass with sufficient observations to evaluate home range size, though the authors have ample observations from many individuals for classifying movement and habitat (Otis & White, 1999; White & Garrott, 1990). Transmitter loss had a lesser effect on the analysis of movement rate and habitat use because each observation was treated as a unique response (i.e., with the individual fish treated as a random effect). Transmitter failure may also have contributed to some tagged individuals never being relocated.

Accounting for fish movements is essential for determining appropriate scales for effective conservation and management and can help balance other management concerns. Movement data provide insight into the range of habitats needed for the completion of the life cycle and the corridors that connect these habitats (i.e., the functional habitat unit; Cooke et al., 2016; Schlosser, 1991; Thurow, 2016). Some individuals moved throughout most of the available riverine corridor, suggesting that efforts to mitigate connectivity loss are particularly important. Because fish in smaller streams move primarily during the spawning season and in response to higher discharge levels, limiting further alteration of the flow regime (e.g., groundwater pumping) could benefit small stream populations. Connectivity between the Elk River and Buffalo Creek populations could be increased by keeping Grand Lake pool levels low (i.e., ≤226 m) during winter and spring, where possible because of flood control limitations, thereby improving access to warmer main stem winter habitats and to a wider range of spawning habitats between the two systems. Such pool levels are typical in winter when precipitation is moderate but rare in the spring because of greater precipitation and seasonal flooding (https://www.swt-wc.usace.army.mil/charts/?monthly&proj=PENS).

Nonetheless, the role of connectivity for the management of smallmouth bass in Elk River and Buffalo Creek is complicated by the risk of introgressive hybridization (Gunn *et al.*, 2020; Taylor *et al.*, 2018). In contrast, the Sycamore Creek population of Neosho smallmouth bass is effectively isolated from other populations by Grand Lake, and shows very little introgression compared to larger, more-connected systems. The long-term consequences of this apparent population fragmentation are unclear. Balancing the protection of physical habitat conditions that allow native stream fish movement while minimizing the effects of non-native invasion or introgression is a difficult task, as management actions that benefit native species (*e.g.*, barrier removal) may also benefit non-native species (Rahel, 2007). Understanding how native smallmouth bass move within these modified river-reservoir systems is important for managing these genetically unique populations in an age of increasing human influence on the environment. Efforts to protect this narrow-range endemic could be valuable to scientists and managers dealing with similar issues (*e.g.*, endemism, hybridization, human alteration of the environment and scale of management), and strategies may be transferrable to other endemic black basses in the face of environmental change.

ORCID

Andrew D. Miller https://orcid.org/0000-0002-0076-9720
Shannon K. Brewer https://orcid.org/0000-0002-1537-3921

REFERENCES

Arnold, T. W. (2010). Uninformative parameters and model selection using Akaike's information criterion. *Journal of Wildlife Management*, 74, 1175–1178.

Bain, M. B. (1999). Substrate. In M. B. Bain & N. J. Stevenson (Eds.), *Aquatic habitat assessment: Common methods* (pp. 95–103). Bethesda, Maryland: American Fisheries Society.

Barthel, B. L., Cooke, S. J., Svec, J. H., Suski, C. D., Bunt, C. M., Phelan, F. J. S., & Philipp, D. P. (2008). Divergent life histories among smallmouth bass *Micropterus dolomieu* inhabiting a connected river-lake system. *Journal of Fish Biology*, 73, 829–852.

Bartoń, K. 2018. MuMIn: multi-model inference. R package version 1.40.4. Retrieved from https://cran.r-project.org/package=MuMIn

Bates, D., Maechler, M., Bolker, B., & Walker, S. (2015). Fitting linear mixed-effects models using lme4. *Journal of Statistical Software*, 67, 1–48.

Benitez, J.-P., & Ovidio, M. (2018). The influence of environmental factors on the upstream movements of rheophilic cyprinids according to their position in a river basin. *Ecology of Freshwater Fish*, 27, 660–671.

Birdsong, T. W., Allen, M. S., Claussen, J. E., Garrett, G. P., Grabowski, T. B., Graham, J., ... Tringali, M. D. (2015). Native black bass initiative: Implementing watershed-scale approaches to conservation of endemic black bass and other native fishes in the southern United States. In M. D. Tringali, J. M. Long, T. W. Birdsong, & M. S. Allen (Eds.), *Black bass diversity: Multidisciplinary science for conservation* (pp. 363–378). Bethesda, Maryland: American Fisheries Society.

Boxrucker, J., Echelle, A. A., & Van Den Bussche, R. A. (2004). *Determining the degree of hybridization in the smallmouth bass population of broken Bow reservoir and the mountain Fork River*. Oklahoma City, Oklahoma: Oklahoma Department of Wildlife Conservation, Final Report F-50-R, Project 19.

Bradford, M. J., & Heinonen, J. S. (2008). Low flows, instream flow needs and fish ecology in small streams. *Canadian Water Resources Journal*, 33, 165–180.

Brewer, S. K. (2011). Patterns in young-of-year Smallmouth Bass microhabitat use in multiple stream segments with contrasting land uses. *Fisheries Management and Ecology*, 18, 506–512.

Brewer, S. K. (2013). Groundwater influences on the distribution and abundance of riverine Smallmouth Bass, Micropterus dolomieu, in pasture landscapes of the midwestern USA. *River Research and Applications*, 29, 269–278.

Brewer, S. K., & Long, J. M. (2015). Biology and ecology of Neosho Smallmouth Bass and the genetically distinct Ouachita lineage. In M. D. Tringali, J. M. Long, T. W. Birdsong, & M. S. Allen (Eds.), *Black bass diversity: Multidisciplinary science for conservation* (pp. 281–296). Bethesda, Maryland: American Fisheries Society.

Bunnell, D. B., & Isely, J. J. (1999). Influence of temperature on mortality and retention of simulated transmitters in rainbow trout. *North American Journal of Fisheries Management*, 19, 152–154.

Chapman, B. B., Skov, C., Hulthén, K., Brodersen, J., Nilsson, P. A., Hansson, L.-A., & Brönmark, C. (2012). Partial migration in fishes: Definitions, methodologies, and taxonomic distribution. *Journal of Fish Biology*, 81, 479–499.

Coble, D. W. (1975). Smallmouth Bass. In H. Clepper (Ed.), *Black bass biology and management* (pp. 21–33). Washington D.C: Sport Fishing Institute.

Cooke, S. J., & Bunt, C. M. (2001). Assessment of internal and external antenna configurations of radio transmitters implanted in smallmouth bass. *North American Journal of Fisheries Management*, 21, 236–241.

Cooke, S. J., Martins, E. G., Struthers, D. P., Gutowsky, L. F. G., Power, M., Doka, S. E., ... Krueger, C. C. (2016). A moving target—Incorporating knowledge of the spatial ecology of fish into the assessment and management of freshwater fish populations. *Environmental Monitoring and Assessment*, 188, 239.

Dauwalter, D. C., & Fisher, W. L. (2007). Spawning chronology, nest site selection and nest success of smallmouth bass during benign streamflow conditions. *American Midland Naturalist*, 158, 60–78.

Dauwalter, D. C., & Fisher, W. L. (2008). Spatial and temporal patterns in stream habitat and smallmouth bass populations in eastern Oklahoma. *Transactions of the American Fisheries Society*, 137, 1072–1088.

Dormann, C. F., Elith, J., Bacher, S., Buchmann, C., Carl, G., Carré, G., ... Lautenbach, S. (2013). Collinearity: A review of methods to deal with it and a simulation study evaluating their performance. *Ecography*, 36, 27–46.

Ettinger-Dietzel, S. A., Dodd, H. R., Westhoff, J. T., & Siepker, M. J. (2016). Movement and habitat selection patterns of smallmouth bass

Micropterus dolomieu in an Ozark river. *Journal of Freshwater Ecology*, *31*, 61–75.

Fausch, K. D., Torgersen, C. E., Baxter, C. V., & Li, H. W. (2002). Landscapes to riverscapes: Bridging the gap between research and conservation of stream fishes. *Bioscience*, *52*, 483–498.

Frissell, C. A., Liss, W. J., Warren, C. E., & Hurley, M. D. (1986). A hierarchical framework for stream habitat classification: Viewing streams in a watershed context. *Environmental Management*, *10*, 199–214.

Gerber, G. P., & Haynes, J. M. (1988). Movements and behavior of Smallmouth Bass, Micropterus dolomieui, and rock Bass, Ambloplites rupestris, in southcentral Lake Ontario and two tributaries. *Journal of Freshwater Ecology*, *4*, 425–440.

Gordon, N. D., McMahon, T. A., Finlayson, B. L., Gippel, C. J., & Nathan, R. J. (2004). *Stream hydrology: An introduction for ecologists* (2nd ed.). Chichester, England: Wiley.

Gowan, C., Young, M. K., Fausch, K. D., & Riley, S. C. (1994). Restricted movement in resident stream salmonids: A paradigm lost? *Canadian Journal of Fisheries and Aquatic Sciences*, *51*, 2626–2637.

Graham, R. J., & Orth, D. J. (1986). Effects of temperature and streamflow on time and duration of spawning by Smallmouth Bass. *Transactions of the American Fisheries Society*, *115*, 693–702.

Gunn, J. C., Berkman, L. K., Koppelman, J., Taylor, A. T., Brewer, S., Long, J. M., & Eggert, L. S. (2020). Complex patterns of genetic and morphological differentiation in the Smallmouth Bass subspecies (*Micropterus dolomieu dolomieu* and *M. d. velox*) of the Central Interior Highlands. *Conservation Genetics*, *21*, 891–904.

Hafs, A. W., Gagen, C. J., & Whalen, J. K. (2010). Smallmouth Bass summer habitat use, movement, and survival in response to low flow in the Illinois Bayou, Arkansas. *North American Journal of Fisheries Management*, *30*, 604–612.

Heim, K. C., Steeves, M. E., McMahon, T. E., Ertel, B. D., & Koel, T. M. (2018). Quantifying uncertainty in aquatic telemetry: Using received signal strength to estimate telemetry error. *North American Journal of Fisheries Management*, *38*, 979–990.

Herbert, M. E., & Gelwick, F. P. (2003). Spatial variation of headwater fish assemblages explained by hydrologic variability and upstream effects of impoundment. *Copeia*, *2003*, 273–284.

Hill, J., & Grossman, G. D. (1987). Home range estimates for three North American stream fishes. *Copeia*, *1987*, 376–380.

Hubbs, C. L., & Bailey, R. M. (1940). *A revision of the black basses (Micropterus and Huro) with description of four new forms. Miscellaneous Publication 48, Museum of Zoology*. Ann Arbor, Michigan: University of Michigan.

Hurst, T. P. (2007). Causes and consequences of winter mortality in fishes. *Journal of Fish Biology*, *71*, 315–345.

Jepsen, N., Koed, A., Thorstad, E. B., & Baras, E. (2002). Surgical implantation of telemetry transmitters in fish: How much have we learned? *Hydrobiologia*, *483*, 239–248.

Koehn, J. D., Eiler, J. H., McKenzie, J. A., & O'Connor, W. G. (2012). An improved method for obtaining fine-scale location of radio tags when tracking by boat. In J. McKenzie, B. Parsons, A. C. Seitz, R. K. Kopf, M. Mesa, & Q. Phelps (Eds.), *Advances in fish tagging and marking technology* (pp. 379–384). Bethesda, Maryland: American Fisheries Society.

Kuechle, V. B., & Kuechle, P. J. (2012). Radio telemetry in fresh water: The basics. In N. S. Adams, J. W. Beeman, & J. H. Eiler (Eds.), *Telemetry techniques: A user guide for fisheries research* (pp. 91–137). Bethesda, Maryland: American Fisheries Society.

Langhurst, R. W., & Schoenike, D. L. (1990). Seasonal migration of smallmouth bass in the embarrass and wolf Rivers, Wisconsin. *North American Journal of Fisheries Management*, *10*, 224–227.

Leasure, D. R., Magoulick, D. D., & Longing, S. D. (2016). Natural flow regimes of the Ozark-Ouachita Interior Highlands region. *River Research and Applications*, *32*, 18–35.

Lucas, M. C., & Baras, E. (2001). *Migration of freshwater fishes*. Oxford, England: Blackwell.

Lyons, J., & Kanehl, P. (2002). Seasonal movements of smallmouth bass in streams. In D. P. Philipp & M. S. Ridgway (Eds.), *Black bass: Ecology, conservation, and management* (pp. 149–160). Bethesda, Maryland: American Fisheries Society.

MacRae, P. S. D., & Jackson, D. A. (2001). The influence of Smallmouth bass (*Micropterus dolomieu*) predation and habitat complexity on the structure of littoral zone fish assemblages. *Canadian Journal of Fisheries and Aquatic Sciences*, *58*, 342–351.

Martin, J. H. (2017). *Neosho Smallmouth Bass movement, spawning, and associated environmental conditions in a seasonally discontinuous stream: The Illinois Bayou, Arkansas*. MS thesis. Russellville, Arkansas: Arkansas Tech University.

McCune, B., & Grace, J. B. (2002). *Analysis of ecological communities*. Gleneden Beach, Oregon: MjM Software Design.

Miller, A. D., & Brewer, S. K. (2021). Riverscape nesting dynamics of Neosho Smallmouth Bass: To cluster or not to cluster? *Diversity and Distributions*, *27*, 1005–1018.

Munther, G. L. (1970). Movement and distribution of Smallmouth Bass in the middle Snake River. *Transactions of the American Fisheries Society*, *99*, 44–53.

Nagrodski, A., Raby, G. D., Hasler, C. T., Taylor, M. K., & Cooke, S. J. (2012). Fish stranding in freshwater systems: Sources, consequences, and mitigation. *Journal of Environmental Management*, *103*, 133–141.

Nakagawa, S., Johnson, P. C. D., & Schielzeth, H. (2017). The coefficient of determination R^2 and intra-class correlation coefficient from generalized linear mixed-effects models revisited and expanded. *Journal of the Royal Society Interface*, *14*, 20170213.

Nigh, T. A., and W. A. Schroeder. 2002. *Atlas of Missouri ecoregions*. Missouri Department of Conservation. Retrieved from https://www.nrc.gov/docs/ML0923/ML092360302.pdf

Otis, D. L., & White, G. C. (1999). Autocorrelation of location estimates and the analysis of radiotracking data. *Journal of Wildlife Management*, *63*, 1039–1044.

Pelicice, F. M., & Agostinho, A. A. (2008). Fish-passage facilities as ecological traps in large Neotropical rivers. *Conservation Biology*, *22*, 180–188.

Pelicice, F. M., Pompeu, P. S., & Agostinho, A. A. (2015). Large reservoirs as ecological barriers to downstream movements of Neotropical migratory fish. *Fish and Fisheries*, *16*, 697–715.

Pert, E. J., Orth, D. J., & Sabo, M. J. (2002). Lotic-dwelling age-0 smallmouth bass as both resource specialists and generalists: Reconciling disparate literature reports. In D. P. Philipp & M. S. Ridgway (Eds.), *Black bass: Ecology, conservation, and management* (pp. 185–190). Bethesda, Maryland: American Fisheries Society.

Peterson, J. T., & Rabeni, C. F. (1996). Natural thermal refugia for temperate warmwater stream fishes. *North American Journal of Fisheries Management*, *16*, 738–756.

Pörtner, H. O., & Peck, M. A. (2010). Climate change effects on fishes and fisheries: Towards a cause-and-effect understanding. *Journal of Fish Biology*, *77*, 1745–1779.

Power, M. E., Matthews, W. J., & Stewart, A. J. (1985). Grazing minnows, piscivorous bass, and stream algae: Dynamics of a strong interaction. *Ecology*, *66*, 1448–1456.

Probst, W. E., Rabeni, C. F., Covington, W. G., & Marteney, R. E. (1984). Resource use by stream-dwelling rock Bass and smallmouth bass. *Transactions of the American Fisheries Society*, *113*, 283–294.

Quinn, J., B. Wagner, and S. Filipek. 2004. Characteristics of black bass populations in the rivers and streams of Arkansas. Arkansas Game and Fish Commission, Stream Fisheries Program Report STP2004-01, Little Rock, Arkansas.

R Core Team. (2018). *R: A language and environment for statistical computing*. Vienna, Austria: R Foundation for Statistical Computing.

Rabeni, C. F., & Jacobson, R. B. (1993). The importance of fluvial hydraulics to fish-habitat restoration in low-gradient alluvial streams. *Freshwater Biology*, *29*, 211–220.

Radinger, J., Essl, F., Hölker, F., Horký, P., Slavík, O., & Wolter, C. (2017). The future distribution of river fish: The complex interplay of climate and land use changes, species dispersal and movement barriers. *Global Change Biology*, 23, 4970–4986.

Radinger, J., & Wolter, C. (2014). Patterns and predictors of fish dispersal in rivers. *Fish and Fisheries*, 15, 456–473.

Rahel, F. J. (2007). Biogeographic barriers, connectivity and homogenization of freshwater faunas: it's a small world after all. *Freshwater Biology*, 52, 696–710.

Rasmussen, J. E., & Belk, M. C. (2017). Individual movement of stream fishes: Linking ecological drivers with evolutionary processes. *Reviews in Fisheries Science & Aquaculture*, 25, 70–83.

Robbins, W. H., & MacCrimmon, H. R. (1977). Vital statistics and migratory patterns of a potamodromous stock of smallmouth bass, *Micropterus dolomieui*. *Journal of the Fisheries Research Board of Canada*, 34, 142–147.

Rodríguez, M. (2002). Restricted movement in stream fish: The paradigm is incomplete, not lost. *Ecology*, 83, 1–13.

Ross, M. J., & Kleiner, C. F. (1982). Shielded-needle technique for surgically implanting radio-frequency transmitters in fish. *The Progressive Fish-Culturist*, 44, 41–43.

Rubenson, E. S., & Olden, J. D. (2017). Dynamism in the upstream invasion edge of a freshwater fish exposes range boundary constraints. *Oecologia*, 184, 453–467.

Schall, M. K., Wertz, T., Smith, G. D., Blazer, V. S., & Wagner, T. (2019). Movement dynamics of Smallmouth Bass in a large river-tributary system. *Fisheries Management and Ecology*, 26, 590–599.

Schlosser, I. J. (1991). Stream fish ecology: A landscape perspective. *Bioscience*, 41, 704–712.

Schwarz, C. J., & Arnason, A. N. (1990). Use of tag-recovery information in migration and movement studies. In N. C. Parker, A. E. Giorgi, R. C. Heidinger, D. B. Jester, Jr., E. D. Prince, & G. A. Winans (Eds.), *Fish-marking techniques* (pp. 588–603). Bethesda, Maryland: American Fisheries Society.

Skalski, G. T., & Gilliam, J. F. (2000). Modeling diffusive spread in a heterogeneous population: A movement study with stream fish. *Ecology*, 81, 1685–1700.

Stark, W. J., & Echelle, A. A. (1998). Genetic structure and systematics of smallmouth bass, with emphasis on interior highlands populations. *Transactions of the American Fisheries Society*, 127, 393–416.

Strahler, A. N. (1952). Hypsometric (area–altitude) analysis of erosional topography. *Bulletin of the Geological Society of America*, 63, 1117–1142.

Sugiura, N. (1978). Further analysis of the data by Akaike's information criterion and the finite corrections. *Communications in Statistics: Theory and Methods*, 7, 13–26.

Taylor, A. T., Long, J. M., Schwemm, M. R., & Brewer, S. K. (2018). Hybridization and genetic structure of Neosho Smallmouth Bass in the Ozark highlands. *North American Journal of Fisheries Management*, 38, 1226–1240.

Taylor, A. T., Long, J. M., Tringali, M. D., & Barthel, B. L. (2019). Conservation of black bass diversity: An emerging management paradigm. *Fisheries*, 44, 20–36.

Taylor, M. K., & Cooke, S. J. (2012). Meta-analyses of the effects of river flow on fish movement and activity. *Environmental Reviews*, 20, 211–219.

The Nature Conservancy, Ozarks Ecoregional Assessment Team. (2003). *Ozarks ecoregional conservation assessment*. Minneapolis, Minnesota: The Nature Conservancy Midwestern Resource Office.

Thorstad, E. B., Økland, F., & Heggberget, T. G. (2001). Are long term negative effects from external tags underestimated? – Fouling of an externally attached telemetry transmitter. *Journal of Fish Biology*, 59, 1092–1094.

Thurow, R. F. (2016). Life history of potamodromous fishes. In P. Morais & F. Daverat (Eds.), *An introduction to fish migration* (pp. 29–54). Boca Raton, Florida: CRC.

Todd, B. L., & Rabeni, C. F. (1989). Movement and habitat use by stream-dwelling smallmouth bass. *Transactions of the American Fisheries Society*, 118, 229–242.

US Fish and Wildlife Service. (2018). *2016 National Survey of fishing, hunting, and wildlife-associated recreation*. Washington, DC: US Department of the Interior and US Department of Commerce.

VanArnum, C. J., Buynak, G. L., & Ross, J. R. (2004). Movement of smallmouth bass in Elkhorn Creek, Kentucky. *North American Journal of Fisheries Management*, 24, 311–315.

Vokoun, J. C., & Rabeni, C. F. (2005). Variation in an annual movement cycle of Flathead catfish within and between two Missouri watersheds. *North American Journal of Fisheries Management*, 25, 563–572.

Vonesh, E. F., Chinchilli, V. P., & Pu, K. W. (1996). Goodness-of-fit in generalized nonlinear mixed-effects models. *Biometrics*, 52, 572–587.

Wagner, T., Hayes, D. B., & Bremigan, M. T. (2006). Accounting for multi-level data structures in fisheries data using mixed models. *Fisheries*, 31, 180–187.

Waldman, J., Wilson, K. A., Mather, M., & Snyder, N. P. (2016). A resilience approach can improve anadromous fish restoration. *Fisheries*, 41, 116–126.

Walsh, M. G., Bjorgo, K. A., & Isely, J. J. (2000). Effects of implantation method and temperature on mortality and loss of simulated transmitters in hybrid striped Bass. *Transactions of the American Fisheries Society*, 129, 539–544.

Warren, M. L., Jr. (2009). Centrarchid identification and natural history. In S. J. Cooke & D. P. Philipp (Eds.), *Centrarchid fishes: Diversity, biology, and conservation* (pp. 375–533). Chichester, England: Wiley.

Webster, D. A. (1954). *Smallmouth Bass, Micropterus dolomieui, in Cayuga Lake: Part I. Life history and environment*. Ithaca, New York: Cornell University Agricultural Experiment Station, Memoir 327.

Westhoff, J. T., Paukert, C., Ettinger-Dietzel, S., Dodd, H., & Siepker, M. (2016). Behavioral thermoregulation and bioenergetics of riverine smallmouth bass associated with ambient cold-period thermal refuge. *Ecology of Freshwater Fish*, 25, 72–85.

White, G. C., & Garrott, R. A. (1990). *Analysis of wildlife radio tracking data*. New York: Harcourt Brace Jovanovich.

Williams, J. D., & Burgess, G. H. (1999). A new species of bass, *Micropterus cataractae* (Teleostei: Centrarchidae), from the Apalachicola River basin in Alabama, Florida, and Georgia. *Bulletin of the Florida Museum of Natural History*, 42, 80–114.

Young, M. K. (1994). Mobility of Brown trout in south-central Wyoming streams. *Canadian Journal of Zoology*, 72, 2078–2083.

Zhou, Y., Fox, G. A., Miller, R. B., Mollenhauer, R., & Brewer, S. (2018). Groundwater flux estimation in streams: A thermal equilibrium approach. *Journal of Hydrology*, 561, 822–832.