

Home Range and Space Use Patterns of Flathead Catfish during the Summer–Fall Period in Two Missouri Streams

JASON C. VOKOUN^{1*}

Department of Fisheries and Wildlife Sciences, the School of
Natural Resources, University of Missouri, 302 Anheuser-Busch
Natural Resources Building, Columbia, Missouri 65211-7240, USA

CHARLES F. RABENI

U.S. Geological Survey, Missouri Cooperative Fish and Wildlife Research Unit,
University of Missouri, 302 Anheuser-Busch Natural Resources Building,
Columbia, Missouri 65211-7240, USA

Abstract.—Flathead catfish *Pylodictis olivaris* were radio-tracked in the Grand River and Cuivre River, Missouri, from late July until they moved to overwintering habitats in late October. Fish moved within a definable area, and although occasional long-distance movements occurred, the fish typically returned to the previously occupied area. Seasonal home range was calculated with the use of kernel density estimation, which can be interpreted as a probabilistic utilization distribution that documents the internal structure of the estimate by delineating portions of the range that was used a specified percentage of the time. A traditional linear range also was reported. Most flathead catfish (89%) had one 50% kernel-estimated core area, whereas 11% of the fish split their time between two core areas. Core areas were typically in the middle of the 90% kernel-estimated home range (58%), although several had core areas in upstream (26%) and downstream (16%) portions of the home range. Home-range size did not differ based on river, sex, or size and was highly variable among individuals. The median 95% kernel estimate was 1,085 m (range, 70–69,090 m) for all fish. The median 50% kernel-estimated core area was 135 m (10–2,260 m). The median linear range was 3,510 m (150–50,400 m). Fish pairs with core areas in the same and neighboring pools had static joint space use values of up to 49% (area of intersection index), indicating substantial overlap and use of the same area. However, all fish pairs had low dynamic joint space use values (<0.07; coefficient of association), indicating that fish pairs were temporally segregated, rarely occurring in the same location at the same time.

The extent to which fishes display home-range behavior reveals not only the space requirements of a species but also is an indication of the scale at which management rules, regulations, and habitat manipulation or restoration might best be implemented. It follows, then, that fisheries researchers are perpetually interested in the concept of home range and restricted movement in fishes (e.g., Gerking 1959; Lewis and Flickinger 1967; Berra and Gunning 1972; Grossman and Freeman 1987; Gowan et al. 1994; Minns 1995). Early definitions of home range were general and lacked objective quantifiers (e.g., Burt 1943). Recently, researchers of terrestrial species have included a

temporal component to their definitions of home range, such as “the extent of area with a defined probability of occurrence of an animal during a specified time period” (Kernohan et al. 2001:126). The inclusion of the temporal component was in response to increasing awareness that many organisms display variable space use and seasonally use different portions of their annual or lifetime range (Kernohan et al. 2001). This is particularly true of stream fishes, many, if not most of which move seasonally within watersheds to meet life requisites (Schlosser and Angermeier 1995; Lucas and Baras 2001; Fausch et al. 2002). Defining the extent of home range area using a probabilistic framework produces estimates of home range that do not place undue importance on relocations near the outer boundary and allows investigation of the internal structure (i.e., differential use) within the home range (Kernohan et al. 2001; Vokoun 2003a).

Because of the popularity of angling for flathead catfish *Pylodictis olivaris* (Fleener 1977; Quinn 1993) and the willingness of anglers to accept low

* Corresponding author: jason.vokoun@uconn.edu

¹ Present address: Department of Natural Resources Management and Engineering, University of Connecticut, W. B. Young Building, 1376 Storrs Road Unit 4087, Storrs, Connecticut 06269-4087, USA

Received April 14, 2004; accepted October 8, 2004
Published online April 6, 2005

catch rates given the opportunity to creel a few large fish (Mayhew 1969; Miranda and Frese 1987), an understanding of the space use of flathead catfish can provide needed ecological information to manage populations in a manner that will support the growth and development of trophy-sized fish. Flathead catfish are long-lived, top-carnivores in many lotic systems (Jackson 1999), and large fish are considered vulnerable to overharvest in at least the northern part of their range (Stauffer et al. 1996). Interest in catfish angling is increasing, as is the interest of fisheries biologists in actively managing catfish fisheries (Michaletz and Dillard 1999; Arterburn et al. 2002; Travniček 2004).

We chose the postspawn summer–fall period to examine extensive home-range data for flathead catfish for two reasons: because the flathead catfish we tracked defined this period with their behavior (see Vokoun and Rabeni *in press*) and because it is during this period that energetic resources are devoted primarily to somatic growth. Our objectives were to (1) use kernel density estimation to create estimates of home range that probabilistically described the internal structure of flathead catfish home range, (2) compare both absolute size and internal structure of their home ranges between rivers, sexes, and size-classes, and (3) provide quantitative measures of space-use sharing by neighboring individuals.

Study Sites

The Cuivre River is a seventh-order Mississippi River tributary draining 3,199 km². The channel is characterized by gravel and sand substrate and scoured pools and sporadic, well-defined riffles. The channel meanders but also follows valley walls along bluff lines, creating long, relatively uniform pools. Flathead catfish were collected for transmitter implantation from the river mouth to 50 river kilometers upstream near Troy, Missouri (Figure 1). The Grand River, an eighth-order Missouri River tributary draining 20,461 km², has a sinuous channel, meandering lateral pools, and few well-defined riffles. The channel is best-described as a regime reach, in contrast to the pool–riffle sequences predominant in the Cuivre River (Montgomery and Buffington 1993). Regime reaches are typical of higher-order rivers flowing in unconstrained valleys typified by sand and silt substrates constantly in a state of transport that results in a bedform regime of ripples, dunes, and antidunes (Knighton 1998). Fish from the Grand River were collected within the section from the mouth to 61

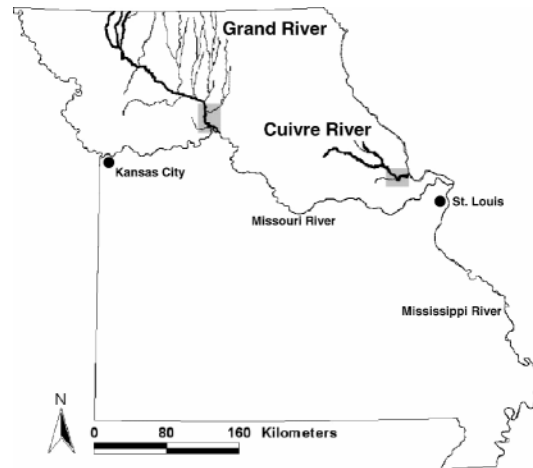


FIGURE 1.—Locations of the Grand River and Cuivre River basins within Missouri. Shaded rectangles highlight the main-stem study reaches in which flathead catfish were radio-tracked during the postspawn (summer–fall) period.

km upstream near Sumner, Missouri. Both streams are within the dissected till plains ecoregion (Hebrank 1989). Large woody debris constituted the predominant structural habitat feature for large fishes in both streams.

Methods

Fish collection and telemetry.—Flathead catfish were surgically implanted with radio transmitters during June and early July 2001 in the Grand River and during the same time period in 2002 in the Cuivre River. Fish were collected using unbaited hoop nets with front hoop diameters of 60 and 90 cm and bar meshes of 2.54, 3.75, and 5 cm. Fish selected for the project were at least 51 cm long (total length) and weighed at least 1.8 kg, a minimum size that was likely to include only sexually mature fish for study (Skains and Jackson 1995). Fish of this size are presumably age 5 or older (Jackson 1999).

Transmitters (Advanced Telemetry Systems Inc., Isanti, Minnesota) had a warranty battery life of 400 d. Surgeries were conducted on-site, and after being held for a 1-h recovery period in a water flow-through pen, fish were released into the pool from which they were captured. Data from the 2 weeks following implantation were not used in analyses to allow a recovery period and avoid potential effects of capture and surgery (Summerfelt 1972).

Fish were relocated from a boat approximately every 30-h on a staggered schedule (not all fish

were relocated at the same time) spanning Monday through Saturday. The schedule resulted in approximately even diel coverage per individual fish. The systematic sampling schedule was chosen to balance achieving independent relocations and the need to acquire enough relocations to facilitate estimation of the home range (Seaman et al. 1999; Kernohan et al. 2001; Vokoun 2003a). Severe weather, low stream stages, and occasional difficulty receiving Global Positioning System (GPS) signals necessitated some deviation from the 30 h staggered schedule. No fish was relocated within an elapsed time of less than 27 h. Blind tests of telemetry accuracy suggested that 95% of relocations were within 5 m of actual hidden transmitter locations, and 80% were within 2 m (Vokoun 2003b). Fish relocations recorded with GPS equipment were later differentially corrected to precisions of 0.68–1.4 m. Only individuals that remained in the Grand or Cuivre river main stems throughout the seasonal period were used in subsequent analyses.

Home range estimation.—Home ranges for individual flathead catfish for the postspawn summer–fall season (mid-July to mid-October) were calculated using two methods. Traditional linear range defined as the distance between the most upstream and most downstream relocation is reported to facilitate comparison with other metrics. The second method, kernel density estimation, is preferable to linear range because it reveals the internal structure of the home range, (i.e., areas of high and low use within the estimate; Vokoun 2003a). Important for accurate kernel density estimation of home range is the accumulation of relocations (Seaman et al. 1999). At least 30 relocations per individual were considered desirable in simulations performed by Vokoun (2003a). Following methods outlined in detail in Vokoun (2003a), we assigned fish relocations to the nearest 10-m point along a thalweg line created for each river (beginning with zero at the river mouth). We used the univariate distribution of relocation points along the thalweg line to calculate a fixed univariate kernel density estimate, defined as

$$\hat{f}(x) = \frac{1}{nh} \sum_{i=1}^n K\left(\frac{x - X_i}{h}\right),$$

where h is bandwidth and $K(x)$ is the Gaussian kernel function. Bandwidth selection was by the Sheather–Jones plug-in method (Jones et al. 1996). Kernel density estimates of home range are an integrated function that sums to 1, allowing inter-

pretation of the estimate as a utilization distribution (van Winkle 1975). A utilization distribution estimates the level of use or amount of time an individual was in a given location or portion of the home range (Worton 1989). Therefore, we reported the 95%, 90%, and 50% level-of-use kernel estimates delineating areas of the home range in which fish were estimated to have spent the respective percentage of the time during the study period. The 50% estimate has been referred to as a core area in other studies (Rodríguez-Robles 2003). The 95% and 90% level-of-use kernel estimates delineate larger portions of home range in which the fish was located throughout almost all of the study period (this includes the 50% use area).

Home range size comparisons.—Home range size estimates for individual flathead catfish were compared using three-way analysis of variance (ANOVA) with main effects of sex, river, and size-class. Sex was assigned to fish during surgical implantation of the radio transmitter. Because of the small size of the incision and recent spawning, we were unable to accurately identify the sex of some fish, and rather than making a larger incision than necessary, we recorded a third, unidentified sex category. River was either the Grand River or Cuivre River. Three size-classes were defined, based on relative stock density lengths evaluated by Quinn (1991): 510–709 mm (quality size), 710–859 mm (preferred size), and 860 mm or larger (memorable and trophy size). Separate ANOVA models were run for the linear range, 95% kernel, 90% kernel, and 50% kernel estimates of home range; each model included both the two-way and three-way interaction terms. Home range data were log-transformed to establish a normal distribution before analysis.

Joint space use calculations.—We calculated both a static and dynamic measure of joint space use between fish pairs with 50% kernel-estimated core areas in the same or neighboring pools. A static measure of joint space use between two animals does not consider temporal aspects of relocation data; in other words, space is considered jointly used if both animals used it at some point during the period of interest, even though they may have never cooccupied the same space at the same time. Dynamic measures of joint space use retain the temporal component of the relocations (Kernohan et al. 2001). For the static measure, we used a univariate version of the volume of intersection index (Seidel 1992) appropriate for the univariate utilization distributions we created for each flat-

head catfish. We termed our reduced index the area of intersection (AI) because it calculated the intersected area under two utilization distribution curves. The AI index is not a simple measure of home range overlap but, rather, a measure of the alignment of use intensity level at locations within the home range used by both individuals. The area of intersection index is given by the integral

$$AI = \int_{-\infty}^{\infty} \min[\hat{f}_1(x), \hat{f}_2(x)] dx,$$

where \hat{f}_1 = the utilization distribution for animal 1, \hat{f}_2 = the utilization distribution of animal 2, and d = the density or height of the distribution. Because the utilization distributions estimated by the kernel density estimation are functions integrated to 1, the AI index will range from 0 (no intersection) to 1 (indicates perfect intersection).

The dynamic measure of joint space use calculated was the coefficient of association (Cole 1949) defined as $2C/A + B$, where, during the period of interest, A = the number of times animal 1 was observed, B = the number of times animal 2 is observed, and C = the number of times animals 1 and 2 were found together. A coefficient of association exceeding 0.5 indicated association among an animal pair in other studies (see Kernohan et al. 2001).

Results

Fish implanted in the Grand River had a mean total length of 77.8 cm (range, 56.5–121.0 cm) and mean weight of 6.6 kg (1.8–21.2 kg); those in Cuivre River were 76.4 cm (55.5–113.0 cm) and 6.5 kg (1.9–20.9 kg). Angler exploitation and the variable annual migratory behavior of the implanted flathead catfish (see Vokoun and Rabeni *in press*) resulted in 13 individuals in the Grand River and 23 in the Cuivre River being used in our analyses.

Home range estimates using univariate kernel density estimation revealed attributes of the internal structure of utilization distributions during the summer–fall restricted movement period (Figure 2). The 95% and 90% kernel estimates represent alternative definitions of the outer home range boundary and are interpreted as the estimated portion of stream in which the flathead catfish spent 95% and 90% of the time during the late-July through late-October seasonal period. The 50% kernel estimate, which represents a length of stream used 50% of the time (typically situated near the middle of the 90% estimate), included 50% of individuals in the Grand River, 62.5% of

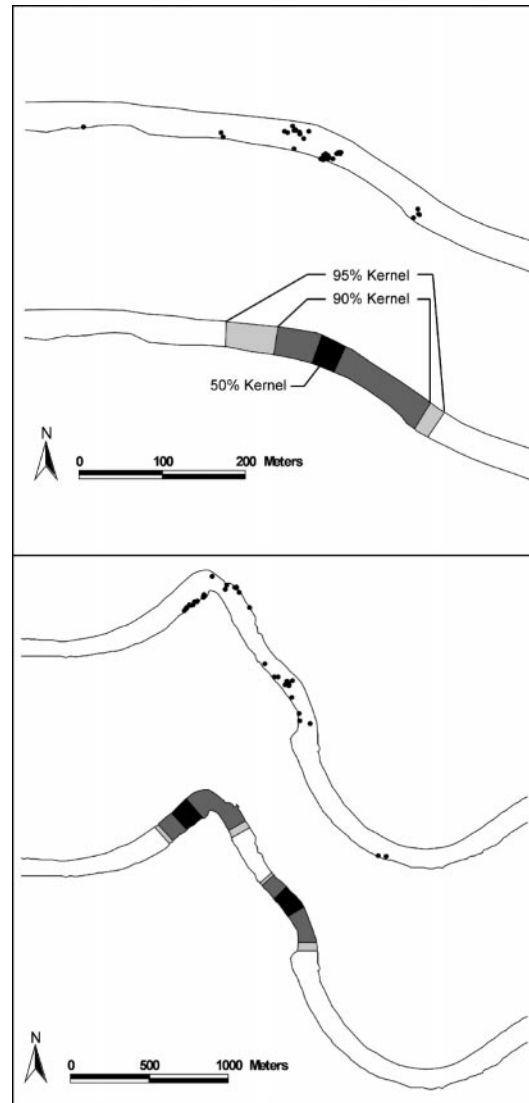


FIGURE 2.—Plan view of the distribution of relocation points and the extent of the 95%, 90%, and 50% kernel home-range estimates calculated from the relocation points for two flathead catfish. The fish in the upper panel had a continuous home range, whereas the fish in the bottom panel had a split home range during the study period. Kernel density home range estimates were univariate and calculated along the thalweg. The full width of the river is shaded for presentational clarity. Stream flow is left to right.

individuals in the Cuivre River, and 58% overall. Other individual fish had 50% estimates situated at or near the upstream end of the 90% estimate: Grand River = 28.5%, Cuivre River = 25%, and overall = 26.3%. Less frequent were fish with downstream 50% estimates: Grand River = 21.5%,

TABLE 1.—Median and range (in parentheses) of estimated linear home-range sizes for flathead catfish radio-tracked in the Grand and Cuivre rivers, Missouri, by river, sex, and size-class. Linear range is the distance between the most upstream and most downstream relocations. Kernel estimates are the 95%, 90%, and 50% levels of use produced by a univariate, fixed kernel density estimate that was calculated on all the distribution of relocations for each individual during the study period.

Variable	N	Linear range (m)	Kernel estimate (m)		
			95%	90%	50%
Cuivre River	23	2,380 (150–29,550)	790 (70–8,640)	720 (50–8,350)	130 (10–2,260)
Grand River	13	7,830 (750–50,400)	1,260 (380–69,090)	1,060 (80–32,860)	140 (20–500)
Male	12	1,425 (150–29,550)	880 (120–8,640)	740 (50–8,350)	110 (10–2,260)
Female	11	8,290 (750–28,970)	1,390 (420–4,910)	1,080 (250–4,910)	200 (40–2,070)
Unidentified sex	13	3,070 (160–50,400)	620 (70–69,090)	410 (70–32,860)	60 (10–500)
510–709 mm	19	1,630 (150–50,400)	790 (120–69,090)	720 (50–32,860)	50 (10–2,070)
710–859 mm	8	7,755 (590–28,970)	710 (70–7,900)	440 (70–6,760)	75 (10–350)
>859 mm	9	6,010 (1,240–29,550)	1,390 (240–8,640)	1,080 (220–8,350)	220 (50–2,260)
All Fish	36	3,510 (150–50,400)	1,085 (70–69,090)	845 (50–32,860)	135 (10–2,260)

Cuivre River = 12.5%, and overall = 15.7%. Most (89%) flathead catfish had a single 50% estimate, but 11% (4 fish: 1 of 13 in Grand River, 3 of 23 in Cuivre River) split their time between two core areas, all occupying an upstream area first and then a second disjointed downstream portion of the seasonal range.

Home-range size differed almost 1,000-fold among individuals (95% kernel estimate). Because our per-fish relocations (mean = 43.6, range = 31–51, collected as 4–5 relocations/week spread throughout the 24-h clock) exceeded minimal sample size recommendations, it was unlikely that the variability was methodological. Median home-range size for all fish was 1,085 m for the 95% kernel estimate, 845 m for the 90% estimate, and 135 m for the 50% estimate. Although the median home range size for these three kernel estimates decreased in size, as expected, the ranges overlapped (Table 1). Median traditional linear range was 3,510 m. Comparison of home-range sizes by sex, river, and size-class showed no significant differences for any category of flathead catfish (three-way ANOVA; all $P > 0.05$). There was some indication of a sex–river interaction in the 95% kernel home-range estimate ($F_{2,21} = 3.41$, $P = 0.052$), the 90% estimate ($F_{2,21} = 2.86$, $P = 0.079$), and the 50% estimate ($F_{2,21} = 3.31$, $P = 0.057$). This can be attributed to four individuals of unidentified sex in the Grand River, all of which had notably

large home ranges. Subsequent removal of all unidentified individuals ($N = 13$) from the data set resulted in no indication of a sex–river interaction (i.e., greater P -values in all cases).

Joint space use calculated using the static area of intersection index ranged from 0.0291 to 0.2051 over the study period for fish pairs with 50% kernel-estimated core areas in neighboring pools and from 0.1007 to 0.4939 for pairs with core areas in the same pool (Table 2). When including the temporal nature of the relocations over the same period, these same fish pairs had low dynamic coefficient of association values that ranged from 0.0 to 0.0208 for fish pairs with core areas in neighboring pools and from 0.0 to 0.0682 for fish pairs with core areas in the same pool (Table 2).

Discussion

The internal home-range structure of flathead catfish during the summer–fall postspawn period in the Grand and Cuivre rivers is difficult to compare with the home ranges reported in other studies because no other study used kernel density estimation. However, the internal structure of flathead home ranges we documented had some relevance to previous statements about the ecology of the species and should prove useful for future comparison. We found that 50% kernel estimates or core areas were most often found in the middle of the 90% estimate. This suggests that departures

TABLE 2.—Measures of joint space use for pairs of flathead catfish having 50% kernel-estimated core home-range areas in the same (S) and neighboring (N) pools of the Grand River (G) Cuivre River (C), Missouri. The area of intersection index is a static measure of joint space use based on the alignment of use intensity across the utilization distributions of two overlapping animals. The coefficient of association is a dynamic measure of joint space use based on how often animal pairs are located together; a value of 0.5 or greater indicates that animals are associated with each other.

Fish pair lengths (mm)	River	Location of home-range core areas	Area of intersection index	Coefficient of association
738; 651	G	S pool	0.4939	0.0294
911; 894	C	S pool	0.3759	0.0000
810; 738	G	S pool	0.3302	0.0682
810; 651	G	S pool	0.2704	0.0244
911; 640	C	S pool	0.2686	0.0215
894; 575	G	N pools	0.2051	0.0208
895; 640	C	S pool	0.1007	0.0000
731; 628	G	N pools	0.0963	0.0000
730; 566	C	N pools	0.0834	0.0256
750; 628	G	N pools	0.0684	0.0000
814; 703	C	N pools	0.0291	0.0000

from the core area were split between upstream and downstream movements. Several studies have reported a similar finding (Robinson 1977; Grace 1985; Skains 1992). We also found that most fish had one core area during the season, to which they regularly returned, even from long distance (up to 50 km) movements associated with sporadic thunderstorm-caused raises in river stage.

Not every catfish made long-distance movements during rises in water, and individual fish that did move did not move during every rise during our study. Flathead catfish are believed to have a sense of environmental recognition (Jackson 1999) and can home to previously used areas after experimental displacement in a reservoir (Hart and Summerfelt 1974). Lotic flathead catfish tracked by Skains (1992) had one to three home sites within the home range, calculated as specific point locations where fish were found greater than three times. Using that criteria, flathead catfish in both the Grand and Cuivre rivers had many more home sites; however, our sampling effort was approximately double that used in the Mississippi study, and the staggered tracking schedule probably provided greater opportunity to relocate individuals in more locations. Based on continuous diel movement paths for 6 of the 36 flathead catfish used in our study, individuals made short, discrete movements from one habitat feature (log complex, clay point, etc.) to another, resulting in 5–13 unique

locations being used and some revisitation of habitat features during the 24-h period (Vokoun 2003b). The four flathead catfish (11% of total) that had split core areas used the two portions sequentially, abandoning the first and establishing the second, and displayed similar movement patterns at both locations. This behavior has been noted in other lotic fish species and has been conceptualized in a home-range-shift conceptual model (Crook 2004).

The variability of home-range sizes found in the Grand and Cuivre rivers was inconsistent with other published studies. Flathead catfish radio-tracked in interior rivers of Mississippi had linear ranges that were less variable (480–1,850 m) than our linear range results (150–50,400 m). The overall median linear range of 3,510 m is higher than the median 865 m reported in Mississippi (Skains and Jackson 1995), although the median kernel-estimate for 95% of time spent home range (1,085 m) was much closer to the Mississippi results. Lentic flathead catfish tracked in Texas also had home ranges that varied less than our results (Weller and Winter 2001). Tag returns from the lower Mississippi River in Kentucky, Tennessee, and Mississippi, documented a maximum range of 6,000 m; however 17 of the 18 tag returns were within 1,000 m of the original tagging location (Pugh and Schramm 1999). In the Missouri River near St. Joseph, Missouri, 80% of tagged flathead catfish moved less than 5,000 m from the tagging location, but some fish moved considerable distances (maximum, 161,000 m) up tributary streams (Travnichek 2004). Reported movements of fish from the Minnesota River that were tagged and recaptured within the summer season ranged from 0 to 42,000 m from the original tagging location (Stauffer et al. 1996), a range of values more consistent with our findings in the Grand and Cuivre rivers. It should be noted, however, that we examined here data-intensive results of a single summer–fall season, but the same flathead catfish we radio-tracked displayed much greater annual movement distances and spatial life history diversity, as reported in Vokoun and Rabeni (*in press*).

Given the high variability of home-range sizes it was not surprising that no differences were found between rivers, sexes, and size-classes of flathead catfish for any kernel home-range estimate of use level or linear range. Linear range was also not different for flathead catfish in two rivers in Mississippi (Skains 1992). In one of these two rivers, flathead catfish with total lengths 710 mm or greater had a larger home range than fish 709 mm and

smaller; however, no such difference was found in the second river. In the Missouri River, Missouri, no home-range differences were found across fish sizes (Robinson 1977). The sex of lentic flathead catfish tracked by Weller and Winter (2001) did produce differences in home range size, similar to our findings in lotic systems.

Flathead catfish are reportedly solitary and aggressive to conspecifics in ponds (Hackney 1966; Swingle 1967). Although we had no knowledge of the locations of nonradiotagged individuals, six pairs of fish had core home-range areas in the same pools and five in neighboring pools. Joint space use among these fish was substantial, especially because the area of intersection index was calculated using kernel density-based utilization distributions, and is thus a measure of the alignment of use intensity and overlap along the linear stream distance used by both fish. This is preferable to a simple measure of linear overlap in which overlapping areas may or may not be areas that received heavy use by one, none, or both individuals (Kernohan et al. 2001). Using the classic ecological definition of a territory—a bounded area that is defended from conspecifics and occupied by a single individual or family group—these data suggest that flathead catfish in the Grand and Cuivre rivers did not display territorial behavior at the home-range scale. Multiple fish were occasionally found occupying the same habitat feature, making it unclear whether, or under what conditions, individuals in streams are aggressive towards one another. When fish jointly used an area, fish-pairs were highly segregated temporally, as measured by the coefficient of association. Therefore, although flathead catfish did use the same areas and even frequented the same habitat features within these areas, they did not occupy locations in association with nearby conspecifics. The combination of the area of intersection index and the coefficient of association explains and quantifies, rather well, the often-quoted statement of Pflieger (1997:212) that the flathead catfish “is a solitary species, and a single unit of cover, such as a drift pile, will usually yield only one or, at most two or three adults.”

Acknowledgments

We received assistance with fish collection, radio-tracking, and data entry from T. Guerrant, Z. Ford, C. Veneble, D. Lemons, M. Combes, A. Rettig, T. Seiler, S. Brewer, G. Pitchford, S. Banks, and M. Leach. Major financial support was provided by the Missouri Department of Conserva-

tion. This manuscript was improved with comments from P. Michaletz, K. Suedkamp-Wells, V. Travnichek, and two anonymous reviewers. This is a contribution of the Missouri Cooperative Fish and Wildlife Research Unit (supported by Biological Resources Division of the U.S. Geological Survey, University of Missouri, Missouri Department of Conservation, and Wildlife Management Institute).

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