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Spatial and temporal use of floodplain habitats by lentic and lotic species of aquatic turtles

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Abstract We investigated the use of aquatic and terrestrial floodplain habitats by lentic and lotic turtles inhabiting the Missouri River, a contemporary, regulated large river. Specifically, we tested whether habitats were used differentially by turtle species, sexes, and life stages over biologically determined spatial and temporal scales. We monitored female and male false map turtles (*Graptemys pseudogeographica*) and slider turtles (*Trachemys scripta*) for 14 months, using radiotelemetry. In addition, over a 3-year period we trapped *G. pseudogeographica* ($n=591$) and *T. scripta* ($n=129$) to supplement data on habitat use. Movements based on radiotelemetry and recaptures were summarized for each individual. Both species of turtles displayed dynamic annual activity patterns and used diverse habitats including those typically considered terrestrial. Although *G. pseudogeographica* and *T. scripta* spent a substantial portion of the year in the Missouri River (primarily in the cool months), newly created scour habitats also appeared to attract turtles during the cool season. However, in the warm months, habitat use became much more diverse, with turtles occupying all identified habitats including flooded agriculture and forest. Relative to their proportions, slough and scour habitats appeared to be highly favored while forests older than 4 years and agricultural habitats were proportionally less favored. We found few differences between species. However, males of both species were consistently more sedentary, used half as many habitats, and moved half as far from the river as did females, especially during May through July. Juveniles of both species were captured on average farther from the river than were adults, perhaps reflecting the close proximity of both nesting areas and shallow, productive habitats free

of aquatic predators. We estimate a riparian zone of 449 m that encompasses 95% of the population movements away from the river and discuss the quality of habitats important to reproduction and survival of lentic and lotic floodplain turtles. These spatial and temporal movement patterns, in light of their potential adaptive costs and benefits to *G. pseudogeographica* and *T. scripta*, are critical to understanding the ecology of long-lived vertebrates that depend on contemporary large rivers.

Key words Floodplain · Habitat use · Telemetry · Turtle · Buffer zone

Introduction

Over 60% of stream flow in the world is projected to be under human regulation by the year 2000 (Gore and Petts 1989). The majority of ecological effects from anthropic manipulation of rivers are related to: modifications of flow regime and water quality, the introduction of barriers, the isolation of rivers from their alluvial plain, loss of lotic surface area, and introduction of exotic species (Gore and Petts 1989). Of these six riverine stresses, all but the introduction of exotic species are related to habitat loss. Basic knowledge of both animal and plant species inhabiting large-river floodplains has largely gone ungathered because of the early and rapid loss of native aquatic and terrestrial floodplain habitats, difficulty of sampling, and lack of functional theory for large-river ecosystems (Johnson et al. 1995).

Among vertebrates that inhabit riverine systems, turtles are a pervasive group whose semi-aquatic behavior makes them especially important for understanding the link between aquatic and terrestrial habitats. Five of the seven freshwater turtle species federally listed in the United States as threatened or endangered are primarily riverine (U.S. Fish and Wildlife Service, Division of Endangered Species, 30 September 1998). Although all turtles use terrestrial habitats for some aspects of their life cycle, many riverine species (e.g., *Graptemys* spp.) are

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tied to specific aquatic conditions, and speciation is thought to have occurred in drainages just a few dozen kilometers apart (Ernst et al. 1994; Lamb et al. 1994). Freshwater turtle species typically inhabit both lentic and lotic habitats with generally stable hydroperiods. These aquatic habitats are used for basking, feeding, mating, and overwintering (Ernst et al. 1994). Males of most species rarely leave these habitats other than to emigrate, search for females, or overwinter terrestrially (Tuberville et al. 1996). Females may leave the wetland to emigrate, overwinter, and oviposit, which occurs once to several times a year (Gibbons et al. 1990). Hatchlings, after emergence from terrestrial nests, migrate to the wetland to feed, grow, and develop (Gibbons et al. 1990). Although referred to as freshwater dwellers, these turtles are actually semi-aquatic, often spending a critical portion of their life cycles on land for incubation, migration, or hibernation (Gibbons 1970; Burke and Gibbons 1995). Hence, riverine turtles depend directly on the quality of both aquatic and surrounding terrestrial habitats.

We investigated the use of aquatic and terrestrial floodplain habitats along the Missouri River, United States, by lentic and lotic turtles. Specifically, we tested whether habitats were used differentially by turtle species, sexes, and life stages over meaningful biological spatial and temporal scales. Analyses of movements provide an understanding of the potential impact of habitats on turtle life histories and also provide direct results for application to conservation and management of large-river floodplain habitats.

Materials and methods

Study area

Data were collected from a 1418-ha portion of the Missouri River and its floodplain in Cooper County (38°55'N, 92°30'W), located in central Missouri, United States (Bodie and Semlitsch 1998). The study area is within the channelized lower 32% (1212 km) of the Missouri River's length, with the middle 35% (1316 km) impounded and the upper 33% (1241 km) free-flowing (Schmulbach et al. 1992). The Missouri is the longest river in the United States (3768 km) and drains one-sixth (1.33×10^6 km²) of the area of the continental United States. Yet, modifications of the lower Missouri River for regulation and navigation have been extensive since 1838 (see Galat et al. 1996 for details of physical, chemical, biological, and social impacts). Our study area is centered within a 55-km length of the Missouri River in which floodplain forests and grasslands have mostly been eliminated, total water surface area has been reduced by 58% (a loss of 2645 ha), and major island complexes including sandbars have been reduced by 100% (a loss of 964 ha) since 1879 (Funk and Robinson 1974).

Despite these modifications, limited new-growth forest and a slough remain in our study area along the Missouri River (Bodie and Semlitsch 1998). Floodplain modifications over the last several decades have included an extensive levee system (Galat et al. 1996). On rare occasions when the Missouri River overtopped levees, scoured wetlands were created by concentrated flow through levee breaks, especially during extensive flooding in 1993 and 1995 (see Galat et al. 1997 for detailed scour descriptions). Scoured wetlands within our study area did not connect directly with the river during our study because they were formed away

from the river margin when cross levees failed. These wetlands were encircled with levees completely following 1993 and 1995, creating relatively deep pondlike habitats that hold water throughout the year. These isolated scours are likely to maintain pondlike processes as aquatic and terrestrial plants colonize wetland margins. Temporary flooding of forest and agriculture habitats occurs during the spring of some years. Hydroperiods of floodplain wetlands in the study area are tied to rainfall and to river stage through a groundwater connection with the Missouri River, with the slough directly connecting to the river and flowing at least annually, while all other wetlands maintain only an indirect connection through groundwater. Vegetative communities within the study area are dominated by active cropland (primary crops are corn, soybeans, and sunflowers), but also include relatively small abandoned agriculture patches 1–20 years old, which are dominated by early- to mid-successional mixed stands of eastern cottonwood (*Populus deltoides*), black willow (*Salix nigra*), and maple (various *Acer* spp.).

Radiotelemetry

Although modification and regulation of the Missouri River have altered the historic hydrologic vicissitude of floodplain wetlands and the river, fluctuation in rainfall and river stage still provide aquatic habitats with a wide range of characteristics. To capture this range of variability, we chose one aquatic turtle species generally associated with lotic habitats and another associated with lentic habitats. False map turtles (*Graptemys pseudogeographica*) inhabit rivers and their backwaters, while slider turtles (*Trachemys scripta*) prefer ponds or slow-moving waters (Ernst et al. 1994). Intraspecific habitat use is potentially different between sexes in some freshwater turtles (Moll and Legler 1971; Vogt 1980; Pluto and Bellis 1988); therefore, we additionally monitored both males and females within each species.

From 18 April to 20 June 1997, ten adult female and five adult male *G. pseudogeographica*, and seven adult female and four adult male *T. scripta* were captured, measured, marked, fitted with radiotransmitters, and released within 1–24 h. All turtles used for radiotelemetry were captured in the slough. Radiotransmitters (ATS Inc., Isanti, Minn., USA) were attached to the upper left posterior margin of the carapace of each turtle with aluminum machine screws, and plumber's epoxy was molded into the seams. Transmitter packages were <5% of each turtle's body mass. All individuals' transmitter frequencies were searched at least monthly until 18 May 1998, and locations were collected via verified fixes (within 3 m) with a Trimble global positioning system (GPS) differentially corrected via fixed base station. Occasional long-range (>2 km) movements by some individuals required that techniques include searches by foot, all-terrain vehicle, boat, and helicopter with mounted antennae. All turtles were located in aquatic or inundated terrestrial habitats (i.e., the radiotelemetry data reflect only aquatic habitat use).

Habitat classification and telemetry analysis

Each telemetry location was overlaid onto a rectified scanned image of a 1996 true-color aerial photograph (scale 1:21,000) of the study area using IMAGINE (ERDAS, Inc., Atlanta, Ga., USA) and ARC/VIEW (Environmental Systems Research Institute, Inc., Redlands, Calif., USA) geographic information system (GIS) software. Comparisons of the underlaid image with field observations indicated that telemetry location displacement was generally <1 m.

Floodplain habitats within the study area were surveyed during 1997–1998 to determine broad habitat types. Seven habitat types were identified: levee (\approx 2-m-high linear earthen embankment rarely breached, and following Missouri River bank stabilization in the 1940s, inundated by floodwater only in 1993), agriculture (land actively farmed at least one season from 1995 through 1997 and annually inundated in discrete to continuous patches), forest

<4 years old (forest patch dominated by sapling cottonwood and willow, inundated less than annually), forest >4 years old (forest patch dominated by mid-successional cottonwood, willow, and maple, inundated less than annually), slough (linear aquatic habitat that connected to the river and dried at least once annually), scour (pond-like aquatic patches of various ages formed through concentrated flow through levee breaks), and river (Missouri River proper with shoreline distinguished by rock stabilization structures).

The perimeter of each landscape element belonging to one of the seven habitat types was digitized into a GIS using the rectified image of the study-area photograph as a template. The proportion of the study area composed of each habitat was calculated using the ARC/VIEW area function. The boundaries of the study area used for habitat proportions were defined to the northeast by a steep limestone bluff and to the northwest, southeast, and southwest by the most distal turtle radiotelemetry location in each direction (Bodie and Semlitsch 1998). Habitats beyond our study area are: to the southwest, 1276 ha of agricultural land bounded by a steep limestone bluff; and to the northwest and southeast, habitats similar in proportion to the study area. Each telemetry location was assigned to a habitat type using the ARC/VIEW feature-join function. Comparisons of the overlaid locations on the digitized habitat types corresponded with field observations. The distance of each telemetry location from the nearest point along the Missouri River boundary and the distance of each consecutive location for each individual was calculated using the ARC/VIEW length function. For each turtle, tracking duration (days), total number of habitats used, mean movement (m), total movement (m), maximum movement (m), mean distance to the river (m), and maximum distance to the river (m) were summarized by month and for the entire study period. Mean residence time per habitat was calculated by averaging total time (days) for two or more consecutive locations in the same habitat for each species. While we do not know whether an individual remained in a habitat between locations, at the very least we know that the habitat was important enough for repeated use.

In order to estimate temporal as well as spatial availability of each habitat type for freshwater turtle use, the area of each habitat was multiplied by the proportion of the tracking period (18 April 1997–18 May 1998) during which each habitat was in some part flooded, based on field observations at least every three weeks. For example, the river was available 100% of the time while agricultural land was flooded only 15% of the time. By adjusting the absolute area of each habitat by the percent of time each habitat was inundated, a more realistic measure of habitat availability for freshwater turtle use was obtained. Likewise, to adjust for uneven tracking effort over time, the number of locations was standardized by dividing the number of telemetry locations per habitat per month by the number of location attempts per month. Monthly Missouri River stage [in feet (1 foot=30 cm) above zero gage; U.S. Army Corps of Engineers, Kansas City, Mo., USA] at Boonville, Missouri (16 km from the study area) and maximum temperature (°C; National Climatic Data Center, Asheville, North Carolina, USA) at New Franklin, Missouri (17 km from the study area) were compared with seasonal movement patterns.

Captures

During March through August each year (1996–1998), all aquatic sites within the study area were trapped for turtles. The study area was sampled twice in 1996 and at least monthly during 1997 and 1998. We sampled sites with equal numbers of large hoop traps (1-m-diameter hoop, 5-cm mesh) and small hoop traps (0.60-m-diameter hoop, 2.5-cm mesh) alternating bait of fresh fish and canned sardines (see Gibbons 1990). Small and large traps were placed alternately in the water around the margin of each site at a density of ≈ 1 trap ha⁻¹ (i.e., a 4-ha site contained four traps). Additionally, we used a more passive drift-type trap composed of a 7.6-m-long net (3-cm mesh) stretched perpendicular to the shoreline with a hoop trap without bait (0.80-m-diameter hoop, 3-cm

mesh) fastened to the end of the net such that turtles swimming either direction along the shoreline would be led into the trap. Each site was trapped continuously for three nights. Sampling was most frequent in the slough (twice during 1996 and at least once monthly during 1997 and 1998), and was interspersed throughout each year for agriculture, scour, and river habitats (sampled at least three times annually during 1997 and 1998 only).

Each captured turtle was measured for plastron and carapace length, pre- and postcloacal tail length, and body mass. Individual captures were summarized for each habitat type by species, sex, and life stage (classification as juvenile or adult was determined by secondary sex characteristics; Ernst et al. 1994). For recaptured individuals, habitat changes between consecutive captures, time since first capture (days), total movement (m), mean distance to the river (m), and maximum distance to the river (m) were summarized for the 3-year sampling period. Proportion of total sampling effort within each habitat type was calculated for the entire sampling period (e.g., sampling of the slough represented 45% of total sampling effort).

Statistical analyses

We analyzed all data with SAS/STAT version 6.12 (SAS 1990). The effects of species and sex, and their interaction (species \times sex) on radiotelemetry variables (tracking duration, total number of habitats used, mean movement, total movement, maximum movement, mean distance to the river, and maximum distance to the river) and recapture variables (time since first capture, total movement, mean distance to the river, and maximum distance to the river), with body mass as a covariate, were analyzed on individuals with two-way analyses of covariance. We used the least-square means procedure to determine which pairs contributed to significant variables with more than two levels. Simple Pearson correlation analysis was performed on body mass and all continuous variables. For radiotelemetry data, differences in habitat use for each species and sex were determined using a log-likelihood contingency *G*-test (Zar 1974) with the null hypothesis that use was randomly distributed among all identified habitats. The “expected” distribution of locations was determined from the adjusted habitat availability variable discussed above. For capture data, differences in habitat association for each species, sex, and life stage were also determined using a log-likelihood contingency *G*-test with the null hypothesis that use was randomly distributed among trapped habitats (only agriculture, slough, scour, and river habitats were trapped; Zar 1974). The “expected” distribution of capture locations was determined in two ways: (1) based on the proportion of total sampling effort in each habitat type and (2) based on the proportion of capture in each habitat type for females and males combined (i.e., immatures versus adults). All continuous variables, with the exception of the *G*-test variables, were log₁₀ transformed to normalize parameters prior to analyses (Zar 1974). Seasonal trends for both species and sexes are presented by month for both radiotelemetry and recapture data but were not analyzed because of heterogeneity of sample sizes among months.

Results

Habitat use from radiotelemetry data

We successfully located turtles with transmitters 362 times out of 488 total attempts (i.e., 126 times during searches, transmitters either were not heard or were impossible to locate precisely). Of 26 individuals, 13 (50%) including representatives from each species and sex were followed until the end of the study (see Fig. 2 in Bodie and Semlitsch 1998). No turtle crossed the width (≈ 425 m) of the Missouri River. Females used sig-

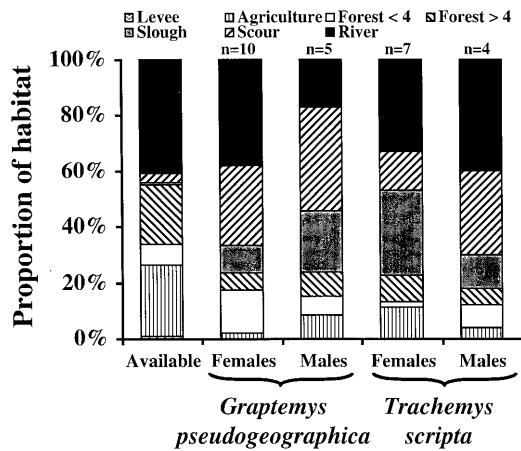


Fig. 1 Proportion of Missouri River floodplain habitat, adjusted for spatial and temporal availability, and habitat use by freshwater turtle species and sexes from radiotelemetry locations over 14 months. See Methods for an explanation of habitat types

nificantly more habitats ($F=5.88$, $df=1,21$, $P=0.03$) and had greater mean movement ($F=4.64$, $df=1,21$, $P=0.04$), mean total movement ($F=5.65$, $df=1,21$, $P=0.03$), and mean maximum movement ($F=10.40$, $df=1,21$, $P=0.004$) than males (Table 1). The effects of species and sex, and the species \times sex interaction on remaining variables (tracking duration, mean distance to the river, and maximum distance to the river) were nonsignificant (all $P\geq 0.07$; Table 1). However, the covariate effect of body mass on mean distance to the river was significant ($F=4.27$, $df=1,21$, $P=0.05$; Table 1). Correlation analysis revealed the relationship between body mass and mean distance to the river was significantly negative ($r=-0.40$,

$P=0.04$), indicating that small turtles were located farther from the river. Correlations between body mass and all other variables (tracking duration, total number of habitats used, mean movement, total movement, maximum movement, and maximum distance to the river) were nonsignificant (all $P\geq 0.12$).

Distribution of turtles among habitats was significantly nonrandom for both female ($G=90.54$, $df=6$, $P<0.001$) and male ($G=33.06$, $df=6$, $P<0.001$) *G. pseudogeographica* and for both female ($G=60.93$, $df=6$, $P<0.001$) and male ($G=28.97$, $df=6$, $P<0.001$) *T. scripta* (Fig. 1). Habitats used most were the river (*G. pseudogeographica* females and *T. scripta* females and males) and scours (*G. pseudogeographica* males) while habitats used least were agriculture (*G. pseudogeographica* females and *T. scripta* males) and forest <4 years old (*G. pseudogeographica* males and *T. scripta* females) even after adjustment for availability. During March through August, turtles used nearly all available habitats equally, in contrast to September through February, when most individuals used scour or river habitats solely (Fig. 2). Number of locations per habitat, adjusted for uneven tracking effort, showed a seasonal trend throughout the period for all species and sexes combined (Fig. 2). Residence time for both species and sexes was longest in scour and river habitats, with the exception of female *T. scripta*, which resided for very short times in all habitats (Fig. 3). Likewise, female and male mean distance to the river per month showed a seasonal trend (Fig. 4). Females of both species moved farther from the river from April through August during increasing temperature and decreasing river level and were relatively close to the river for the remaining months, whereas males showed little seasonal pattern (Fig. 4). Mean distance of monthly movement for

Table 1 Summary of radiotelemetry variables by freshwater turtle species and sexes^a

Variable	<i>Graptemys pseudogeographica</i>		<i>Trachemys scripta</i>		Species combined	
	Females	Males	Females	Males	Females	Males
Number of individuals	10	5	7	4	17	9
Mean turtle mass (g) ^b	1241.0 (353.4)	419.0 (325.0)	1109.3 (596.0)	1575.0 (518.8)	1186.8 (455.8)	932.8 (724.5)
Mean tracking duration (days)	306.0 (113.6)	186.0 (120.4)	300.0 (88.3)	270.0 (127.3)	303.4 (101.1)	222.0 (123.9)
Mean number of habitats used	3.9 (1.0)	2.4 (0.9)	4.1 (1.3)	3.3 (1.7)	4.0 ^c (1.1)	2.8 (1.3)
Mean movement (m)	386.7 (176.5)	364.8 (127.2)	427.6 (207.3)	151.8 (88.6)	403.5 ^d (184.6)	270.1 (153.8)
Mean total movement (m)	5151.8 (3149.0)	3752.6 (1476.5)	5652.3 (2372.5)	2126.5 (1809.5)	5357.9 ^d (2784.5)	3029.9 (1747.0)
Mean maximum movement (m)	1620.3 (763.4)	1204.8 (734.6)	2084.1 (937.4)	537.5 (306.1)	1811.3 ^c (844.2)	908.2 (654.7)
Mean distance to the river (m)	317.4 (212.8)	512.0 (327.7)	346.1 (149.8)	304.0 (167.4)	329.3 (184.7)	419.6 (276.1)
Mean maximum distance to river (m)	807.3 (392.5)	732.2 (371.1)	900.4 (324.3)	593.8 (271.2)	845.6 (358.2)	670.7 (319.1)

^a SDs in parentheses

^b Significant covariate on mean distance to the river

^c Females significantly greater than males at $P<0.01$

^d Females significantly greater than males at $P<0.05$

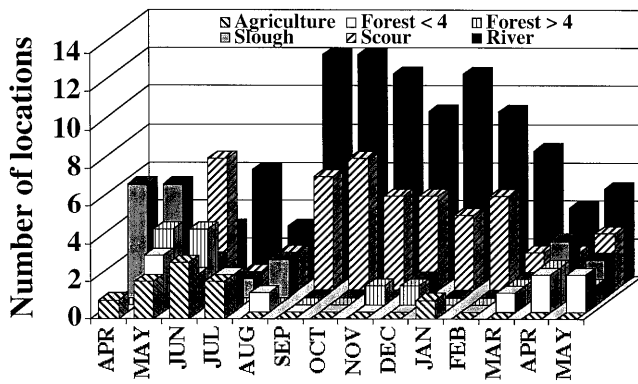


Fig. 2 Number of freshwater turtle radiotelemetry locations, adjusted for uneven tracking effort, by Missouri River floodplain habitats over 14 months. See Methods for an explanation of habitat types

both sexes of *G. pseudogeographica* and males of *T. scripta* was near zero from October to January during low temperature and low river stage, with only short movements by female *T. scripta* during that time.

The distances that these turtles moved from the river were normally distributed (test of normality for mean distance to the river by both species and sexes combined; $W=0.927$, $P=0.0720$). Therefore, by definition, the mean ($\bar{x}=360.5$ m) represents a distance encompassing only 50% of the populations' movements from the river. A riparian zone encompassing the majority [95% confidence limits= $\bar{x}\pm 2.06$ ($\alpha=0.05$, $df=25$) \times standard deviation/ \sqrt{n}] of the populations' mean movements from the river would have to encompass floodplain habitats 449.1 m from the river's edge.

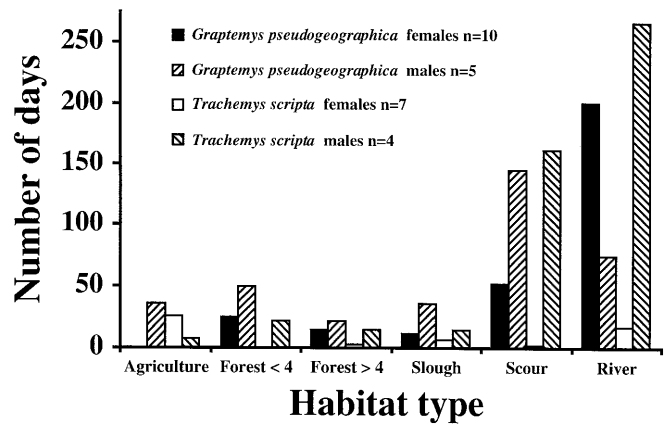


Fig. 3 Residence time (the number of consecutive radiotelemetry locations) within Missouri River floodplain habitats by freshwater turtle species and sexes over 14 months. See Methods for an explanation of habitat types

Habitat use from trapping data

We captured 591 individual *G. pseudogeographica* (142 females, 157 males, and 292 immatures) of which 49 were recaptured (7 females, 33 males, and 9 immatures), and 129 original *T. scripta* (41 females, 42 males, and 46 immatures) of which 17 were recaptured (9 females, 5 males, and 3 immatures; Table 2). Recaptures in different habitats from the original habitats of capture were proportionally higher for *G. pseudogeographica* (females, 57%; males, 47%; immatures, 33%) than for *T. scripta* (females, 33%; males, 40%; immatures, 0%; Table 2). Three individuals (all female *G. pseudogeographica*) were captured on maintained levee tops. There was a significant species \times sex in-

Table 2 Summary of recapture variables by freshwater turtle species, sexes and life stages^a

Variable	<i>Graptemys pseudogeographica</i>			<i>Trachemys scripta</i>		
	Females	Males	Immatures	Females	Males	Immatures
Number of individuals	7	33	9	9	5	3
Proportion that changed habitats between consecutive captures (%)	57	47	33	33	40	0
Mean turtle mass (g)	1250.0 (246.6)	218.1 (55.1)	149.8 (108.7)	1569.9 (830.4)	935.4 (340.8)	320.0 (105.4)
Mean time since first capture (days)	67.9 (27.8)	55.2 (33.1)	43.0 (22.2)	42.3 (30.3)	51.6 (41.9)	27.0 (24.8)
Mean total movement (m)	904.1 (432.4)	754.7 (709.4)	719.3 (569.0)	1270.7 (682.4)	769.8 (721.4)	621.0 (606.6)
Mean distance to the river (m)	680.8 (236.4)	581.5 (227.6)	683.0 ^b (270.0)	539.2 (205.8)	657.7 (221.8)	756.8 (311.0)
Mean maximum movement (m)	1620.3 (763.4)	1204.8 (734.6)	2084.1 (937.4)	537.5 (306.1)	1811.3 ^c (844.2)	908.2 (654.7)
Mean maximum distance to the river (m)	851.9 (216.6)	734.7 (247.1)	895.1 (219.6)	660.8 (250.7)	750.6 (218.6)	830.3 (259.9)
Mean maximum distance to river (m)	807.3 (216.6)	732.2 (247.1)	900.4 (219.6)	593.8 (250.7)	845.6 (218.6)	670.7 (259.9)

^a SDs in parentheses

^b Significantly farther from the river than *G. pseudogeographica* females and *T. scripta* females and males at $P<0.05$

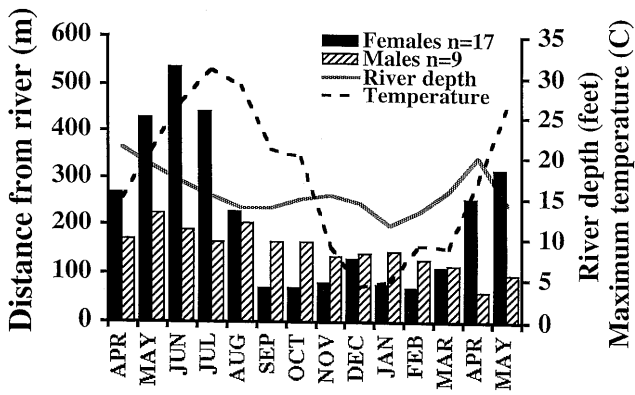


Fig. 4 Mean monthly distance to the Missouri River from radiotelemetry locations of freshwater turtle females and males, and mean monthly maximum temperature and river stage over 14 months

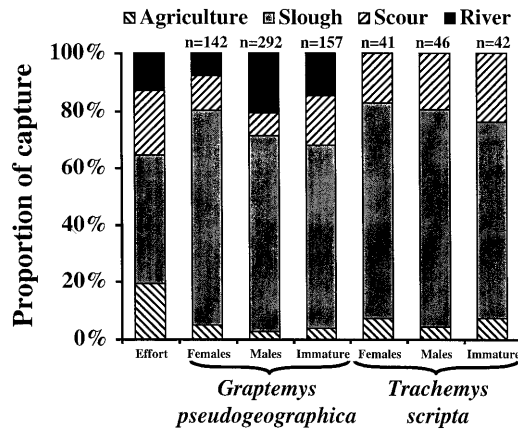


Fig. 5 Proportion of trapping effort and proportion of capture in Missouri River floodplain habitats by freshwater turtle species and sexes from recaptures over 1996–1998. See Methods for an explanation of habitat types

teraction for mean distance from the river ($F=3.62$, $df=2$, 59 , $P=0.03$; Table 2). *G. pseudogeographica* immatures were found significantly farther from the river than were *G. pseudogeographica* females and *T. scripta* females and males, contributing to the significant interaction term (all $P<0.05$; Table 2). Correlations between body mass and all recapture variables were nonsignificant (all $P\geq 0.15$).

Distribution of turtles among habitats sampled based on effort was significantly different for male *G. pseudogeographica* ($G=47.37$, $df=3$, $P<0.001$) and male *T. scripta* ($G=13.95$, $df=3$, $P=0.004$), but not for female ($G=3.17$, $df=3$, $P=0.35$) or immature ($G=2.98$, $df=3$, $P=0.40$) *G. pseudogeographica* and female ($G=6.55$, $df=3$, $P=0.09$) or immature ($G=5.50$, $df=3$, $P=0.11$) *T. scripta* (Fig. 5). Both sexes and life stages of *G. pseudogeographica* were captured most in slough and least in agriculture habitats, while both sexes and life stages of *T. scripta* were captured most in slough and least in the river habitats (Fig. 5). *T. scripta* were not captured in the Missouri River during the summer trapping period and

were captured proportionally more in scour habitats than were *G. pseudogeographica* (Fig. 5). Additionally, immature *G. pseudogeographica* were captured significantly more in scour and less in slough habitats than were adult *G. pseudogeographica* ($G=17.26$, $df=3$, $P<0.001$) while immature *T. scripta* did not differ from adult *T. scripta* ($G=6.10$, $df=3$, $P=0.11$).

Discussion

Patterns of habitat use

Our direct monitoring and multiple-habitat trapping of freshwater turtles showed two species with dynamic annual activity patterns and use of some habitats that were terrestrial for most of the year. Although *G. pseudogeographica* and *T. scripta* spent a substantial portion of the year in the river (primarily in the cool months of September through February), the newly created scour habitats also appeared to attract turtles during these cool months. However, in the warm months, habitat use became much more diverse, with turtles occupying all identified habitats including flooded agriculture and forest habitats. Relative to their proportions, slough and scour habitats appeared to be highly favored while forests older than 4 years and agricultural habitats were proportionally less favored. We found few differences between species, although *G. pseudogeographica* were more predictable in their seasonal activity patterns, with all movement occurring from January through September and no movement occurring from October through December. It is notable, however, that *T. scripta* were not found in the Missouri River by trapping methods during the summer months. Yet, they were found there numerous times using radiotelemetry, emphasizing the importance of multiple sampling techniques, including radiotelemetry, when describing habitat use by any animal. More differences were found between the sexes of both species. The most striking of these was that males were consistently more sedentary, used half as many habitats, and moved half as far from the river as did females, especially during May through July. Juveniles of both species were captured on average farther from the river than were adults, potentially reflecting the close proximity of both nesting areas and shallow productive habitats free of aquatic predators. These spatial and temporal movement patterns, in light of their potential adaptive costs and benefits to *G. pseudogeographica* and *T. scripta*, are critical to understanding the ecology of long-lived vertebrates that depend on contemporary large rivers.

The movements described herein generally are termed extrapopulational (*sensu* Gibbons et al. 1990), defined as (1) searches for habitats with seasonally available food; (2) migration to nesting habitats by females; (3) searches for mates by males; (4) migration to hibernation and estivation habitats; (5) migration from nests by hatchlings; and (6) emigration from unsuitable habitats. Seasonal floodplain wetlands are some of the most productive

freshwater habitats; hence, it is likely that turtles move en masse to these habitats from March through August to take advantage of the seasonal flush of productivity that is realized during these warmer months (Brinson et al. 1981). Additionally, because mortality of hatchling and juvenile turtles is high primarily due to their small size (Gibbons and Semlitsch 1982; Iverson 1991), pressure to grow rapidly may force turtles in these early life stages to seek seasonal wetlands with high food resources. These seasonal wetlands fill from precipitation or groundwater intrusion, therefore small turtles may benefit from a lack of fish predators in these sites, although bird predation may be high especially during bird migrations (Hart 1983; Congdon et al. 1992; Smith 1996). Migration of adult turtles among habitats for seasonally available resources has been described for *T. scripta* in Panama (Moll and Legler 1971) and for western pond turtles, *Clemmys marmorata* (Reese 1996), where in each case riverine individuals moved to connected marshes when these habitats were flooded. Likewise, lentic turtle species such as painted turtles, *Chrysemys picta* (Sexton 1959; Parker 1984) and spotted turtles, *Clemmys guttata* (Graham 1995) have been shown to migrate from permanent ponds or lakes to adjacent seasonal wetlands. Conversely, Moll (1990) found that adult mud turtles (*Kinosternon scorpioides*, *K. leucostomum*) moved into a stream from nearby ephemeral habitats that dried during the prolonged spring dry season. Vertebrates other than turtles also exploit seasonally available wetlands. Similar patterns of migration to vernal wetlands are found for feeding in waterfowl (Reid et al. 1989) and for spawning in fishes (Galat et al. 1998).

However, migration by females during May through July may also be related to searches for suitable nesting habitats. While aspects of nesting were not part of our study, three gravid *G. pseudogeographica*, all >1 km from the river, were captured on levee tops. These individuals were collected during May and June, which corresponds with the months when females of both species contain shelled eggs and are farthest from the river, suggesting that nesting habitats are also far from the river. In our study area, the levee is set back from the river to provide protection from flooding in the slough. Additionally, depredated nests were found solely on levees, despite searches for signs of depreciated nests throughout all habitats.

Mating in *G. pseudogeographica* and *T. scripta* occurs during warm periods within the cool months (September through March), but primarily during fall and spring (Cagle 1950; Vogt 1980). This mating time corresponds with the period of minimum movement and greatest residence time when both sexes were congregated in scours or in the river. In addition, no turtle was tracked even 25% of the way across the Missouri River, suggesting that turtle density could be high along the shoreline during hibernation. Vogt (1980) described similar hibernation patterns for *G. pseudogeographica* and for the Ouachita map turtle, *G. ouachitensis*, inhabiting the Mississippi River in Wisconsin. Therefore, mate

searches are probably localized within these habitats, benefitting males by reducing movements for the purpose of finding mates. This is in direct contrast to studies of lentic populations of *T. scripta*, *Chrysemys picta*, and striped mud turtles, *Kinosternon baurii*, in which most long-range movements are typical of males, and have been attributed to the potential for increased encounter rates, and consequently, mating events with females (Morreale et al. 1984; Gibbons 1986; Tuberville et al. 1996).

However, the trade-off for increasing mating potential in distant communal hibernation sites is that predation risk is increased during migration (Gibbons 1970) and substantial energy is devoted to migration (Congdon et al. 1982). Yet, migration was demonstrated by peak long-distance movements during fall and spring months when both species and sexes moved to and from scours or the Missouri River. These migrations may also be a necessity for avoiding freezing and desiccation that can occur in hydrologically unstable habitats (Bodie and Semlitsch, in press). Seasonal migration to aquatic hibernation sites also occurs with *C. picta* (Sexton 1959), *C. marmorata* (Reese 1996), and Blanding's turtle, *Emydoidea blandingii* (Butler and Graham 1995). Based upon comparisons of movement with average maximum air temperature, estivation by *G. pseudogeographica* was not evident. However, *T. scripta* movements steadily decreased as temperature rose during April through July, and sharply increased as temperature began dropping during August, possibly reflecting a temperature cue for migration. Migrations across the width of the Missouri River to floodplain habitats on the other side were not recorded in our study area. We were unable to determine if turtles do not cross the contemporary high-velocity river or if the quantity of floodplain habitats on the opposite side (55 ha), which is a small fraction (5%) of the amount of floodplain habitats in our study area (1064 ha), was not worth the energy expenditure and risk of predation.

Although hatchling migrations from nest to water were not directly observed in this study, we suggest that nests are placed far from the river, based on observations of females. This implication was corroborated by juveniles being significantly farther from the river on average than adults of both species and by body mass being negatively correlated with distance to the river (i.e., smaller turtles were farther from the river). Small, immature turtles typically do not migrate very long distances (Moll and Legler 1971; Bury 1972; Butler and Graham 1995; Reese 1996), and choose shallower habitats than do adults (Moll and Legler 1971; Pluto and Bellis 1988; Congdon et al. 1992) because immature turtles are more vulnerable to predation and lack energy reserves for long-distance travel. We also found that immature turtles of both species were more likely than adults to be located in the same habitat when recaptured, further suggesting that immature turtles move less than adults. While shallow habitats may provide abundant resources for juveniles, the risk of mortality due to desiccation and/or

freezing may be greatly increased, particularly in river floodplains that are regulated for navigation (Bodie and Semlitsch, in press).

Emigration from habitats that are unsuitable (e.g., Moll 1990) can be considered similar to emigrations from one habitat to another for finding food, nests, mates, and hibernation and estivation sites, each of which has been addressed above. The potential to dry for habitats such as seasonally available agriculture, forest, and sloughs likely forces adults to choose hydrologically stable habitats such as scours and the Missouri River for hibernation. Likewise, juveniles may choose shallow habitats to avoid predation and particularly flooding in the river, which because of the strong current can passively displace small turtles to unsuitable habitats (Moll and Legler 1971). However, floodplain wetlands with the highest frequency of flooding do support greater numbers of turtle species overall (Bodie et al. 1998).

Conservation and management implications

Freshwater turtles utilized all seven identified habitats in this large-river floodplain and can therefore provide lessons for conservation and management of river systems on both spatial and temporal scales. Spatially, annual movements by freshwater turtles spanned several kilometers of the river's length, bounded on one side by the river, which was not crossed, and on the other by a 449-m riparian zone encompassing 95% of the populations' movements. The amount of floodplain used was most likely reflective of the overall heterogeneity of habitat types near the Missouri River, because beyond this to the southwest of our study area is a relatively large, homogeneous agriculture patch bounded by a bluff. It is also important to note that radiotelemetry locations collected at least monthly are minimum estimates of movement and consequently, distances moved from the river should also be considered minimum. Therefore, the measured distances from the river likely underestimate the actual riparian zone needed to encompass 95% of the movements away from the river, so our riparian zone of 449 m is a minimum estimate. Alternatively, the riparian zone utilized by these freshwater turtles may simply reflect the available habitats within this portion of the Missouri River floodplain.

However, the quality of habitats included within the riparian zone is as important as, or more important than, the quantity. River sloughs or side channels appeared to be favored and should be targeted for floodplain conservation. Interestingly, newly created scour sites, which have been subjects of many floodplain land purchases by state and federal agencies since flooding in 1993 and 1995 (Galat et al. 1998), also attracted turtles and may be good surrogates for some of the diverse floodplain wetlands that have been converted to agriculture during the past 150 years. Both slough and scour habitats in general have also been shown to support high turtle species diversity among a gradient of floodplain wetland types (Bodie et al. 1998). However, scour wetlands with

a direct connection to the river are rapidly sedimenting and with time may become structurally very different.

The most striking feature of freshwater turtle floodplain use was the use of all available floodplain habitats, including flooded forest and agriculture. What is most important for management of these typically terrestrial habitats is that they are allowed to flood rather than being ditched and drained as happens elsewhere along the floodplain. Flooding of habitats in large-river floodplains is the key process responsible for their productivity (Junk et al. 1989) and is associated with increased turtle species richness (Bodie et al. 1998). The importance of seasonal floodplain wetlands also has been well documented for several species of fishes (reviewed in Galat et al. 1996) and many groups of birds including waterfowl, shorebirds, wading birds, and waterbirds (reviewed in Smith 1996).

Temporally, river and scour habitats were used almost exclusively during cool months while a diversity of habitats, especially more ephemeral ones, was used in warm months. However, juveniles may select shallow wetlands farther from the river for hibernation during cool months. Artificial decreases in river depth during mid-winter following the commercial navigation season may strand these small, young turtles without moisture and insulation from freezing temperatures. Bodie and Semlitsch (in press) showed that substantial mortality of small size and age classes of turtles occurs within shallow wetlands along the Missouri River floodplain during winter months. Therefore, while adults exclusively utilize river and scour habitats during cool months, juveniles occupy shallow wetlands, effectively making both the river and floodplain habitats that hold water important during this season.

Floodplain and wetland managers have very few data on which to base decisions for management of nongame wildlife such as turtles (Galat et al. 1998). Managers of these habitats must recognize the needs of organisms throughout their life cycles, both spatially and temporally. Organisms that utilize both aquatic and terrestrial habitats in dynamic river floodplains are particularly sensitive to alterations of the large-river system on nearly every level because reproductive success and survival are predicated on the availability of aquatic and terrestrial habitats throughout the year. We encourage further studies in other river systems that relate directly to management, particularly on organisms that depend solely on floodplain habitats.

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