# SPATIOTEMPORAL ECOLOGY OF *Apalone spinifera* in a Large, Great Plains River Ecosystem

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Abstract.—Sparse information exists about the ecology of Spiny Softshell Turtles (Apalone spinifera) in large rivers, at the northwestern extent of their natural range, and in Montana, where they are disjunct from downstream populations and a State Species of Concern. We determined spatiotemporal ecology of 47 female and 12 male turtles from 2009 through 2012 and identified fundamental habitats in the Missouri River in east-central Montana. Movement rates of females were greater than those of males and peaked before nesting. Movement rates of males peaked before overwintering, and movement rates of both sexes were minimal in winter. Home range sizes were not different between sexes, varied among individuals and seasons, and were similar to those reported elsewhere in their northern range. Turtles aggregated and showed interannual fidelity to separate and disparate habitats in different seasons. Turtles often chose fine substrates, tributary confluences, and reaches with islands during summer and mainstem outside bends in the winter. They inhabited shallow, slow water velocity areas from May to September. They inhabited deeper, moderate velocity areas from October to April. We did not observe ice jams and associated riverbed scour at hibernacula, but did observe them elsewhere. Ice jams may be spatially predictable and influence the distribution of riverine turtles during autumn and winter. Preservation of dissimilar habitats used during major portions of the life cycle (lateral habitats, islands, and hibernacula) and natural streamflow patterns, which influenced timing of habitat availability and turtle movement, may facilitate continued existence of Spiny Softshell Turtles in the Missouri River in Montana.

Key Words.—disjunct population; habitat selection; hibernacula; home range; ice dynamics; Missouri River; movement; Spiny Softshell Turtle

# INTRODUCTION

Large river ecosystems are dynamic and complex. Species in floodplain rivers often require multiple habitat types during their life history and thus exhibit morphological and behavioral adaptations to flourish in these highly variable systems. Aquatic turtles in particular probably use all major habitat types that occur in floodplain rivers during their life cycle (Leopold et al. 1964; Welcomme 1979). Turtles in large rivers use islands, offshore areas, and bars for feeding, thermoregulation, and nesting, and a reduction of these habitats could decrease annual survival and nesting success (Moll and Moll 2004; Barko and Briggler 2006). Large rivers are especially susceptible to anthropogenic disturbances such as dam operations (Funk and Robinson 1974; Graf 2006), managed flows (Tracy-Smith et al. 2012), and river channelization (Funk and Robinson 1974; Hesse et al. 1989).

Dams and dam operations can have varied effects on riverine turtles (reviewed by Moll and Moll 2004). Regulated downstream reaches of rivers in six ecoregions had less island and bar areas, fewer bars, less active floodplain areas, and less geomorphic complexity than upstream unregulated reaches (Graf 2006). Dams can influence growth rates (Snover et al. 2015), demography (Melancon et al. 2013), diets (Tucker et al. 2012), spatial ecology and genetics (Bennett et al. 2010), and nesting ecology (Riley et al. 2005) of riverine turtles. Dams convert lotic to lentic habitats, prevent migrations, fragment populations, and alter hydrologic cycles and geomorphology (Ward and Stanford 1983; Hesse et al. 1989), thereby changing the availability of riverine habitats (Sanford 2007; Bowen et al. 2003) and altering the dynamics of riverine ice. Altering, eliminating, or changing the locations of habitats important to the life cycles of riverine turtles may cause local population declines or extirpation.

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**FIGURE 1.** Study area for Spiny Softshell Turtles (*Apalone spinifera*) on the Missouri River in Montana, USA. Black circles represent the locations of remote telemetry stations and solid lines perpendicular to the river represent the locations of bridges. One remote telemetry station lies outside the Missouri River on the Judith River.

Spiny Softshell Turtles (Apalone spinifera; herein SSTs) are native to the east-central United States, west of the Appalachian Mountains, and south to the Gulf Coast and South Atlantic states; disjunct natural populations exist in Montana and elsewhere. Populations typically occur in rivers, the majority of which have been affected by dams, but also occur in lentic and ecotonal habitats (reviewed by Ernst and Lovich 2009). The ecology of this species has been studied in several regions of the United States and Canada, but in only two studies in the northern range. Both studies were conducted in lentic ecosystems on Lake Champlain in Québec, Canada, and Vermont, USA (45°N; Graham and Graham 1997; Galois et al. 2002). Moreover, the ecology and life history of SSTs have never been documented in large prairie or snowmelt-dominated floodplain-river ecosystems.

Overwintering of aquatic turtles at high latitudes can be prolonged and severe. Overwintering may be a particularly critical time for SSTs in large rivers at their northern range limit because they spend five to seven months overwintering (Werner et al. 2004; Ultsch 2006). Turtles in rivers often overwinter underwater in deep pools with flowing well-oxygenated water and fine substrates (Moll and Moll 2004; Ultsch 2006). Riverine turtles may inhabit such areas to avoid freezing and destructive ice scour (Scrimgeour et al. 1994), because they are intolerant of anoxia, and must avoid displacement from hibernacula during ice-breakupinduced flood events (Graham and Graham 1997; Reese et al. 2003; Ultsch 2006). Riverine ice dynamics can increase local current velocity and scour riparian areas, river channels, and riverbeds (Scrimgeour et al. 1994; Beltaos 2003) where SSTs overwinter; consequently, river-ice breakup may influence SST winter distribution and abundance. However, ice dynamics are rarely investigated as a potential factor influencing the distribution of hibernating riverine turtles.

Two disconnected SST populations occur in Montana; the Missouri River population occurs upstream of Fort Peck Reservoir, and the Yellowstone river population occurs above the confluence of the Missouri River. Both populations are isolated from downstream populations because the species is ostensibly absent in about 600 km of the Missouri River below Fort Peck Dam to the Missouri River near Bismarck, North Dakota (LeClere et al. 2009; Arnold Dood et al., unpubl. report). Spiny Softshells in the Missouri River in Montana may be vulnerable to declines or extirpation because they are isolated from downstream populations, are influenced by upstream dam operations, and are at the northern range limit of the species.

Variable discharge patterns, a short active season, and ice dynamics may influence movement and habitats of SSTs in large northern rivers. Our goal was to determine spatiotemporal patterns in SST movements and habitats and their relationships with natural factors and dam operations in a large northwestern Great Plains river. We investigated differences in SST movements and habitats between males and females, between years with varied annual river discharge, and among seasons. We also identified high-use habitat areas to guide river management decisions and conservation efforts.

#### MATERIALS AND METHODS

Study site.—Our study was conducted on 130 river kilometers (rkm) of the Missouri River above Fort Peck Reservoir in central Montana, USA, in the Upper Missouri River Breaks National Monument and Charles M. Russell National Wildlife Refuge. We selected this reach because it had the highest catch rates of SSTs in Montana in a 2004-2008 survey (Arnold Dood et al., unpubl. report). The reach extended from 10 rkm upstream of the Judith River confluence (rkm 3194; measured from the confluence with the Mississippi River) downstream to 20 rkm below the Fred Robinson Bridge (US Route 191; rkm 3093; Fig. 1). The river channel is largely canyon-bound by the Missouri Breaks, which are eroding bluffs of Judith and Fox-Hills sandstone transitioning to a wider valley with badlands of Bearpaw shale in the downstream reaches (Vuke et al. 2007). Channel-bottom substrate is largely gravel, cobble, and occasional boulders in the upper portion and predominately sand in the lower portion of the study site (Richards 2012). Numerous low-order intermittent or ephemeral tributaries enter the study area, and their confluences typically form lateral areas of near-lentic water when they are backwatered during high flows on the Missouri River.

Several hydroelectric dams affect the hydrology of the Missouri River in our study area, but three dams



**FIGURE 2**. Mean daily discharges in the Missouri River at the Fred Robinson Bridge near Landusky, Montana, USA, from 2010–2012.

(Canyon Ferry Dam on the Missouri River, Gibson Dam on the Sun River, and Tiber Dam on the Marias River) operated by the U.S. Bureau of Reclamation probably most influence streamflow and habitat (Michael Ramey et al., unpubl. report). Downstream of these dams, mean monthly discharge in spring has been reduced by an average of 28% and can be reduced by up to 53%; however, regulated discharge can be up to 55% higher than natural discharge in summer and autumn (Michael Ramey et al., unpubl. report; William Gardner and Casey Jensen, unpubl. report). Despite these alterations, the Missouri River in our study area is considerably less hydrologically altered than rivers that have been converted to lentic settings, have highly altered flows, are channelized, or a combination thereof (Pegg et al. 2003; Galat et al. 2005; Sanford 2007). Discharge patterns of the Missouri River differed substantially among 2010, 2011, and 2012 (Fig. 2) as judged by daily discharge data from the U.S. Geological Survey (USGS) flow gauge on the Missouri River at the Fred Robinson Bridge near Landusky, Montana. Median daily flow, maximum daily mean flow, and annual runoff were highest in 2011 and lowest 2012.

*Turtle capture and radio telemetry.*—We documented movement patterns of SSTs using radio telemetry. We captured turtles with hoop traps baited with dead fish in August 2009 (model TN330, Memphis Nets, Memphis, Tennessee, USA; Appendix). We weighed turtles, measured curved carapace length (CCL), determined sex (e.g., by tail length, presence of ocelli, or probe), and clasped Monel tags with distinct codes onto their carapace for identification. We used nylon-coated stainless steel wire to fit individually coded, 19.0 g (in air), external radio transmitters to selected turtles (model Lotek SR-M16-25; Lotek Wireless, Inc., Newmarket, Ontario, Canada; Appendix). Selection of SSTs for radio transmitter attachment was intentionally biased towards females and large size in both sexes to increase the probability of obtaining information on timing and location of nesting and to ensure that transmitter mass was < 10% of body mass (actual,  $\leq$  4% of body mass; Tornabene 2014). We equipped 12 male and 47 female SSTs with radio transmitters. We distributed radio transmitters evenly throughout the study site resulting in an average of about one radio transmitter per 1.6 rkm (Appendix).

We located turtles using a portable receiver (model SRX-400, Lotek Wireless Inc., Newmarket, Ontario, Canada) equipped with a boat-mounted, four-element Yagi antenna. From 2009 through 2012, at least eight field excursions of 7-10 d to locate telemetered SSTs occurred from each spring through autumn (May-September) and at least once each early spring (April) and late autumn (October or November). We determined precise point locations by passing the boat directly over or triangulating SSTs using a hand-held, three-element Yagi antenna. Point location accuracy, based on blind trials with transmitters, was  $\leq 10$  m. We deemed point locations approximate if SSTs could not be located within about 20 m because of obscured telemetry signals or inability to access the specific area (e.g., extensive mudflats or logiams). We recorded latitude and longitude of SST point locations using a hand-held Global Positioning System (Garmin GPS eTrex Legend, ± 15 m; Garmin Ltd., Olathe, Kansas, USA), converted these to river kilometer (rkm), and projected them onto 5-m orthoimagery using ArcMap version 10.0 (Esri, Redlands, California, USA). We recorded as aggregated two or more telemetered SSTs found within 50 m of each other. We documented macro- and microhabitat characteristics at each location. We recorded telemetered turtles that passed any of six remote radio telemetry stations managed by MTFWP (Fig. 1); stations included two four-element Yagi antennas that were connected to receivers and installed on riverbanks. We randomly selected only one telemetry fix per remote station per turtle per day in analyses to reduce autocorrelation and bias; some SSTs spent considerable time near remote stations.

We described locations of turtles as main channels, braided channels (channel segments with islands, bars, and multiple channels), lateral habitats, or outside bends (mainstem outside bends, with moderate depth and water velocity). Lateral habitats included tributaries confluences (ephemeral or intermittent streams that are generally backwatered, slow velocity, and near-lentic at the mouth), ephemeral side channels, backwaters, and floodplains. We described microhabitat characteristics by recording distance to each shore, depth, water velocity, and water temperature at each SST point location (Appendix). *Movement and home range.*—We calculated weekly movement rates for each SST by dividing the river distance (km) between sequential point locations (marked along the center of the river) by the number of weeks elapsed (White and Garrott 1990). We categorized the direction of movement as upstream or downstream. We calculated weekly movement rates (km/week) because two or more weeks typically elapsed between subsequent relocations. Movement rates represent minimum estimates because other movements could have occurred between sampling events (Rogers and White 2007).

We grouped movement rates and home ranges into four temporal periods differentiated by streamflow and thermal patterns. Spring began at river ice-off (early April), was characterized by increasing temperatures and streamflow, and continued until peak discharge (mid-June). Summer began immediately after peak discharge, continued to mid-September, and was characterized by decreasing streamflow and stable high water temperatures. Autumn extended from mid-September until the river was ice covered (mid-November) and was characterized by low discharge and decreasing water temperatures. Winter began when ice formed on the surface of the river and was characterized by the lowest water temperatures, and continued until the ice melted in early April. We typically calculated winter movement rates and home ranges from two points for each SST, the first just before ice formed and the second just after ice melted, because most of the study area was inaccessible during winter. Some winter movements may therefore have gone undetected.

We calculated linear home range (LHR) of each telemetered SST by subtracting its furthest downstream rkm location from its furthest upstream rkm location, both overall and by season. We added distances moved into tributaries to mainstem LHRs for SSTs (sensu Ouellette and Cardille 2011). We calculated areal home range (AHR) by multiplying the mean of main-channel river widths at point locations of each turtle, both overall and by season, by the corresponding LHR. We added mean tributary width multiplied by the maximum distance moved into each tributary to AHR for SSTs that were found in tributaries.

*Habitat selection.*—We evaluated habitat selection by SSTs at three different spatial scales. First, we classified geomorphic reach types as straight (with or without islands) or meander (with or without islands). Second, the habitat unit was classified as riffle or run (with or without islands). Third, we divided river bends mid-stream and classified bend type as inside or outside bend. We classified the entire 130-rkm study area using aerial imagery and field observations and conducted all spatial analyses with ArcMap. In our study area, the Missouri River is laterally confined by canyons and badlands and does not have a typical riffle-pool sequence. Instead, straight and meandering runs are present, both with and without islands and riffles. Small rapids occur sporadically where tributaries contribute gravel, cobble, or boulders to the mainstem.

We determined substrate selection by SSTs by comparing substrate at SST point locations to substrate availability in the study area (Richards 2012). We detected the predominant substrate by probing the river channel bottom at point locations (Bramblett and White 2001). We classified substrates as fine (clay, silt, sand, or a combination thereof; 0–4 mm in diameter), gravel (5–64 mm), or cobble (65–300 mm). We validated this method with blind tests in areas with known substrates.

To meet assumptions of habitat selection analyses and reduce bias, we randomly selected one point location for each SST for each month that it had an active transmitter for annual and seasonal selection analyses. We did not detect all SSTs every sampling occasion and the numbers of detections for individual animals were unequal. We considered habitats occupied directly before ice-on (autumn) and after ice-off (spring) as winter habitats. Moreover, we assumed that the availability of geomorphic reach types, habitat units, river bends, and substrates did not change throughout the duration of our study.

Ice dynamics.---We used remote cameras and river gauge data to determine if river-reach characteristics influenced occurrence of ice jamming and suitability as turtle hibernacula. We placed remote trail cameras (Moultrie, EBSCO Industries, Inc., Birmingham, Alabama, USA) at three SST hibernacula (identified using radio telemetry) and at three control reaches without telemetered overwintering SSTs where we expected active ice dynamics. Presence or absence of non-telemetered SSTs at control reaches was unknown. Control reaches were shallower with higher water velocities than hibernacula, and were located at river constrictions or below tributary confluences. Remote trail cameras had wide views of the river, typically from high vantage points, and took pictures every four hours November to April (or until batteries were drained) of 2010-2011 and 2011-2012. Two of the six cameras we deployed each winter malfunctioned or were lost because of eroding riverbanks or ice floes, one each at a hibernaculum and a control site. Cameras at two hibernacula and two control areas remained active in both years and the numbers of usable pictures and timeframes (November-April) were nearly equal among cameras. We counted days with complete ice cover among all cameras, freeze and thaw events, and ice jams and compared between years and between known hibernacula and control areas. We accessed river stage height data from November through April 2010–2011 and 2011–2012 from the U.S. Geological Service gauge on the Missouri River at the Fred Robinson Bridge near Landusky, Montana. We identified increases and decreases in stage height at the downstream flow gauge and attributed them to river-wide freeze and thaw events (observed with remote cameras) that occurred in the same time period (sensu Prowse 1986).

Statistical analyses.--We examined the normality of all variables using histograms, Q-Q plots, and Shapiro-Wilk tests. We examined homoscedasticity using Levene, Brown-Forsythe, or Bartlett's tests (Zar 1999). The majority of telemetry surveys occurred in April-November of 2010 and 2011. Telemetry surveys occurred only in August and November in 2009, and occurred only in April, May, and June of 2012, when just 28% (n = 16) of transmitters remained active. We compared variables between years with similar sampling intensity (2010 and 2011), between sexes (males and females), and among seasons (for home range, movement rates, and habitat selection) or months (for habitat characteristics). We did not compare home ranges and movement rates among months because they were calculated from sequential points sometimes separated by several months. We made habitat selection comparisons among years and seasons because of our interest in this temporal variation and limited statistical power for monthly comparisons.

We examined variables that were non-normal, heteroscedastic, had unequal group sample sizes, or a combination thereof using non-parametric tests; medians were used for these comparisons (Zar 1999). We used Mann-Whitney U-tests to compare movement rates, LHR, AHR, upstream and downstream movements, distance between spring-summer activity areas and hibernacula, and microhabitat characteristics between sexes and between years. We also used Mann-Whitney U-tests to compare monitoring period and number of telemetry fixes between sexes. We tested for correlations between monitoring duration and number of telemetry fixes, and monitoring duration and number of telemetry fixes and LHR and AHR with Spearman's rank correlation coefficients. We used Wilcoxon signedranked tests to compare paired depth, velocity, and temperature between thalweg (defined as the deepest point in a cross section of the river) and main channel measurements. We used Kruskal-Wallis (KW) one-way analysis of variance tests to compare movement rates, LHR, AHR, upstream and downstream movements, and microhabitat characteristics among seasons or months. We used linear regression to investigate the relationship between the number of SSTs in lateral habitats with river discharge. We conducted multiple comparisons following KW tests with pairwise Wilcoxon ranksum tests, or Dunn's multiple comparisons tests for movement rate comparisons (Jaeger et al. 2005), with Bonferroni's confidence interval adjustment (Zar 1999). We tested for population-level annual and seasonal selection of habitat types using Manly's resource selection function for design II on SST habitat-use data collected in situ and habitat-availability data derived from ArcMap (Manly et al. 2002). We also calculated selection ratios with 95% simultaneous Bonferroni confidence intervals for each comparison to identify preference (ratio greater than one) or avoidance (ratio less than one) of habitats and substrate types using program R and package adehabitat (Manly et al. 2002; Calenge 2006; Rogers and White 2007; R Development Core 2013). We conducted all analyses in R (v3.0.1) or SigmaPlot (v11; Systat Software, San Jose, California, USA). Statistical significance level for all analyses was  $\alpha = 0.05.$ 

#### RESULTS

**Radio telemetry.**—We obtained 1,269 telemetry fixes, with 801 precise hand fixes from boat or shore with associated habitat information, 174 approximate point locations, and 294 fixes from remote stations. Mean monitoring period of individual turtles was 721 d (range 37–1,064 d). Mean number of telemetry fixes per turtle was 23 (range 4–76) fixes. Median monitoring period and number of fixes did not differ between sexes (W = 174 and 182, P = 0.112 and 0.156). On an average excursion, 69% of turtles were located (range 46–90%).

Movement and home range.--Movement rates varied widely among individuals, between sexes, and among seasons. Median weekly movement rates were not significantly different between years 2010 and 2011 (W = 121210, P = 0.440), but varied between sexes (W = 333, P < 0.001) and among seasons (H = 134, df = 3, P < 0.001; Fig. 3). Median and maximum movement rates of females were higher than those of males during each season, especially during spring and summer. Median movement rates of females varied widely from spring through autumn, were highest in the summer (0.31 km/week) and lowest in the winter (0.00 km/week), and were similar between spring and autumn (0.06 km/week). Movement rates of males varied the most in summer (range 0.00-68.54 km/week) and were highest in autumn (median 0.09 km/week) and lowest in winter (median 0.00 km/week). Median upstream and downstream movements were not significantly different overall (W = 305880, P = 0.916), in years 2010 (W =74546, P = 0.826) or 2011 (W = 31210, P = 0.980), between sexes (downstream and upstream; W = 34282and 39168, P = 0.793 and 0.780), or among any seasons (W = 5915 - 96437, all P > 0.050).



**FIGURE 3.** Lognormal median weekly movements of 47 female and 11 male telemetered Spiny Softshell Turtles (*Apalone spinifera*) in the Missouri River in Montana, USA, 2009–2012, by season (Sp = spring, Su = summer, Au = autumn, and Wi = winter). Total weekly movement labels (y-axis) were back-transformed for clarity. Median weekly movement rates of seasons sharing the same letter are not significantly different from one another and those with different letters are significantly different from one another (P < 0.05).

Linear and areal home ranges (LHRs and AHRs) of both sexes were highly variable among individuals and different among seasons. Most (88%, n = 51) SSTs were located on both sides of the river and only seven (12%, n = 6 females and 1 male) were found exclusively on one side of the river, which justified our use of mean channel width to estimate AHR. Neither median LHR nor median AHR were different between years 2010 and 2011 (*W* = 1253 and 1131, *P* = 0.939 and 0.979) or between males and females (W = 231 and 251, P = 0.668and 0.976). Median LHR was 6.98 km (0.85-86.85 km) and median AHR was 1.01 km<sup>2</sup> (0.08-16.95 km<sup>2</sup>). Median LHR and median AHR were both different among seasons (H = 72.2 and 74.2, df = 3, P < 0.001), but trends were similar between the two home range estimators. Median LHR and median AHR were largest in summer (4.99 km and 0.73 km<sup>2</sup>) and smallest in winter (0.02 km and 0.01 km<sup>2</sup>). Median LHR differed among all seasons, but median AHR in spring and

autumn were similar. No correlation existed between monitoring duration or number of telemetry fixes and LHR ( $\rho = 0.050$  and 0.090, P = 0.712 and 0.226) or AHR ( $\rho = 0.067$  and 0.083, P = 0.618 and 0.541).

Most individual SSTs occupied and moved between different habitats from spring through summer (May-August) and autumn through winter (September-April) of each year. Some SSTs remained close to their original trapping locations, whereas others made sizeable movements upstream or downstream, or both, away from their initial location from spring through autumn of each year. We identified three common movement trends that were often small scale (< 2 km): (1) moving upstream during summer and downstream before winter each year, (2) moving downstream in summer and upstream before winter each year, or (3) a combination of the preceding two or vice versa in subsequent years. The majority of SSTs (81%, n = 42) generally made reciprocal movements each year from May through July, and August through September. Ten turtles (eight female and two male) moved more than 10 km (range 10.4-86.8 km) from May-July, typically immediately before or after peak streamflow.

Numbers of SSTs found in lateral habitats were positively related to discharge ( $F_{1,27} = 76.69, P < 0.001$ ,  $r^2 = 0.74$ ; Fig. 4) and generally increased from spring to summer and decreased thereafter in 2010 and 2011. Numbers of SSTs in lateral habitats in 2010 increased in May (17%), peaked in June (76%), and decreased in July (18%) and August (2%). However, numbers of SSTs in lateral habitats peaked earlier and in May (76%) in 2011. an above average discharge year, and then decreased from June (50%) to July (14.5%) and August (2%). Mean movement to reach these lateral habitats from the main channel was 2.24 km (range 0.02-54.59 km) by water. Mean absolute distance from the main channel to lateral habitats was 0.30 km (range 0.01-7.71 km). Hibernacula of individual SSTs were either consistently upstream (39%, n = 16) or downstream (43%, n = 18) of summer areas in both winters or varied between years



**FIGURE 4**. (A) Relationship between discharge and the percent of telemetered Spiny Softshell Turtle (*Apalone spinifera*; n = 58) in lateral habitats (i.e., tributary confluences, ephemeral side channels, and floodplain) and (B) temporal patterns of the percentage of telemetered *Apalone spinifera* (n = 58) in lateral habitats in the Missouri River in Montana, USA, from January 2010 to November 2011.

| TABLE 1. Summary statistics describing fidelity and homing to overwintering sites of telemetered Spiny Softshell Turtles (Apalone spinifera) |
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| in the Missouri River in Montana, USA, monitored for three consecutive years split into two rows (for 2010-2011, and 2011-2012) and any      |
| two consecutive years (Years = 2; i.e., 2009 and 2010, 2010 and 2011, or 2011 and 2012). Abbreviations and acronyms are n = number of        |
| turtles, Within 1 km describes the number and percentage of animals monitored that were within 1 km of their previous overwintering site,    |
| and Parsed describes, of those animals within 1 km of their previous site, the number and percentage of animals that were within 1 km, <     |
| 0.5 km, < 0.1 km, or < 0.05 km of their previous site. Range describes the minimum and maximum rkm distance between previous and             |
| subsequent overwintering sites.  |

|             |      |    | Within   |         | Par      | Range (rkm) |           |         |         |
|-------------|------|----|----------|---------|----------|-------------|-----------|---------|---------|
|             | Year | n  | 1 km     | < 1 km  | < 0.5 km | < 0.1 km    | < 0.05 km | Minimum | Maximum |
| 2010-2011   | 3    | 22 | 15 (68%) | 0 (0%)  | 3 (20%)  | 4 (27%)     | 8 (53%)   | 0.006   | 25.9    |
| 2011-2012   | 3    | 22 | 13 (59%) | 2 (15%) | 4 (31%)  | 3 (23%)     | 4 (31%)   | 0.010   | 22.7    |
| Either year | 2    | 19 | 11 (58%) | 1 (9%)  | 3 (27%)  | 1 (9%)      | 6 (55%)   | 0.010   | 7.7     |
| Total       |      |    | 39       | 3 (8%)  | 10 (26%) | 8 (20%)     | 18 (46%)  | 0.006   | 25.9    |

(19%, n = 8). Median distance between spring-summer habitats and hibernacula was variable (3.43 km; range 0.02–23.27 km) and did not differ between years 2010 and 2011 (W = 517, P = 0.923) or between males and females (W = 177, P = 0.329)

Interannual site fidelity and aggregation.— Individual SSTs inhabited and showed fidelity to tributaries in spring-summer and hibernacula in winter among years. We observed 60% (n = 34) of telemetered SSTs inhabiting at least one tributary during May to July of 2010–2012, and 32% (n = 18) inhabited a tributary in consecutive years. Thirteen SSTs (72%) occupied the same tributary in two consecutive years and two (11%) occupied the same tributary in three consecutive years; three SSTs (17%) inhabited different tributaries in consecutive years. Two larger tributaries were inhabited in May-July of all three years, and 13 unique tributaries were inhabited over the course of the study.

We observed 41 turtles before and after overwintering in more than one year, 19 for two years and 22 for three years (Table 1). Turtles occupied 38 unique (< 1 km river stretches) overwintering sites from 2010 through 2012. Several turtles hibernated close (e.g., 6 m) to their previous overwintering sites, whereas others hibernated considerable distances away (e.g., 25.9 km) in consecutive years. Turtles overwintered an average of 1.7 km (range < 0.05–25.90 km) from their previous hibernaculum in consecutive years. However, more than half 58% of SSTs we observed in consecutive years overwintered within one km of their previous location, often (46%) within 50 m of their previous location.

Telemetered SSTs aggregated, but some SSTs were initially trapped together when transmitters were attached. However, the percentage of instances of SSTs aggregating with SSTs they were not trapped with was higher (69%) than the percentage aggregating with SSTs they were trapped with (2%). The percentage of SSTs aggregating with both SSTs that they were and were not trapped was 29%. We detected aggregations with the same group of turtles multiple times in a season, but

only included one of those detections per unique group of turtles into aggregation analyses.

We observed 66 aggregations of two or more telemetered SSTs from October 2009 through June 2012. Median aggregation size was two and ranged from two to six SSTs, but aggregations including nontelemetered SSTs in tributaries exceeded 30 turtles. Turtles aggregated in different habitats at different times of the year, but generally used the same habitats at the same time of the year among years. We located unique aggregations in four general areas: in outside bends of the main channel at hibernacula (36%, n=24), in braided main channels (27%, n=18), in main channels other than at hibernacula (21%, n = 14), and in tributary confluences (15%, n = 10). Turtles aggregated in outside bends in the autumn and winter (November-April), in braided main channels and tributary confluences during the spring and early summer (May-July), and in nearshore main channels in summer (August-September; Fig. 5). However, the exact timing and progression of these events differed slightly among years. Fewer turtles remained in outside bends following overwintering in April of 2011 (36%) than in 2010 (60%), SSTs inhabited braided main channels earlier in 2011 (May-June) than in 2010 (June-July), and main channel aggregations did not persist in a unique location for a month or longer in any year. Fewer aggregations of telemetered SSTs were located in each habitat type in each subsequent year, probably as a result of attrition of transmitters throughout the study. Interannual fidelity (two or three years) of SST aggregations occurred at five hibernacula, two tributary confluences, two braided main-channel locations in island complexes downstream of a tributary, and one main-channel area (Fig. 5).

**Habitat selection.**—Habitat and substrate selection of telemetered SSTs were similar among years. Strong annual selection was observed in all years for substrate (P < 0.001) and bend type (P < 0.039), but no evidence of selection existed for geomorphic reach type (P < 0.294) or habitat unit (P < 0.232); Table 2 and Fig. 6).



**FIGURE 5**. Aggregations of two or more telemetered Spiny Softshell Turtles (*Apalone spinifera*) in the Missouri River in Montana, USA, October 2009 to June 2012, in four different habitat types. Solid lines connecting points indicate aggregations of turtles at specific sites in consecutive years.

Selection ratios less than one indicate a reach is used less than expected (avoidance), and values greater than one indicate a reach is used more than expected (preference). Turtles avoided cobble and chose fine substrates in 2010, 2011, and 2012 (selection ratios; cobble,  $< 0.2 \pm 0.0-0.1$  [SE]; fine,  $> 3.4 \pm 0.1-0.3$ ). Gravel was avoided in 2011 ( $0.6 \pm 0.1$ ) and 2012 ( $0.7 \pm 0.4$ ), but was used in proportion to its availability in 2010 ( $1.0 \pm 0.2$ ). Turtles avoided inside bends ( $0.6 \pm 0.1$ ) and chose outside bends in 2010 ( $1.3 \pm 0.1$ ), but were less selective in 2011 (0.9 and  $1.1 \pm 0.1$ ). Low sample sizes in 2012 precluded calculation of estimates of habitat selectivity for bend types and resulted in wide confidence intervals for estimates of selectivity of geomorphic reach types and habitat units.

We observed strong seasonal selection for substrate type in all seasons (P < 0.001) and for bend type in autumn (P < 0.001; Table 3 and Fig. 7). Only moderate evidence of seasonal selection existed for geomorphic reach type and habitat unit in spring, summer, and autumn (P < 0.001). Turtles had the highest preference for outside bends ( $1.5 \pm 0.1$ ) and the greatest avoidance

of inside bends in autumn  $(0.5 \pm 0.1)$ . Fine substrate was highly selected (>  $2.8 \pm 0.1$ –0.2) and cobble substrate was avoided (<  $0.2 \pm 0.0$ –0.1) in all seasons. Moderate preference was observed for riffles in the spring (1.6  $\pm 0.5$ ), but riffles were avoided in autumn ( $0.6 \pm 0.3$ ). Bends with islands were selected moderately in spring ( $1.5 \pm 0.3$ ) prior to the nesting season, whereas straight reaches without islands were avoided ( $0.6 \pm 0.2$ ). Gravel substrate was moderately selected in the summer and autumn (1.3 and  $1.9 \pm 0.3$  and 0.4), but strongly avoided in spring ( $0.3 \pm 0.2$ ).

**Microhabitat characteristics.**—Microhabitat characteristics at SST point locations did not differ between sexes (P>0.089; Table 4), but varied among years for delta depth (difference between depth at SST point locations and in the adjacent thalweg) and mean column velocity. Microhabitat characteristics also differed between point locations and the immediate thalweg (defined as the deepest point in a cross section of the river) or main channel, and varied regularly among months. Depth and velocity at point locations were lower than in adjacent

**TABLE 2.** Summary statistics for chi-square ( $\chi^2$ ) tests (including degrees of freedom, df, and *P* values) of annual overall habitat selection by telemetered Spiny Softshell Turtles (*Apalone spinifera*) monitored in the Missouri River in Montana, USA, 2010–2012. Bold font indicates statistical significance of  $P \le 0.05$ .

|                       | 2010     |     |         |          | 2011 |         | 2012     |    |         |
|-----------------------|----------|-----|---------|----------|------|---------|----------|----|---------|
|                       | $\chi^2$ | df  | Р       | $\chi^2$ | df   | Р       | $\chi^2$ | df | Р       |
| Bend type             | 92.0     | 54  | < 0.001 | 59.4     | 42   | 0.039   |          |    |         |
| Habitat unit          | 308.9    | 108 | < 0.001 | 193.1    | 84   | < 0.001 | 16.3     | 14 | 0.294   |
| Geomorphic reach type | 520.7    | 162 | < 0.001 | 327.4    | 126  | < 0.001 | 25.4     | 21 | 0.232   |
| Substrate type        | 447.3    | 100 | < 0.001 | 479.0    | 92   | < 0.001 | 96.8     | 40 | < 0.001 |



**FIGURE 6**. Annual habitat-type selection (rows) by telemetered Spiny Softshell Turtles (*Apalone spinifera*) in the Missouri River in Montana, USA, 2010–2012, for four habitat type comparisons (columns). For geomorphic reach type and habitat unit, Isl. = with islands. The horizontal dashed line in each figure represents a selection ratio of one (no preference). Values less than one indicate a reach is used less than expected (avoidance), and values greater than one indicate a reach is used more than expected (preference). Error bars describe 95% Bonferroni confidence intervals. Note the different scales for each habitat type comparison (columns).

thalweg locations (P < 0.001). Overall median depth and velocity in the adjacent thalweg were 3.3 and 5.7 times greater than at point locations, respectively (Fig. 8). Microhabitat characteristics of locations occupied were generally similar spring through summer (May-August) and autumn through winter (October-April), but were different between these two groups of seasons.

Differences between years existed only for median mean-column water velocity and median delta depth, and both were greater in 2011 than in 2010 (P < 0.044). Median velocity was 1.8 times greater in 2011 (0.2; range 0–1.5 m/sec) than in 2010 (0.1; range 0.0–1.3 m/sec) and median delta depth was 2.4 times greater in 2011 (2.1 m; range 0–5.7 m) than in 2010 (0.8 m; range 0–4.5 m). No thalweg velocity measurements were made before April 2011 or in October of 2011, because of velocity meter malfunctions, so comparisons between years could not be made for delta velocity (difference between velocity at SST point locations and in the adjacent thalweg).

Median distance to shore (DTS), depth, velocity, delta depth, and delta velocity at point locations often differed among months (P > 0.001; Fig. 8). Median depth, velocity, and DTS at point locations were lowest spring through summer (< 0.6 m, < 0.1 m/sec, < 2.0 m; May-August) and greatest autumn through winter (> 1.7 m, > 0.3 m/sec, > 13.7 m; September-April). Conversely, delta depth and velocity were greatest in spring and summer (> 1.3 m, > 1.4 m/sec) and lowest in autumn and winter (< 0.4 m, < 0.4 m/sec), indicating that occupied habitats were more similar to the thalweg in autumn through winter and less similar to the thalweg in spring through summer.

Median water temperature at point locations, when SSTs inhabited lateral habitats, (point temperature; 17.9° C) was higher than median temperature in the adjacent main channel (main temperature; 15.1°C; P <0.001; Fig. 9). Delta temperature (difference between point temperature and main temperature) varied among months (P = 0.034), was highest in June (1.9° C), and

**TABLE 3.** Summary statistics for chi-square ( $\chi^2$ ) tests (including degrees of freedom, df, and *P* values) of seasonal overall habitat selection by telemetered Spiny Softshell Turtles (*Apalone spinifera*) monitored in the Missouri River in Montana, USA, 2009–2012. Bold font indicates statistical significance of  $P \le 0.05$ .

|                       | Spring   |     |         | Summer   |     |         | Autumn   |     |         | Winter   |     |       |
|-----------------------|----------|-----|---------|----------|-----|---------|----------|-----|---------|----------|-----|-------|
|                       | $\chi^2$ | df  | Р       | $\chi^2$ | df  | Р       | $\chi^2$ | df  | Р       | $\chi^2$ | df  | Р     |
| Bend type             | 37.1     | 55  | 0.969   | 44.3     | 55  | 0.847   | 109.3    | 55  | < 0.001 | 37.1     | 55  | 0.969 |
| Habitat unit          | 190.7    | 110 | < 0.001 | 232.5    | 110 | < 0.001 | 197.0    | 110 | < 0.001 | 110.6    | 110 | 0.466 |
| Geomorphic reach type | 267.7    | 165 | < 0.001 | 445.2    | 165 | < 0.001 | 326.9    | 165 | < 0.001 | 162.5    | 165 | 0.539 |
| Substrate type        | 199.9    | 112 | < 0.001 | 286.7    | 112 | < 0.001 | 224.0    | 112 | < 0.001 | 95.6     | 112 | 0.866 |



**FIGURE 7**. Seasonal habitat-type selection (rows) by telemetered Spiny Softshell Turtles (*Apalone spinifera*) in the Missouri River in Montana, USA, 2009–2012, for four habitat type comparisons (columns). For geomorphic reach type and habitat unit, Isl. = with islands. The horizontal dashed line in each figure represents a selection ratio of one (no preference). Values less than one indicate a reach is used less than expected (avoidance) and values greater than one indicate a reach is used more than expected (preference). Error bars describe 95% Bonferroni confidence intervals. Note the different scales for each habitat type comparison (columns).

lowest in May (0.5° C). Turtles were generally active before and after overwintering when temperatures were greater than about  $6^{\circ}$  C.

*Ice dynamics.*—Ice conditions on the river differed during the two winters we monitored. The winter of 2010–2011 was colder, had more precipitation, and had ice cover for more days than did the winter of 2011–2012. Remote cameras revealed formation and breakup of ice jams (Figs. 10 and 11) that were concurrent with large fluctuations in stage height (Fig. 12) recorded at the gauge station. Only a single major freeze-and-thaw event occurred in the winter of 2010–2011, whereas three freeze-and-thaw events occurred in 2011–2012.

Complete ice cover on the river at camera locations averaged 95 d (range 24–126 d) in the winter of 2010–2011 and 29 d (range 4–88 d) in 2011–2012.

River geomorphology generally differed at hibernacula and control reaches. Hibernacula were usually found in outside bends of relatively wide sections of the river with moderate depths and current velocities. Control sites were more constricted and shallow, with moderate to high water velocities, and were located downstream from tributary deltas in braided riffles. Accordingly, ice formation and breakup also differed at hibernacula and control reaches. In hibernacula, frazil ice aggregated and created border ice and eventually spanned the width of the river; subsequent floes of

**TABLE 4.** Summary statistics for Mann-Whitney U-tests (W, and P values) by sex and year, paired Wilcoxon signed-rank (Thalweg), or Kruskal-Wallis one-way analysis of variance tests (Month) comparing microhabitat variables between males and females (Sex), between years 2010 and 2011 (Year), between point locations and the adjacent thalweg (Thalweg), and among months (Month; April-November) for telemetered Spiny Softshell Turtles (*Apalone spinifera*) monitored in the Missouri River in Montana, USA, 2009–2012. Bold font indicates statistical significance of  $P \le 0.05$ .

|                      | Sex    |       | Year   |         | Tha  | alweg   | Month |    |         |
|----------------------|--------|-------|--------|---------|------|---------|-------|----|---------|
|                      | W      | Р     | W      | Р       | V    | Р       | Н     | df | Р       |
| Distance to shore    | 19,777 | 0.529 | 37,576 | 0.465   |      |         | 216.8 | 6  | < 0.001 |
| Depth                | 26,059 | 0.766 | 38,861 | 0.428   |      |         | 346.8 | 6  | < 0.001 |
| Delta depth          | 17,784 | 0.212 | 13,082 | < 0.001 | 0.0  | < 0.001 | 166.9 | 6  | < 0.001 |
| Mean-column velocity | 9,585  | 0.089 | 15,604 | 0.044   |      |         | 119.8 | 6  | < 0.001 |
| Delta velocity       | 3,708  | 0.959 |        |         | 98.0 | < 0.001 | 98.9  | 5  | < 0.001 |
| Delta temperature    | 393    | 0.543 | 498    | 0.103   | 78.5 | < 0.001 | 6.8   | 2  | 0.034   |



**FIGURE 8**. Left; overall depth and velocity at point locations of telemetered Spiny Softshell Turtles (*Apalone spinifera*) in the Missouri River in Montana, USA, 2009–2012, in the adjacent thalweg, and the difference between them (Delta). Middle; depth and velocity at point locations by month (April-November; Point). Right; delta depth and velocity (value at point location subtracted from value in adjacent thalweg; Delta) by month (April-November). Median values of months or locations sharing the same letter are not significantly different from one another and those with different letters are significantly different from one another (P < 0.05).

frazil then often overtopped existing ice without causing ice breakup or jamming. In control reaches, anchor ice formed on mainstem riffles and island margins; subsequent frazil and ice floes accumulated on existing ice, caused ice jams, and disturbed the streambed and riverbanks.

Breakup of ice at hibernacula sites appeared to be primarily caused by melting (thermal breakup sensu Beltaos 2003), whereas mechanical breakup of ice commonly occurred at control reaches. At hibernacula, the ice at the thalweg typically melted first and then large sections of thermally degraded border ice broke off and were slowly carried downstream by main channel flows. At control reaches, adjacent upstream tributaries contributed melt water that overtopped and broke up main-channel ice, created ice jams that partially or entirely dammed the river, and subsequently broke and cleared the reaches of ice. Following initial breakup, ice floes from upstream often grounded on riffles and islands near control sites creating new ice jams. We observed seven major ice jams in or adjacent to the main channel thalweg at all control sites; five ice jams occurred in winter 2010-2011 and two ice jams occurred in winter 2011–2012. Only one small ice jam was observed near a hibernaculum, in 2010-2011, and it was upstream and on the opposite bank from the hibernaculum location. Following ice breakup in late March 2011, some islands were completely covered by ice up to 1.5 m thick that scoured vegetation from these islands. Moreover, ice jams and floes scoured riverbed and riparian areas. Ice scour occurred most often at riffles, constrictions, and upstream points of islands.



**FIGURE 9.** Overall temperature (left, Overall) at point locations in tributary confluences (Point), in adjacent main channels (Main), and the difference between them and (right, Delta) delta temperature at point locations, when animals were located in tributary confluences, by month (April-November) for telemetered Spiny Softshell Turtles (*Apalone spinifera*) in the Missouri River in Montana, USA, 2009–2012. Median values of locations or months sharing the same letter are not significantly different from one another and those with different letters are significantly different from one another (P < 0.05).

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**FIGURE 10**. Photographs from remote trail cameras on the Missouri River in Montana, USA, demonstrating the general progression of freeze (A and B) and thaw and breakup (C and D) at a control site that did not contain telemetered Spiny Softshell Turtles (*Apalone spinifera*) from 19 November 2010 through 20 March 2011. Ice jams occurred in the main channel and on the margin during freeze (B) and on the margin (C) and in the main channel (D) during breakup.

### DISCUSSION

Activity, behavior, and habitats.--Riverine turtles are seasonally and ontogenetically dependent on various habitats throughout their life cycles (Bodie and Semlitsch 2000; Anderson et al. 2002; Moll and Moll 2004). At the northern extent of their range, SSTs experienced high and variable river discharges, indeterminate timing of habitat availability, cold and prolonged winters, and powerful ice dynamics. We observed movement, aggregation, and fidelity of SSTs to spatiotemporally separated fundamental habitats (e.g., inundated floodplain and tributary confluences, nesting habitats [Tornabene 2014], post-nesting habitats, and hibernacula) that were required to complete lifehistory processes, as observed in other riverine turtles (reviewed by Moll and Moll 2004). Biological function and environmental conditions (e.g., streamflow, temperature, substrate, and ice conditions) strongly influenced movements and habitat use of SSTs. We posit that the fundamental periods in the annual cycle of adult SSTs in this ecosystem were runoff, nesting, postnesting, and overwintering.

Turtles dispersed from main-stem hibernacula, following ice-off and preceding runoff, as water

temperatures increased above those that inhibit SST motor function (< 5° C; Jackson et al. 2001). Rising temperature is probably the first environmental cue that initiates SST movement in this lotic system. Increasing dissolved oxygen concentrations that occur when ice cover recedes has also been attributed to cue postoverwintering movements in more lentic environments (Ultsch 1989, 2006), but temporal fluxes in dissolved oxygen concentration are probably less pronounced in rivers. Increasing discharge and availability of habitats during runoff influenced timing of movements and habitat selection of riverine SSTs. Most turtles moved out of mainstem hibernacula into inundated lateral habitats such as tributary confluences, floodplains, and backwaters coincident with peaking river discharges during runoff. Such near-shore habitats with shallow water, slow to no flow, and fine substrates seemed to be important during this period because SSTs moved up to several kilometers to occupy and aggregate in them.

Turtles may occupy lateral habitats to avoid peak flows and displacement (MacCulloch and Secoy 1983), to seek areas with warmer temperatures (Moll and Legler 1971), or to occupy habitats that provide increased productivity and food availability (Brinson et al. 1981; Galat et al. 1998). However, displacement may



**FIGURE 11**. Photographs from remote trail cameras on the Missouri River in Montana, USA, demonstrating the general progression of freeze (A and B), thaw (C), and swift breakup (D) at a hibernaculum containing three telemetered Spiny Softshell Turtles (*Apalone spinifera*) 19 November 2010 to 29 March 2011. The letter X = general location denoted in each image. Four hours elapsed between photographs (C) and (D).

be relatively unimportant given that SSTs are highly adapted to lotic conditions; Smooth Softshell Turtles, *Apalone mutica*, quickly returned upstream following displacement (Plummer and Shirer 1975). Moreover, movements and use of lateral and microhabitats differed little between an average (2010) and high water (2011) year.

Occupation of lateral habitats with higher water temperatures may facilitate metabolism and growth, similar to basking (Congdon 1989; Huey 1982; Dubois et al. 2009). Additionally, occupation of these areas could decrease predation risk (e.g., by Coyotes, Canis latrans) relative to basking on land. In our study area, which was largely canyon-bound, many of the lateral habitats used by SSTs were backwaters located at intermittent or ephemeral tributary confluences. Prey fish densities can be high in lateral habitats in large river-floodplains, particularly during high water periods (Galat et al. 1998; Reinhold et al. 2016), and may provide a reliable seasonal food source (Gibbons and Semlitsch 1982; Iverson 1991). Lateral habitats were generally dominated by fine substrates that SSTs could bury into as observed in previous studies with SSTs (Graham and Graham 1991, 1997). We frequently found telemetered turtles buried in 5 to 10 cm of fine or mixed (gravel and sand) substrate in shallow water where they could extend their neck to reach the water surface, and ambush prey swimming near them. Turtles may also exploit carrion that deposits in slow velocity and calm tributary confluences. We located SST feeding on partially submerged carcasses of White-tailed Deer (*Odocoileus virginianus*) on three separate occasions, two of which were in tributary confluences, and dead fish were effective bait for capturing SSTs in hoop nets. Aggregation in lateral habitats preceding nesting could also provide an opportunity for mating (Moll and Moll 2004; Tornabene 2014). We did not observe mating during our study, but mating probably occurs in the autumn or spring at communal hibernacula or lateral habitats (Ernst and Lovich 2009).

During runoff, riffles and braided reaches were preferred habitats. These usually were located downstream of tributaries. Although SSTs may have only passed through and briefly inhabited riffles and braided reaches when moving to and from tributary confluences, riffles and braided reaches are complex and provide heterogeneous habitats. Additionally, these areas probably provide benefits similar to lateral habitats and may provide easier access to terrestrial nesting habitats.



**FIGURE 12.** River stage height (Stage height) on the Missouri River at the Fred Robinson Bridge near Landusky, Montana, USA, in the overwintering period from November-April 2010–2011 (top) and 2011–2012 (bottom). Solid vertical lines represent the beginning of major freeze events with complete ice cover, and vertical dashed lines represent major thaw events when ice no longer completely covered the view of the river at any remote trail camera locations.

Female movements before and after peak streamflow were probably associated with nest-site selection. Movements probably increase before peak streamflow to facilitate arrival at nesting habitats as they become exposed by receding streamflow. During the 2011 flood event, we observed females arriving in reaches with known nesting habitats (Tornabene 2014) prior to the exposure of nesting beaches. Increasing-topeak and decreasing-from-peak streamflows may cue nesting-related movements and nesting. However, large movements by both sexes during this period could also be exploratory or temporally irregular movements (extrapopulational movements sensu Gibbons et al. 1990) in search of mates, food, or shelter (Moll and Moll 2004).

Female SSTs moved furthest during the nesting period, probably as a result of exiting lateral habitats and movement to nesting sites along shorelines. Behavior of SSTs in Lake Champlain was similar, although females there had higher movement rates (about 2.8 km/week; Galois et al. 2002) than females in our study (about 0.3 km/week). Contrary to our findings, male SSTs moved more than females in a small Arkansas stream (Plummer et al. 1997). However, our sample was intentionally biased towards females; therefore, our observations of male SST movements were limited.

During the post-nesting period, most SSTs moved out of braided reaches and towards hibernacula as stream discharges stabilized to base flow (late July) and water temperatures decreased (late August-September). Turtles may move out of shallow nearshore areas to avoid freezing and predation during the winter when low temperatures limit locomotion. Decreasing temperatures may be an environmental cue to initiate movement to hibernacula, along with decreasing discharge (Ultsch 1989). Migration of riverine SSTs to aquatic hibernacula also occurred in Lake Champlain (Graham and Graham 1997; Galois et. al 2002), but not in a small creek in Arkansas (Plummer and Burnley 1997; Plummer et al. 1997). However, shorter duration and magnitude of freeze events at lower latitudes probably allowed SSTs to hibernate at shallower depths in Arkansas.

Distances of SST movements to hibernacula in the Missouri River (median 3.4 km) were similar to those in central Lake Champlain (3-4 km; Graham and Graham 1997), but shorter than those in northern Lake Champlain (mean 13.7 km; Galois et al. 2002). Movements in northern Lake Champlain may have been longer because turtles were observed to move from many locations in the lake to a single hibernaculum located under a causeway that may have had optimal habitat for overwintering (Galois et al. 2002). In contrast, we located numerous hibernacula. Female movement decreased during this period, suggesting that movement for nest-site selection was more intense than movement to hibernacula. Conversely, male movement rates were highest in the post-nesting period when they probably located hibernacula and mates, and because they do not move for nesting. Males of other turtle species, in other locations, make long-range movements to increase female encounter rates and mating events (Morreale et al. 1984; Gibbons 1986; Tuberville et al. 1996).

Aggregation during the overwintering period suggests that hibernacula provide specific characteristics facilitating overwinter survival, provide opportunities to mate immediately before or after overwintering, or are limited throughout the study site (Moll and Moll 2004; Ultsch 2006). Aggregation may facilitate reproduction and allow sufficient time for egg production, incubation, and emergence of hatchlings before low temperatures arrest hatchling development at the extreme northern range of the species (Kuchling 1999; Bodie and Semlitsch 2000; Tornabene 2014). Females typically ovulate in May or June but sperm does not mature in males until July or August (Robinson and Murphy 1978). This asynchrony suggests that mating probably occurs in late autumn or early spring at communal hibernacula in our study area, which is consistent with observations from other parts of the species range (Graham and Graham 1997; Galois et al. 2002), rather than in late spring during peak runoff when turtles aggregated in lateral habitats. Furthermore, we observed higher numbers of males in aggregations in hibernacula than in lateral habitats. However, both sexes can store sperm through winter and may mate at other times (Robinson and Murphy 1978; Gist and Jones 1989).

Hibernacula of SSTs in the Missouri River were similar to others in the northern range of the species. Hibernacula were usually in outside bends of main channel reaches without islands, between shore and the river thalweg, with ample depth, and moderate water velocity. Turtles in central Lake Champlain occupied lentic habitats during the active season, but moved upstream into lotic habitats for overwintering (Graham and Graham 1997). Conversely, SSTs in northern Lake Champlain that inhabited lotic habitats during the active season moved into lentic habitats for overwintering; however, the single known overwintering site reportedly resembled a lotic habitat more than a lentic habitat, was the deepest portion of the bay, and was cleared of ice earlier (Galois et al. 2002). Turtles may remain in a state of metabolic depression for several months at the northern extent of the range of the species and habitat characteristics at hibernacula ostensibly facilitate survival (Ultsch 2006). Spiny Softshell Turtles are among the most anoxia-intolerant turtles, but can survive more than six months without atmospheric oxygen because they can acquire sufficient oxygen directly from well-oxygenated water (Jackson et al. 2001; Reese et al. 2003). As a consequence, moderate water velocity is probably the major determinant in the distribution of hibernacula of riverine SSTs at their northern range limit (Ultsch 1989, 2006). Moderate velocity would provide adequate dissolved oxygen for SSTs without displacing them. High velocity and river stage changes during runoff, and ice formation and breakup, could displace hibernating SSTs when low water temperatures inhibit locomotory activity. Turtles may therefore anchor or bury in substrate to avoid displacement, which may explain why friable substrates were preferred during this period. However, complete burial in fine substrates during overwintering is unlikely for SSTs in this and other systems because it would reduce efficiency of cutaneous gas exchange and could preclude buccopharyngeal gas exchange (reviewed by Ultsch 2006).

Choice of hibernacula by SSTs may also be influenced by riverine ice dynamics. Hibernacula were relatively deep and devoid of ice jams, in contrast to control sites that were shallow and frequently scoured by ice jams. Turtles may have avoided riffles and other shallow water habitats to avoid freezing and deep ice scour (Scrimgeour et al. 1994; Ultsch, 2006). Riverine fish similarly occupy deep areas below rocks, debris, and vegetation seemingly to avoid ice scour, high water velocity, predation, or a combination thereof (Swales et al. 1986; Ultsch 1989; Mitro and Zale 2002; Karchesky and Bennett 2004; Muhlfeld and Marotz 2005). However, other habitat characteristics that facilitate SST winter survival may coincidentally be similar to those that reduce the chance of ice scour. We observed a longer period of ice cover and higher number of ice jams in the colder winter because ice cover was greater and thicker. The severity of ice dynamics, and therefore SST distribution, may change in the future as a function of thermal and hydrologic trends.

implications.—Spiny **Conservation** Softshell Turtles have inhabited the Missouri and Mississippi rivers for millions of years (Parmley 1992; Holman and Andrews 1994) and their life history, like those of all riverine biota, has evolved in the context of natural flow regimes (Bunn and Arthington 2002; Wildhaber et al. 2011). Spiny Softshell Turtle populations in the Missouri River in Montana are probably vulnerable to disturbances because they are disjunct from the nearest downstream SST populations by over 600 km and two large dams and reservoirs (Fort Peck Dam in Montana and Garrison Dam in North Dakota), are at the extreme northern extent of the range of the species, and use different habitats for mating, nesting (Tornabene 2014), and overwintering. Flood pulses are an important riverine ecological process (Junk et al. 1989) that maintain and create diverse habitats used by SSTs such as inundated floodplains, tributary confluences, and sparsely vegetated islands and bars (Tornabene 2014). Flood pulses probably also play an important role in cuing movement of SSTs between dissimilar habitats used for feeding, thermoregulation, nesting, and overwintering. Further modification of the quasi-natural flow regime (e.g., to peak streamflow timing, duration, or magnitude) or the construction of additional dams could reduce or eliminate critical habitats, create asynchrony between environmental cues and SST movements, reduce survival by altering seasonal temperatures and the availability and suitability of habitats, reduce sinuosity and habitat heterogeneity, alter ice dynamics and locations of ice scour, or a combination thereof. Maintaining near-natural streamflow with a small peak in spring and a large peak in early summer promotes sinuosity and habitat heterogeneity, preserves possible movement cues, provides SSTs access to shallow lateral habitats in the summer, reduces the possibility of nest inundation by late flows, and maintains diverse habitats fundamental for feeding, mating, nesting, and overwintering.

Dams or channelization can fragment populations, decrease habitat heterogeneity, and alter habitats used by SSTs for feeding, reproduction, and overwintering (Plummer et al. 1997; Barko and Briggler 2006). Fragmentation of populations increases the likelihood of a genetic bottleneck and inbreeding depression (Soulé and Wilcox 1980), makes populations more vulnerable to environmental stochasticity and disease (Gilpin and Soulé 1986), and reduces the ability of turtles to colonize new areas (Moll and Moll 2004). Disjunct populations are especially vulnerable to extirpation because of limited possibilities for recolonization; turtle movements, over large adverse stretches, are typically inadequate to colonize new or formerly occupied patches (Shively and Jackson 1985). Demographic and genetic studies would enhance understanding of the vulnerability of this disjunct population.

River-floodplain ecosystem managers typically have sparse data to guide management of nongame wildlife such as turtles. Spiny softshell turtles moved between, aggregated in, and showed fidelity to many diverse habitat types in this pseudo-natural, large, Great Plains river to complete their life histories successfully. Conservation and restoration of such diverse habitats may therefore be key to conservation of turtles in the Missouri and other large river systems.

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#### **Appendix: Supplemental Methods**

*Turtle capture and radio telemetry.*—We set 60 traps at intervals of about one per 1.6 rkm. Additional turtles were trapped, hand-caught, or recovered from Montana Fish, Wildlife & Parks (MTFWP) trotline by-catch in June and July of 2010. Transmitter frequency was 147.400 MHz, individual transmitters had unique codes within this frequency, and maximum battery life was an estimated 1,443 d. Mortality sensors indicated if transmitters had not moved in 24 h or more. We telemetered up to five turtles from some traps to compensate for proximate traps that did not capture individuals or only captured individuals unsuitable for transmitter attachment. Confirmation of shed transmitters was in situ when possible, typically by finding a transmitter on the shoreline or buried in mud; otherwise, transmitters were considered shed after about six months of immobility in spring, summer, autumn, or a combination thereof and were parsed out retroactively.

*Microhabitat characteristics.*—We recorded distance to each shore, depth, water velocity, and water temperature at each SST point location to describe microhabitat characteristics. We measured distance to each riverbank with a laser range finder (model RX-1000; Leupold & Stevens, Inc., Beaverton, Oregon, USA; http://www.leupold.com), and total river width was calculated as the sum of these two measurements. We measured depth and velocity at point locations and in the adjacent river thalweg, defined as the deepest point in a cross section of the river, using a boatmounted depth sounder (Eagle Cuda 350; NAVICO, Catoosa, Oklahoma, USA), wading rod, boat-mounted velocity meter (Marsh-McBirney Flo-Mate 2000; HACH Company, Loveland, Colorado, USA), or a combination thereof.

At each location, we took velocity measurements at the surface, mid-depth, and bottom of the water column. We calculated the mid-depth velocity from a single measurement, at 60% of depth, if depth was less than 1 m and from two measurements, at 20% and 80% of depth, if depth was greater than 1 m. We calculated the mean water-column velocity at each location as the mean of surface, middle, and bottom velocity measurements. We subtracted the depth and velocity at each point location from depth and velocity in each adjacent thalweg to calculate delta depth and delta velocity. We measured surface water temperature using a handheld or boat-mounted thermometer at SST point locations and in the adjacent main channel when we located SSTs in lateral habitats in 2011 and 2012. To calculate delta temperature, we subtracted the water temperature at each adjacent main channel from water temperature at each point location.

# Tornabene et al.—*Apalone* spatiotemporal ecology in a large-river ecosystem.



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