

MOVEMENTS, HABITATS, AND NESTING ECOLOGY OF
SPINY SOFTSHELLS IN THE MISSOURI RIVER:
THE INFLUENCE OF NATURAL AND
ANTHROPOGENIC FACTORS

by

Brian James Tornabene

A thesis submitted in partial fulfillment
of the requirements for the degree

of

Master of Science

in

Fish and Wildlife Management

MONTANA STATE UNIVERSITY
Bozeman, Montana

April 2014

©COPYRIGHT

by

Brian James Tornabene

2014

All Rights Reserved

ACKNOWLEDGMENTS

I first thank my advisors, Dr. Bob Bramblett and Dr. Al Zale, who were supportive, steadfast, and provided invaluable insight on study design, analysis, and production of this thesis; I was honored to work with both of you. I thank Dr. Jay Rotella, for his insight on study design, analysis, and for comments on this thesis. This project would not have been possible without the support of Steve Leathe from PPL Montana and Jo Ann Dullum from USFWS who helped initiate the study, secured funding, and provided invaluable logistical support for this project. Additionally, I thank my field technicians Colin Manning and Zach Wenderott, and volunteers through the years that were indispensable in collecting and entering three years of telemetry data and hundreds of thousands of photos.

Innumerable thanks go to all my fellow Montana State University graduate students from 2010–2014, especially to David Ritter, Brittany Mosher, Mariah Mayfield, Ann Marie Reinhold, Mike Duncan, Jim Junker, and Ryan Richards for their help with study design, equipment needs, and volunteer time. I wholeheartedly thank Erin Kenison for providing insight and constructive criticism on analyses and drafts and providing undying emotional and mental support. Last, but not least, I thank my family—Tom, Pam, Chris, and Sarah Tornabene—with my every molecule for their love, support, and unwavering thirst for knowledge; my thesis is dedicated to them.

This study was completed with generous grants from PPL Montana, United States Fish and Wildlife Service, United States Bureau of Reclamation, United States Bureau of Land Management, Montana Fish, Wildlife, and Parks, and Montana State University.

TABLE OF CONTENTS

1. INTRODUCTION TO THESIS	1
Literature Cited	5
2. MOVEMENT PATTERNS AND HABITAT SELECTION OF THE TURTLE <i>APALONE SPINIFERA</i> IN THE MISSOURI RIVER IN MONTANA: IMPLICATIONS FOR CONSERVATION	9
Contribution of Authors and Co-Authors	9
Manuscript Information Page	10
Abstract	11
Introduction	12
Materials and Methods	15
Study Area	15
Turtle Capture and Radio Telemetry	17
Movement and Home Range	20
Longitudinal Distribution and Habitat Selection	21
Microhabitat Characteristics	22
Ice Dynamics	24
Statistical Analyses	24
Results	26
Movement and Home Range	26
Interannual Site Fidelity and Aggregation	29
Longitudinal Distribution and Habitat Selection	32
Microhabitat Characteristics	34
Ice Dynamics	38
Mortality	39
Discussion	40
Implications for Conservation	48
Acknowledgments	51
Tables	53
Figures	55
Literature Cited	82
3. NESTING ECOLOGY OF THE TURTLE <i>APALONE SPINIFERA</i> IN A LARGE RIVER-FLOODPLAIN ECOSYSTEM	88
Contribution of Authors and Co-Authors	88
Manuscript Information Page	89
Abstract	90
Introduction	91
Materials and Methods	94

TABLE OF CONTENTS – CONTINUED

Study Site.....	94
Describing Nesting Timing and Behavior	96
Describing Nesting, Emergence, and Basking Habitats	98
Describing Incubation Period and Emergence Timing and Behavior	100
Incubation and Overwintering Temperatures	101
Statistical Analyses.....	103
Results	104
Nesting Timing And Behavior, and Recreation	104
Predation, Incubation Period, and Emergence Timing and Behavior	107
Nest Site Distribution, Aggregation, Fidelity, and Macrohabitat Characteristic.....	109
Basking Site Distribution and Macrohabitat Characteristics.....	110
Microhabitat Characteristics at Nest Sites and Basking Sites	111
Incubation and Overwintering Substrate Temperatures	113
Discussion.....	115
Acknowledgments	123
Tables	125
Figures	133
Literature Cited.....	155
4. CONCLUSIONS AND MANAGEMENT RECOMMENDATIONS.....	162
Conclusions	162
Implications for Management and Conservation	165
Literature Cited.....	169
REFERENCES	172
APPENDICES	184
APPENDIX A: Spiny Softshell Turtle Morphology, Movement, Home Range, Habitat Selection, and Microhabitat Tables	185
APPENDIX B: Spiny Softshell Turtle Movement Figures.....	196

LIST OF TABLES

Table	Page
2.1. Missouri River discharge summary statistics from USGS gaging station 06115200 on the Missouri River at the Fred Robinson Bridge near Landusky, Montana, for water years 2010–2012 and the average at this site (1934–2012).....	53
2.2. Numbers of <i>Apalone spinifera</i> fitted with radio transmitters (Fitted), numbers that became undetectable or were unconfirmed shed transmitters (Lost), and numbers of confirmed shed transmitters (Shed) by year	53
2.3. Means and standard deviations of mass, curved carapace length (CCL), curved carapace width (CCW), monitoring period in days, and number of point locations, and standard deviations of 46 female and 11 male telemetered <i>Apalone spinifera</i> in the Missouri River in Montana from 2009 through 2012.....	54
2.4. Minimum, maximum, median, and standard deviation of total weekly movement rates (km/week) by sex and season of telemetered <i>Apalone spinifera</i> in the Missouri River in Montana from 2009 through 2012	54
3.1. Discharge summary statistics for the Missouri River from USGS gaging station 06115200 on the Missouri River at the Fred Robinson Bridge near Landusky, Montana, for water years 2010–2012 and the average at this site (1935-2012)	125
3.2. Start and end dates of nesting and emergence periods in 2011 and 2012, number of nests (<i>n</i>) and duration (d) of the nesting, incubation (Inc.), and emergence periods in 2011 and 2012.	125
3.3. Minimum, maximum, and mean time for each nesting step (1–4; <i>n</i> = 8) and all steps (Total) of the nesting process and number of test digs during step 1	126
3.4. Numbers of observed nests (N), emergences (E), and nest predations (P) at 18 nesting areas used in 2011, or 2012, or both	126
3.5. Island locations, characteristics, and dimensions for those nested upon in 2012 including number of nests and nest density per site (# of nests/m ²). Island type indicates if the nest was on a mature (M), pioneer (P), or bare (B) island.....	127
3.6. Number of observations, minimum, maximum, median, and standard deviation (SD) for microhabitat variables at <i>Apalone spinifera</i> nests during the nesting and emergence periods in 2011 and 2012	128

LIST OF TABLES – CONTINUED

Table	Page
3.7. Number of observations, minimum, maximum, median, and standard deviation (SD) for microhabitat variables at <i>Apalone spinifera</i> nests during the nesting and emergence periods.....	129
3.8. Number of observations, minimum, maximum, median, and standard deviation (SD) for microhabitat variables at <i>Apalone spinifera</i> nests and basking site parameters	130
3.9. Summary statistics for potential freezing episodes (PFE) at known <i>Apalone spinifera</i> nesting sites in simulated nests in mixed (predominantly gravel and sand) and pure sand substrates on the Missouri River in Montana from November 9, 2011 to June 1, 2012.....	131

LIST OF FIGURES

Figure	Page
2.1. Study site on the Missouri River, Montana, including major tributaries inhabited by telemetered <i>Apalone spinifera</i>	55
2.2. Distribution of substrate types in the Missouri River, Montana, upstream of Fort Peck Reservoir estimated by (Richards et al., 2012)	56
2.3. Average (1934–2012; dashed line) and January 2010 through November 2012 mean daily discharges in the Missouri River, Montana, at the Fred Robinson Bridge near Landusky, Montana	57
2.4. Initial distribution of telemetered <i>Apalone spinifera</i> in the Missouri River in Montana in August 2009	58
2.5. Relationships among curved carapace width (CCW), curved carapace length (CCL), and mass of 11 adult male and 47 female telemetered <i>Apalone spinifera</i> in the Missouri River, Montana	59
2.6. Numbers of active telemetered <i>Apalone spinifera</i> (i.e., have not shed transmitters, been lost because of weakened signals, or died) in the Missouri River, Montana, from August 2009 through July 2012	60
2.7. Log-normal median weekly movements of 47 female and 11 male telemetered <i>Apalone spinifera</i> in the Missouri River, Montana, from 2009 through 2012 by season	61
2.8. Movement patterns of 11 male and 47 female telemetered <i>Apalone spinifera</i> on the Missouri River, Montana, from 2009 through 2012	62
2.9. River-kilometer-standardized movements of 11 male and 47 female telemetered <i>Apalone spinifera</i> on the Missouri River, Montana, from 2009 through 2012	63
2.10. Individual movement plots for four female <i>Apalone spinifera</i> in the Missouri River, Montana, from 2009 through 2011 displaying four common movement trends	64
2.11. Temporal pattern of the percent of telemetered <i>Apalone spinifera</i> (N=58; 11 male and 47 female) in lateral habitats (i.e., tributaries, ephemeral side channels, and floodplain) in the Missouri River, Montana, from 2010 through 2011	65

LIST OF FIGURES – CONTINUED

Figure	Page
2.12. Relationship between the percent of telemetered <i>Apalone spinifera</i> (N = 58; 11 male and 47 female) in lateral habitats (i.e., tributaries, ephemeral side channels, and floodplain) and discharge in the Missouri River, Montana, from 2010 through 2011	66
2.13. Mean linear and areal home ranges (km and km ² , respectively) of 11 male and 47 female telemetered <i>Apalone spinifera</i> in the Missouri River, Montana, by season.....	67
2.14. Aggregations of 2 or more telemetered <i>Apalone spinifera</i> in the Missouri River, Montana, from 2009 through 2010 in four different habitat types	68
2.15. Initial tagging (i.e., origin) and seasonal frequency distributions of 11 male and 47 female telemetered <i>Apalone spinifera</i> on the Missouri River, Montana, from 2009 through 2012 categorized by 10-kilometer river sections	69
2.16. Annual habitat-type selection by telemetered <i>Apalone spinifera</i> on the Missouri River, Montana, from 2010 through 2012 for four habitat type comparisons.....	70
2.17. Seasonal habitat-type selection by telemetered <i>Apalone spinifera</i> on the Missouri River, Montana, from 2010 through 2012 for four habitat type comparisons.....	71
2.18. Median distances to shore from point locations of 11 male and 47 female telemetered <i>Apalone spinifera</i> from April through November on the Missouri River, Montana, from 2009 through 2012	72
2.19. Median water depths at point locations of 11 male and 47 female <i>Apalone spinifera</i> from April through November on the Missouri River, Montana, from 2009 through 2012	73
2.20. Median water depths at point locations of 11 male and 47 female <i>Apalone spinifera</i> by habitat type on the Missouri River, Montana, from 2009 through 2012	74

LIST OF FIGURES – CONTINUED

Figure	Page
2.21. Top: median water depths at point locations and in the immediate thalweg and the differences between depths at these locations of 11 male and 47 female <i>Apalone spinifera</i> from April through November on the Missouri River, Montana, from 2009 through 2012. Bottom: median differences between depths in the immediate thalweg and at point locations from 2009 through 2012 by month	75
2.22. Median mean-column (top) and bottom (bottom) water velocities at point locations of 11 male and 47 female <i>Apalone spinifera</i> from April through November on the Missouri River, Montana, from 2009 through 2012	76
2.23. Median mean-column (top) and bottom (bottom) water velocities at point locations of 11 male and 47 female <i>Apalone spinifera</i> by habitat type on the Missouri River, Montana, from 2009 through 2012	77
2.24. Top: median mean-column water velocities at point locations, median mean-column water velocities in the immediate thalweg, and median difference between the two of 11 male and 47 female <i>Apalone spinifera</i> from April through August and November on the Missouri River, Montana, from 2011 through 2012. Bottom: median differences between mean-column water velocities in the immediate thalweg and point locations from 2010 through 2012 by month	78
2.25. Top: median temperatures, in degrees Celsius, in main channel and lateral habitats and the median differences between temperatures in the two habitat types in the Missouri River, Montana, in May, June, and July of 2011 and 2012. Bottom: median difference between temperatures in main channel and lateral habitats in the Missouri River, Montana, in May, June, and July of 2011 and 2012	79
2.26. Relationship between percent of active (had moved within 24 h of being located) telemetered <i>Apalone spinifera</i> and temperatures during October and November winter excursions on the Missouri River, Montana, in 2009, 2010, and 2011	80
2.27. Gauge height on the Missouri River at the Fred Robinson Bridge near Landusky, Montana, in the overwintering period from November through April 2010 through 2011 (top) and 2011 through 2012 (bottom)	81

LIST OF FIGURES – CONTINUED

Figure	Page
3.1. Study site on the Missouri River in Montana	133
3.2. Distribution of channel bottom substrate types in the Missouri River in Montana upstream of Fort Peck reservoir estimated by Richards (2012)	134
3.3. Average (1934–2012) and January 2010 through November 2012 mean daily discharge in the Missouri River at the Fred Robinson Bridge near Landusky, Montana	135
3.4. Nesting and emergence periods of <i>Apalone spinifera</i> in 2011 (top) and 2012 (bottom) plotted against annual discharge (solid line), average discharge (1935-2012; dashed line), annual water temperature (dot-dash line), and average water temperature (2002-2012; dotted line).....	136
3.5. Frequency distribution of <i>Apalone spinifera</i> nesting (n = 482) and human recreation activity (n = 208) observed by remote cameras from 16 June to 9 July 2012 binned by day	137
3.6. Frequency distribution of <i>Apalone spinifera</i> nesting (n = 482) and human recreation activity (n = 208) observed by remote cameras from 16 June to 9 July 2012 by time of day (h)	138
3.7. Frequency of <i>Apalone spinifera</i> exhibiting nesting behavior from remote cameras (n = 482) by lunar phase, cloud cover, precipitation, if an animal was in view, if humans were in view, and temperature.....	139
3.8. Relationship between nesting date and incubation period for <i>Apalone spinifera</i> nests laid in 2011 (n = 10) and 2012 (n = 23)	140
3.9. Frequency of <i>Apalone spinifera</i> hatchlings or hatchling tracks emerging from nests from remote cameras (n = 74) by temperature (°C), time of day (h), and lunar phase	141
3.10. Longitudinal distribution of <i>Apalone spinifera</i> nests in 2011 (n = 25) and 2012 (n = 97)	142
3.11. Longitudinal density distribution of <i>Apalone spinifera</i> nests in 2011 (n = 25), 2012 (n = 97), and of islands (n = 111).....	143

LIST OF FIGURES – CONTINUED

Figure	Page
3.12. Relationship between potential area for nesting (nesting area) and total island area (island area) and number of <i>Apalone spinifera</i> nests laid in that location (n = 13).....	144
3.13. Channel types at <i>Apalone spinifera</i> nests in 2011 (n = 25) and 2012 (n = 97).....	145
3.14. Channel types, longitudinal distribution, and dominant substrate types at <i>Apalone spinifera</i> basking sites (n = 70) from May through August 2010 and May and late June of 2011	146
3.15. Microhabitat characteristics of <i>Apalone spinifera</i> nests in 2011 and 2012	147
3.16. Microhabitat characteristics of <i>Apalone spinifera</i> nests during emergence in 2011 and 2012	148
3.17. Microhabitat characteristics of <i>Apalone spinifera</i> nests during nesting and emergence.....	149
3.18. Microhabitat characteristics of <i>Apalone spinifera</i> nesting and basking sites	150
3.19. Mean daily substrate temperatures in simulated nests from 16 June through 30 September 2012 in mixed gravel with sand (mixed; top) and pure sand (bottom) substrates at known nesting sites on the Missouri River in Montana	151
3.20. Mean daily substrate temperatures in simulated nests from 16 June through 30 September 2012 in mixed gravel with sand (mixed; top) and pure sand (bottom) substrates by depth at known nesting sites on the Missouri River in Montana	152
3.21. Mean daily overwintering substrate temperatures in simulated nests from 11 November through 30 May 2012 in mixed gravel with sand (mixed; solid line) and sand (dotted line) substrates at known nesting sites on the Missouri River in Montana	153
3.22. Mean daily overwintering substrate temperatures in simulated nests from 11 November through 30 May 2012 in mixed gravel with sand (mixed; top) and pure sand (bottom) substrates by depth at known nesting sites on the Missouri River in Montana	154

ABSTRACT

Sparse information exists about the ecology of spiny softshell turtles in large rivers and in Montana where they are at the northern extent of their range, disjunct from downstream populations, and a Montana species of concern. We described spatial and temporal patterns in movements, habitats, and nesting ecology of spiny softshell turtles in relation to natural and anthropogenic factors in the Missouri River from August 2009 through July 2012. Movement rates and home ranges were generally highest in summer, and lowest in winter. Turtles aggregated and showed interannual fidelity to active-period and overwintering-period habitats that were distinct and separated by 0.2–23.3 km. Microhabitat characteristics at turtle locations varied between active and overwintering periods; shallow and slow velocity areas were inhabited from May–September whereas deeper areas with moderate water velocities were inhabited from October–April. We located 25 nests in 2011 and 97 in 2012. Nesting followed peak river stage, and occurred mostly in the afternoon when no humans were present. Nesting and emergence occurred later in 2011 than in 2012, but incubation periods for successfully-emerged nests were similar between years, and fewer nests were successful in 2011. Nearly all nests were in mixed-gravel substrates with sparse vegetative cover. Nest sites during the nesting period were lower and closer to water than nest sites during the emergence period. More islands were nested on in 2012 than 2011 and depredation rate was three times lower on islands than mainland shores in both years. Substrate temperatures in simulated nests during the incubation period were warmer in gravel than sand substrates. Flooding in 2011 probably decreased nesting success by inundating potential nesting habitats and reducing habitat availability thereby delaying the onset of nesting. However, nesting habitats are created and maintained by floods. During winter, freezing episodes occurred at all depths in all simulated nests. The northern range of the species is probably limited by incubation period because hatchlings are unable to overwinter in the nest. Preservation of natural streamflow regimes and protection of habitats from anthropogenic disturbance may facilitate continued existence of spiny softshell turtles in the Missouri River in Montana.

CHAPTER ONE

INTRODUCTION TO THESIS

Annual variation in streamflow shapes the physical environment and ecosystem configuration of river-floodplain ecosystems (Leopold et al., 1964; Hupp and Osterkamp, 1985; Ward, 1989) and determines the location and timing of optimal habitat patches (Bain et al., 1988; Auble et al., 1994; Poff and Allen, 1995) and species distribution, abundance, and biodiversity (Poff et al., 1997; Poff and Zimmerman, 2010). Streamflow and flood pulses play a central role in sediment transport, structuring river geomorphology, creating and shaping islands (Leopold et al., 1964), and exposing bare substrate on shorelines essential for the reproduction of many riparian species such as shorebirds (Smith and Renken, 1991; Sidle and Kirsch, 1993) and turtles (Kuchling, 1999; Moll and Moll, 2004;).

Life history characteristics of riverine species have evolved in response to natural flow regimes, thereby facilitating survival through natural disturbances such as floods and droughts (Welcomme, 1979; Bunn and Arthington, 2002). Organisms cope with natural disturbances by exhibiting behavioral responses, physical adaptations, synchronized life history strategies, or a combination thereof (Humphries and Baldwin, 2003; Lytle and Poff, 2004). Turtle species that occupy large and dynamic river-floodplain ecosystems have developed similar adaptations in response to variable streamflow, drought, and indeterminate timing, magnitude, and length of flood pulses (Moll and Moll, 2004).

Riverine turtles are seasonally or ontogenetically dependent on multifarious habitats in river-floodplain ecosystems to complete their life cycle (Bodie and Semlitsch, 2000; Anderson et al., 2002; Moll and Moll, 2004; Ernst and Lovitch, 2009). Limited and spatiotemporally separated fundamental habitats often necessitate turtle movement, aggregation, and fidelity to locate optimal habitats and obtain specific resources in order to complete life history processes (Gibbons et al., 1990; Graham and Graham, 1997; Bodie, 2001; Galois et al., 2002; Moll and Moll 2004).

Spiny softshell turtles (herein SSTs or turtles) have inhabited the Missouri and Mississippi rivers for thousands of years or more (Parmley, 1992; Holman and Andrews, 1994) and their life-history strategies are probably influenced by local environmental conditions, natural streamflow patterns, and disturbance events such as flood pulses (Kuchling, 1999; Bunn and Arthington, 2002; Moll and Moll, 2004). However, despite being the most widespread species of the genus *Apalone* in North America (Webb, 1962, 1973), scarce information exists concerning the ecology of SSTs in river-floodplain ecosystems. Information about the ecology and life history of SSTs in Montana is also sparse and limited to incidental presence records (Werner et al., 2004) and systematic sampling that determined longitudinal distribution and relative abundance of SSTs in the Yellowstone and Missouri rivers in Montana from 2004–2008 (Dood et al., 2009). Of the populations of SSTs in Montana, the Missouri River population is probably most vulnerable to declines or extirpation because it is separated from downstream populations by Fort Peck Dam, is influenced by upstream dam regulation, may be negatively influenced by river recreation (Bolton, 2007), and is at the northern range limit of the species.

Information on the ecology of SSTs in the northwestern portion of their range is limited to two studies conducted on Lake Champlain in Quebec, Canada, and Vermont, USA (45° N; Graham and Graham, 1997, Galois et al., 2002). No movement or nesting ecology studies have been conducted in a large river in the western part of the range of SSTs. Turtles occupying the extreme northern portion of their range may have a truncated active season and fewer degree-days available for egg incubation; nevertheless, temperature influences general timing and nest success in temperate-region turtles (Kuchling, 1999). Moreover, populations in their northern range may have lower annual growth, delayed maturity, and lower relative clutch mass (Larsen and Gregory, 1989; Bobyn and Brooks, 1994).

Dams can influence riverine turtles by altering flood-pulse cycles, converting lotic to lentic habitats, influencing timing and availability of habitats, and fragmenting populations (Ward and Stanford, 1983; Moll and Moll, 2004). The installation of dams in lower reaches of the Missouri River has altered natural flow cycles (Ward and Stanford, 1983), influenced sandbar migration (Sanford, 2007), and influenced distribution and abundance of fish communities (Hesse et al., 1989; Bowen et al., 2003; Galat et al., 2005). Dams and channelization have also reduced islands and sand bars by 98% in a 740-km reach of the Lower Missouri River from 1879–1954 (Funk and Robinson, 1974). A reduction of these habitats, commonly basked and nested upon by river turtles (Moll and Moll, 2004), could decrease annual nesting success and fitness (Moll and Moll, 2004; Barko and Briggler, 2006). Moreover, if extirpation occurs, dams and reservoirs could obstruct recolonization by downstream populations.

The relationships between variable streamflow and a truncated active season and movements, habitat selection, and nesting ecology of SSTs in a large river-floodplain ecosystem at the northwestern range limit of the species are not known. A fundamental requisite for management and conservation of a species is a more complete understanding of the relationship between life history characteristics of that species and anthropogenic and natural factors.

Our objectives in Chapter Two were to determine seasonal patterns in SST movements and habitat use in relation to natural and anthropogenic factors and to identify fundamental habitats for SSTs in the Missouri River above Fort Peck Reservoir. The objective of Chapter Three was to document SST nesting ecology and habitats in relation to natural and anthropogenic factors in a large river-floodplain ecosystem in the Missouri River above Fort Peck Reservoir.

Literature Cited

- Auble, G. T., J. M. Friedman, and M. L. Scott. 1994. Relating riparian vegetation to present and future streamflows. *Ecological Applications* 4:544–554.
- Bain, M. B., J. T. Finn, and H. E. Brooke. 1988. Streamflow regulation and fish community structure. *Ecology* 69:382–392.
- Barko, V. A., and J. T. Briggler. 2006. Midland smooth softshell (*Apalone mutica*) and spiny softshell (*Apalone spinifera*) turtles in the middle Mississippi River: habitat associations, population structure, and implications for conservation. *Chelonian Conservation and Biology* 5:225–231.
- Bobyn, M. L., and R. J. Brooks. 1994. Incubation conditions as potential factors limiting the northern distribution of snapping turtles, *Chelydra serpentina*. *Canadian Journal of Zoology* 72:28–37.
- Bodie, J. R., and R. D. Semlitsch. 2000. Spatial and temporal use of floodplain habitats by lentic and lotic species of aquatic turtles. *Oecologia* 122:138–146.
- Bolton, R. M. 2007. Effects of anthropogenic disturbance, nest-site selection, and dipteran infestation on spiny softshells (*Apalone spinifera*). M.S. Thesis, The University of Guelph, Ontario, Canada.
- Bowen, Z. H., K. D. Bovee, and T. J. Waddle. 2003. Effects of flow regulation on shallow-water habitat dynamics and floodplain connectivity. *Transactions of the American Fisheries Society* 132:809–823.
- Bunn, S. E., and A. H. Arthington. 2002. Basic principles and ecological consequences of altered flow regimes for aquatic biodiversity. *Environmental Management* 30:492–507.
- Dood, A. R., B. Schmitz, V. Riggs, N. McClenning, M. Jaeger, D. Fuller, R. Rauscher, S. Leathe, D. Moore, J. Dullum, J. Ensign, S. Story, and M. Backes. 2009. Relative abundance of spiny softshell turtles (*Apalone spinifera*) on the Missouri and Yellowstone rivers in Montana, Final Report. Montana Fish, Wildlife & Parks, Helena, Montana.
- Ernst, C. H., and J. E. Lovich. 2009. Turtles of the United States and Canada. The Johns Hopkins University Press, Baltimore, Maryland.
- Funk, J. L., and J. W. Robinson. 1974. Changes in the channel of the lower Missouri River and effects on fish and wildlife. Missouri Department of Conservation, Aquatic Series 11, Jefferson City, Missouri.

- Galat, D. L., C. R. Berry, W. M. Gardner, J. C. Hendrickson, G. E. Mestl, G. J. Power, C. Stone, and M. R. Winston. 2005. Spatiotemporal patterns and changes in Missouri River fishes. *American Fisheries Society Symposium* 45:249–291.
- Galois, P., M. Léveillé, L. Bouthillier, C. Daigle, and S. Parren. 2002. Movement patterns, activity, and home range of the eastern spiny softshell turtle (*Apalone spinifera*) in northern Lake Champlain, Québec, Vermont. *Journal of Herpetology* 36:402–411.
- Gibbons, J. W., J. L. Greene, and J. D. Congdon. 1990. Temporal and spatial movement patterns of sliders and other turtles. Pp. 201–215 In J. W. Gibbons (Ed.), *Life History and Ecology of the Slider Turtle*. Smithsonian Institution Press, Washington D.C., USA.
- Graham, T. E., and A. A. Graham. 1997. Ecology of the eastern spiny softshell, *Apalone spinifera spinifera*, in the Lamoille River, Vermont. *Chelonian Conservation and Biology* 2:363–369.
- Hesse, L. W., J. C. Schmulbach, J. M. Carr, K. D. Keenlyne, D. G. Unkenholz, J. W. Robinson, and G. E. Mestl. 1989. Missouri River fishery resources in relation to past, present, and future stresses. Pp. 352–371 In D. P. Dodge (Ed.), *Proceedings of the International Large River Symposium*. Canadian Special Publication of Fisheries Aquatic Science 106.
- Holman, J. A., and K. D. Andrews. 1994. North American quaternary cold-tolerant turtles: distributional adaptations and constraints. *Boreas* 23:44–52.
- Humphries, P., and D. S. Baldwin. 2003. Drought and aquatic ecosystems: an introduction. *Freshwater Biology* 48:1141–1146.
- Hupp, C. R., and W. R. Osterkamp. 1985. Bottomland vegetation distribution along Passage Creek, Virginia in relation to fluvial landforms. *Ecology* 66:670–681.
- Hynes, H. B. N. 1970. *The ecology of running waters*. University of Toronto Press, Canada.
- Jackson, D. C., and G. R. Ultsch. 2010. Physiology of hibernation under the ice by turtles and frogs. *Journal of Experimental Zoology* 313A:311–327.
- Kuchling, G. 1999. *The reproductive biology of chelonian-zoophysiology*. Springer-Verlag, New York, USA.
- Larsen, K. W., and P. T. Gregory. 1989. Population size and survivorship of the common garter snake, *Thamnophis sirtalis*, near the northern limit of its distribution. *Holarctic Ecology* 12:81–86.

- Leopold, L. B., M. G. Wolman, and J. P. Miller. 1964. Fluvial processes in geomorphology. Dover Publications, Inc., Mineola, New York.
- Litzgus, J. D., and T. A. Mousseau. 2004. Home range and seasonal activity of southern spotted turtles (*Clemmys guttata*): implications for management. *Copeia* 2004:804–817.
- Lytle, D. A., and N. L. Poff. 2004. Adaptation to natural flow regimes. *Trends in Ecology and Evolution* 19:94–100.
- Moll, D., and E. O. Moll. 2004. The ecology, exploitation, and conservation of river turtles. Oxford University Press, New York, USA.
- Parmley, D. 1992. Turtles from the late Hemphillian (latest Miocene) of Knox County, Nebraska. *Texas Journal of Science* 44:339–348.
- Plummer, M. V., N. E. Mills, and S. L. Allen. 1997. Activity, habitat, and movement patterns of softshell turtles (*Trionyx spiniferus*) in a small stream. *Chelonian Conservation Biology* 2:514–520.
- Poff, N. L., and J. D. Allen. 1995. Functional organization of stream fish assemblages in relation to hydrological variability. *Ecology* 76:606–627.
- Poff, N. L., J. D. Allen, M. B. Bain, J. R. Karr, K. L. Prestegard, B. D. Richter, R. E. Sparks, and J. C. Stromberg. 1997. The natural flow regime. *BioScience* 47:769–784.
- Poff, N. L., and K. H. Zimmerman. 2010. Ecological responses to altered flow regimes: a literature review to inform the science and management of environmental flows. *Freshwater Biology* 55:194–205.
- Reese, S. A., D. C. Jackson, and G. R. Ultsch. 2003. Hibernation in freshwater turtles: softshell turtles (*Apalone spinifera*) are the most intolerant of anoxia among North American species. *Journal of Comparative Physiology B: Biochemical, Systemic, and Environmental Physiology* 173:263–268.
- Sanford, J. P. 2007. Dam regulation effects on sand bar migration on the Missouri River: Southeastern South Dakota. M.A. Thesis, University of Montana, Missoula, USA.
- Scrimgeour, G. J., T. D. Prowse, J. M. Culp, and P. A. Chambers. 1994. Ecological effects of river ice break-up: a review and perspective. *Freshwater Biology* 32:261–275.
- Sidle, J. G., and E. M. Kirsch. 1993. Least tern and piping plover nesting at sand pits in Nebraska. *Colonial Waterbirds* 16:139–148.

- Smith, J. W., and R. B. Renken. 1991. Least tern nesting habitat in the Mississippi River valley adjacent to Missouri. *Journal of Field Ornithology* 62:497–504.
- Ultsch, G. R. 2006. The ecology of overwintering among turtles: where turtles overwinter and its consequences. *Biological Reviews* 81:339–367.
- Ward, J. V. 1989. The four-dimensional nature of lotic ecosystems. *Journal of the North American Benthological Society*, 8:2–8.
- Ward, J. V., and J. A. Stanford. 1983. The serial discontinuity concept of lotic ecosystems. Pp. 29-42 in T. D. Fontaine and S. M. Bartell (Eds.), *Dynamics of lotic ecosystems*. Ann Arbor Science Publishers Inc., Michigan, USA.
- Webb, R. G. 1962. North American recent soft-shelled turtles (family Trionychidae). *University of Kansas Publications Museum of Natural History* 13:429–611.
- Webb, R. G. 1973. *Trionyx spiniferus*. *Catalog of American Amphibians and Reptiles*, 140:1–4.
- Welcomme, R. L. 1979. *Fisheries ecology of floodplain rivers*. Longman, New York, New York.
- Werner, J. K., B. A. Maxell, P. Hendricks, and D. L. Flath. 2004. *Amphibians and reptiles of Montana*. Mountain Press, Missoula, Montana.

CHAPTER TWO

MOVEMENT PATTERNS AND HABITAT SELECTION OF THE TURTLE

APALONE SPINIFERA IN THE MISSOURI RIVER IN MONTANA:

IMPLICATIONS FOR CONSERVATION

Contributions of Authors and Co-Authors

Manuscript in Chapter 2

Author: Brian J. Tornabene

Contributions: Conceived the study, collected and analyzed data, interpreted analyses, and authored the manuscript

Co-author: Robert G. Bramblett

Contributions: Conceived the study, obtained funding, collected data, and assisted with study design and interpretation of analyses. Discussed results and implications and edited the manuscript.

Co-author: Stephen A. Leathe

Contributions: Conceived the study, obtained funding, collected data, and discussed results and implications.

Co-author: Alexander V. Zale

Contributions: Assisted with study design and interpretation of analyses. Discussed results and implications and edited the manuscript.

Manuscript Information Page

Brian J. Tornabene, Robert G. Bramblett, Stephen A. Leathe, Alexander V. Zale
Copeia

Status of Manuscript:

- ☒ Prepared for submission to a peer-reviewed journal
- ☐ Officially submitted to a peer-review journal
- ☐ Accepted by a peer-reviewed journal
- ☐ Published in a peer-reviewed journal

Published by the American Society of Ichthyologists and Herpetologists

Abstract

Sparse information exists about the ecology of spiny softshell turtles in large rivers and in Montana where they are at the northern (45–47° N) and western extent of their natural range, disjunct from downstream populations, and a State species of concern. We described spatial and temporal patterns in movements and habitats of spiny softshell turtles in relation to natural and anthropogenic factors and identified fundamental habitat areas in the Missouri River in east-central Montana from August 2009 through July 2012. Forty-seven female and twelve male turtles were equipped with radio transmitters and monitored for 5 to 152 weeks. Movement rates of females were greater than those of males and movement rates of both sexes peaked in summer and were minimal in winter. Median home range sizes were not significantly different between sexes, varied among seasons, were larger than reported elsewhere (linear 7 km; areal 1 km²), and were highly variable among individuals (linear 0.9–87.0 km; areal 0.1–17.0 km²). Turtles aggregated and showed interannual fidelity to active and overwintering-period habitats that were distinct and separated by long distances in some cases (median 3.4 km, range 0.02–23.27 km). Turtles preferred tributaries or reaches with islands in the spring and summer, outside bends in the winter, and fine substrates in both periods. Microhabitat characteristics at turtle locations varied among months; shallow, slow velocity, near-shore areas were inhabited from May through September whereas deeper areas, with moderate water velocities, that were located furthest from shore were inhabited from October through April. Thermally and mechanically-induced ice breakup occurred in winter of 2010 and 2011 causing ice jams in the river channel, bed and riparian scour,

and flood events; however, ice jams were never observed at turtle hibernacula. The locations of initial ice breakup and jams are predictable and both may influence the distribution of turtles during autumn and winter. Preservation and protection of areas inhabited during major portions of the life cycle (lateral habitats and hibernacula) from anthropogenic disturbance may facilitate continued existence of spiny softshell turtles in the Missouri River in Montana.

Introduction

Spiny softshell turtles (*Apalone spinifera*; herein SSTs or turtles) occur in the east-central U.S. west of the Appalachian Mountains and south to the Gulf Coast and South Atlantic states; disjunct populations exist in Montana and Vermont and the species has been introduced in New Jersey and the Gila-Lower Colorado watershed (in Arizona, California, Nevada, Utah, and New Mexico). Populations are typically concentrated around lakes and river drainages in these regions (Ernst and Lovitch, 2009). The ecology and life history of SSTs have been studied in the United States and Canada, but never in Montana where they are a BLM Sensitive Species and a Montana Species of Concern (Maxell, 2013). Information about the ecology and life history of SSTs in Montana is sparse and was limited to incidental presence records and systematic sampling of the Yellowstone and Missouri rivers in Montana from 2004 through 2008 (Werner et al., 2004; Dood et al., 2009). Systematic sampling identified a longitudinal distribution of SST catch per unit effort in both rivers that generally increased moving west to east and decreased near the North Dakota border (Dood et al., 2009). In Montana, SST populations in the Missouri River above Fort Peck Reservoir may be most vulnerable to

declines or extirpation because they are separated from downstream populations by Fort Peck Dam, influenced by upstream dam regulation, and are at the northern range limit of the species.

Dam operations can affect riverine turtles by preventing migrations and fragmenting populations, altering flood cycles, converting lotic habitats to lentic habitats, changing the availability of habitats, and altering riverine ice dynamics (Moll and Moll, 2004). The installation of dams in lower reaches of the Missouri River has altered natural flow cycles (Ward and Stanford, 1983), influenced sandbar migration (Sanford, 2007), and influenced distribution and abundance of fish communities (Hesse et al., 1989; Bowen et al., 2003; Galat et al., 2005). Islands, island complexes, offshore areas, and sandbars are commonly used for feeding, basking, and nesting by most riverine turtle species (including SSTs) and a reduction of these habitats could decrease annual survival and nesting success (Moll and Moll, 2004; Barko and Briggler, 2006). These habitats are especially susceptible to anthropogenic disturbance; for example, islands and sand bars were reduced by 98% in a 740-km reach of the Lower Missouri River from 1879 to 1954 (Funk and Robinson, 1974). Altering, eliminating, or changing the location of habitats important to the life cycle of SSTs may cause declines or local extirpations.

Information on the ecology of this species in its northern range is limited to two studies conducted on Lake Champlain in Quebec, Canada, and Vermont, USA (45° N; Graham and Graham, 1997, Galois et al., 2002), and no movement studies have been conducted in a large river in the western part of the range of SSTs. Overwintering may be a particularly critical time for SSTs in large rivers in Montana because they are at the extreme northern and western extent of the range of the species (47° N) and can spend up

to 6 months overwintering (Werner et al., 2004; Ernst and Lovitch, 2009). Riverine turtles typically overwinter underwater and SSTs in rivers often overwinter in deep pools with flowing well-oxygenated water and fine substrates to bury themselves in, probably because they must avoid freezing and destructive ice scour, are intolerant of anoxia, and must prevent being displaced from hibernacula during breakup-induced flood events (Ultsch, 2006; Reese et al., 2003; Graham and Graham, 1997; Plummer and Burnley, 1997; Scrimgeour et al., 1994). Overwintering in northern climates is prolonged and more severe than in the southern range of the species; consequently, overwintering is probably more difficult and more pivotal to the annual survival of turtles in northern climates (Hynes, 1970; Litzgus et al., 1999; Ultsch, 2006; Jackson and Ultsch, 2010). Occasional overwintering mortality events can occur because of predation, anoxia, and freezing at sometimes-communal hibernacula, but turtle mortality during overwintering is usually lower than during spring, summer, and autumn (Ultsch, 2006). Riverine ice dynamics can cause local increases in current velocity and scour riparian areas, river channels, and riverbeds where SSTs overwinter (Scrimgeour et al., 1994; Beltaos, 2003); consequently, river-ice breakup may influence SST winter distribution and abundance. However, ice dynamics are rarely addressed as a factor explaining the distribution of riverine turtles. Upstream dam operations may also influence riverine ice dynamics and SST distribution by controlling the timing and amount of water released each year.

The relationships between hydrograph and movements and habitat selection by SSTs in the Missouri River in Montana for feeding, nesting, and overwintering are not known. A more complete understanding of the life history characteristics of a species and the relationship among these characteristics and anthropogenic stressors and natural

factors is a fundamental requisite for management and conservation. Our goals were to determine spatial and temporal patterns in SST movements and habitat use in relation to natural and anthropogenic factors and to identify fundamental habitats for SSTs in the Missouri River above Fort Peck Reservoir.

Materials and Methods

Study Area

Our study was conducted on 130 river kilometers (rkm) of the Missouri River above Fort Peck Reservoir in central Montana extending from 10 rkm upstream of the Judith River confluence (rkm 3,194; measured from the confluence with the Mississippi River) downstream to 20 rkm below the Fred Robinson Bridge (rkm 3,093; Fig. 2.1). We selected this reach because it had the highest catch rates of SSTs on the Missouri and Yellowstone rivers in Montana during systematic sampling surveys conducted from 2004 through 2008 by Montana Fish, Wildlife and Parks (MTFWP), PPL Montana, and the U.S. Fish and Wildlife Service (USFWS; Dood et al., 2009).

Several regulated hydroelectric dams affect the hydrology of the Missouri River in our study area, but three dams (Canyon Ferry, Gibson Dam on the Sun River, and Tiber Dam on the Marias River) operated by the U.S. Bureau of Reclamation ostensibly have the most influence on streamflow and habitat. Peak flows in spring have been reduced to 70–80% of natural flows and base flows in autumn and winter have been increased downstream of these dams (Ramey et al., 1993; Gardner and Jensen, 2011). However, our study area is considerably less hydrologically altered than downstream reaches that have been converted to lentic settings, are highly flow-altered, channelized,

or a combination thereof (Pegg et al. 2003; Galat et al., 2005; Sanford, 2007). We used daily discharge data from the United States Geological Survey (USGS) flow gauge on the Missouri River at the Fred Robinson Bridge near Landusky, Montana, to calculate average (1935 – 2012) mean daily discharge for comparison among years and to assess the influence of discharge on SST ecology.

Our study area was located within the Upper Missouri River Breaks National Monument and Charles M. Russell National Wildlife Refuge, and is part of a designated Wild and Scenic River (USHR, 1976). The Lewis and Clark Expedition explored, mapped, and described this area in 1805 and it remains one of the most pristine locations in Montana. The river channel is largely canyon-bound by the “Missouri Breaks” – 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 reaches and predominately sand in the lower reaches (Fig. 2.2; Richards, 2012). Numerous intermittent or ephemeral tributaries enter the study area and their confluences typically form lateral pools of near-lentic water during high flows on the Missouri River. The six largest tributaries within the study site are the Judith River and Antelope, Bullwhacker, Cow, Dog, Two Calf, and Woodhawk creeks (Fig. 2.1). The creeks generally flow from April through June, range in length from about 30 to 70 km, range in width from about 5 to 20 m, are less than about 2 m deep, and are dominated near their confluences by silt and sand substrates with occasional gravel and cobble deposits.

Discharge patterns of the Missouri River differed substantially among 2010, 2011, and 2012 (Fig. 2.3). Annual median flow, maximum daily mean flow, and annual runoff

were highest in 2011 and lowest 2012 (Table 2.1). Median daily flow rate differed among years (Kruskal-Wallis test; $\chi^2 = 219.02$, $df = 2$, $P < 0.001$) and was 1.3 times greater in 2011 than in 2010, 2012, and compared to the 79-year average. Annual runoff in 2011 was 1.6 and 1.8 times higher than in 2010 and 2012. Maximum daily mean flow was 2.1 and 3.9 times higher in 2011 than in 2010 and 2012 and occurred on June 20 in 2010, but occurred 9 d earlier and on the same date (June 11) in 2011 and 2012.

Turtle Capture and Radio Telemetry

We documented spatial and temporal patterns in SST habitats and movement using radio telemetry. Turtles were captured using hoop traps baited with dead fish in August 2009. Hoop traps had 5.1-cm mesh, three 0.9-m metal hoops, and were about 2.1 m long when fully extended. Sixty traps were set at intervals of about one per 1.6 rkm. Additional turtles were trapped, hand-caught, or recovered from Montana Fish, Wildlife & Parks trotline by-catch in June and July of 2010. Captured SSTs were weighed, curved carapace length (CCL) and curved carapace width (CCW) were measured, sex was determined, and Monel tags inscribed with distinct six-digit alphanumeric codes were clasped onto the posterior right side of the carapace of the turtle for individual identification. We used nylon-coated stainless steel wire to fit individually coded external radio transmitters (model Lotek SR-M16-25; Lotek Wireless, Inc., Newmarket, Ontario, Canada) weighing 8.5 g in water and 19.0 g in air to selected turtles. Transmitter weight in air averaged 4% of body weight for males and 0.8% of body weight for females. Mortality sensors indicated if transmitters had not moved in 24 h or more. Transmitter frequency was 147.400 MHz and maximum battery life was an estimated 1,443 d.

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 (Chapter 3) and to ensure that individuals were sexually mature. Radio transmitters were distributed at an average of about 1 tag per 1.6 rkm; however, up to five turtles were telemetered from a single trap to compensate for proximate traps that did not capture individuals suitable for transmitter attachment (Fig. 2.4). Twelve male and forty-seven female SSTs were equipped with radio transmitters (Tables 2.2 and 2.3). Mass, CCL, and CCW were different between male and female telemetered SSTs and were greater for females. Median CCL of females was 1.8 times larger than that of males (Mann-Whitney U-test; $W = 517, 506, \text{ and } 517$; $P < 0.01$; Fig. 2.5) and variance in mass, CCL, and CCW of telemetered SSTs were also greater for females (Brown-Forsythe test; $F = 9.14, 4.57, \text{ and } 4.17$; $P < 0.01$). Mass and CCL, mass and CCW, and CCL and CCW of both sexes were highly correlated with each other (Linear regression; $P > 0.01$, $R^2 > 60.3$; Fig. 2.5)

Turtles were located using a portable receiver (Lotek model SRX-400) equipped with a boat-mounted four-element Yagi antenna. At least 8 excursions of 7 to 10 d to locate telemetered SSTs occurred each summer (May through September) and at least once each spring (April) and autumn (October or November) from October 2009 through July 2012. Precise point locations were determined by passing the boat directly over SSTs or walking the riverbank and pinpointing SSTs using a hand-held three-element Yagi antenna. Point location accuracy, based on blind-trials with dummy tags, was ± 10 m. Point locations were deemed approximate if SSTs could not be located within about 25 m because of obscured telemetry signals or inability to access the specific area.

Latitude and longitude of SST point locations were recorded using a hand held Geographic Positioning System (Garmin GPS eTrex Legend, ± 15 m; Garmin Ltd., Olathe, KS; <http://www.garmin.com>) and converted to river kilometer (rkm) and projected onto 5-m orthoimagery using ArcMap version 10.0 (ESRI, Redlands, CA; <http://www.esri.com>). Two or more telemetered SSTs found within 50 m of each other were considered aggregated and recorded as such. We noted if each SST had moved in 24 h (using the transmitter mortality sensor) when SSTs were located during the onset of overwintering (October or November or both) in 2009, 2010, and 2011. Macro and microhabitat characteristics were documented at each location (see below). Telemetered turtles passing six remote radio telemetry stations managed by MTFWP (Fig. 2.1) were recorded; stations included two four-element Yagi antennas installed on riverbanks connected to receivers. Only one telemetry fix per remote station per turtle per day was included in analyses because SSTs could spend considerable time near remote stations.

The mean monitoring period of individual turtles was 721 d and ranged from 37 to 1,064 d. Mean number of telemetry fixes per turtle was 23 and ranged from 4 to 76 fixes. Median monitoring period and number of fixes did not differ between sexes (Mann-Whitney U-test; $W = 333$ and 352 , $P = 0.14$ and 0.06). Confirmation of shed transmitters was done 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. On an average excursion, 69% of turtles were located (range 46–90%). A total of 1,269 telemetry fixes were obtained with 801 precise hand fixes from

boat or shore with associated habitat information, 174 approximate point locations, and 294 fixes from remote stations.

Movement and Home Range

Weekly movement rates were calculated 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); the direction of movement was noted as upstream or downstream. Weekly movement rates (km/wk) represent minimum estimates because other movement could have occurred between sampling events (Rogers and White, 2007).

Movement rates were grouped into four temporal periods differentiated by streamflow and thermal patterns. Spring began at about river ice-off (early April), was characterized by increasing temperatures, and continued until peak streamflow (mid-June). Summer began immediately after peak streamflow, 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-flow and decreasing water temperatures. Winter began about 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. Winter movement rates were calculated from two points, the first obtained about immediately before ice formed and the second about immediately after ice melted.

Linear home range (LHR) of each telemetered SST was calculated by subtracting its furthest downstream rkm location from its furthest upstream rkm location, both overall

and by season. Distances moved into tributaries were added to mainstem LHRs for SSTs that were located in tributaries. Areal home range (AHR) of each turtle was calculated by multiplying the mean of main-channel stream widths at point locations of that turtle in that period, both overall and by season, by the corresponding LHR. Mean tributary width multiplied by the maximum distance moved into each tributary was added to AHR if the SST was located in tributaries.

Longitudinal Distribution and Habitat Selection

Longitudinal distribution was evaluated by dividing the study reach into 11 segments—i.e., ten 10-km main channel segments and one segment for all tributaries—and summing SST point locations per segment per season and for the original tagging locations to calculate frequencies. The original tagging distribution was then compared to seasonal distributions with chi-square tests (Manly et al., 2002).

Habitat selection by SSTs was evaluated at three different spatial scales. The Missouri River in our study area is largely laterally confined by canyons and badlands and does not have a typical alluvial alternating riffle-pool sequence. However, straight reaches and meandering reaches, reaches with and without islands, and riffles or small rapids occur where intermittent or ephemeral tributaries contribute large substrates (gravel, cobble, and boulder) to the main-stem river; runs occur otherwise. The entire 130-rkm study area was classified using aerial imagery and field observations and all spatial analyses were done using ArcMap. First, the geomorphic reach type was classified as straight (with or without islands) or meanders (with or without islands). Second, the

habitat unit was classified as riffle or run (with or without islands). Third, river bends were divided in the center and bend type was classified as inside or outside bends.

Selection of substrate was determined by comparing substrate at SST point locations to substrate availability in the study area. The predominant substrate at a point location was detected by probing (“feeling”) the river channel bottom at point locations with a hollow 1.2-cm wide and 3.5-m long electrical conduit (Bramblett and White, 2001; Bellgraph et al., 2008, Richards, 2012) and classified as fines (clay, silt, sand, or a combination thereof; 0–4 mm in diameter), gravel (5–64 mm), or cobble (65–300 mm). This method was validated with blind tests in areas with known substrates. Richards (2012) described the availability of substrate classes within the study reach (Fig. 2.2) and these data were used in this analysis. A point location for each month that each SST was alive was randomly chosen for annual and seasonal selection analyses to eliminate bias because all SST were not detected on every sampling occasion and the numbers of detections for individual animals were unequal (Rogers and White, 2007). Habitats occupied directly before ice-on (autumn) and after ice-off (spring) were considered winter habitats; most of the study area was inaccessible during winter. We assumed that the availability of geomorphic reach types, habitat units, river bends, and substrates did not change between years or among seasons.

Microhabitat Characteristics

We recorded channel type, distances to shore, depth, water velocity, and water temperature at each point location to describe SST microhabitat characteristics. Channel types were main channel, side channel, backwater, floodplain, and tributary.

Aggregations were described as in main channels, braided main channels, tributaries, or hibernacula (i.e., where and when they were found to occur). Distance to right and left riverbanks and total river width were measured using a laser range finder (model RX-1000; Leupold & Stevens, Inc., Beaverton, OR; <http://www.leupold.com>). Depth and velocity at point locations and in the adjacent river thalweg were measured using a boat-mounted depth sounder (Eagle Cuda 350; NAVICO, Catoosa, OK) or wading rod and boat-mounted velocity meter (Marsh-McBirney Flo-Mate 2000; HACH Company, Loveland, CO) or wading rod. Velocity measurements at each location were taken at the surface, mid-depth, and bottom of the water column. The mid-depth velocity was calculated from a single measurement, at 0.6 of depth, if depth was less than 1 m and from two measurements, at 0.2 and 0.8 of depth, if depth was greater than 1 m. We analyzed only bottom and mean-column water velocity at point locations because SSTs are largely located on the river bottom, but probably experience mean-column velocities when feeding, surfacing for air, and travelling (Graham and Graham, 1991; Graham and Graham, 1997). The mean-column velocity at each location was calculated from measurements made at the surface, middle, and bottom. Water temperature was measured, using a handheld or boat-mounted thermometer, at SST point locations and in the immediate main channel when SSTs were located in lateral habitats in May, June, and July of 2011 and 2012. Water temperature was also measured when SSTs were located during the onset of overwintering (October or November or both) in 2009, 2010, and 2011.

Ice Dynamics

Remote trail cameras (Moultrie, EBSCO Industries, Inc., Birmingham, AL) were placed at three SST overwintering reaches that we identified using radio telemetry and at three control reaches that we expected to experience more active ice dynamics. Control reaches were shallower with faster water velocities than hibernacula, and were located at river constrictions or tributary confluences (M. Scott, USGS, pers. comm.). Presence of untagged SSTs at control reaches was unknown. Remote trail cameras had wide views of the river, typically from high vantage points, and took pictures every 4 h from November through April 2010–2011 and 2011–2012 (or until batteries were drained). Two of the six cameras deployed each winter malfunctioned or were lost, 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 were nearly equal among cameras. Days with ice cover, freeze and thaw events, and ice jams at known hibernacula and control areas were counted and compared between years. We used stage height data from November through April of 2010–2011 and 2011–2012 from the USGS gauge on the Missouri River at the Fred Robinson Bridge near Landusky, Montana, to identify major freeze and thaw events and associated increases in discharge within the study site.

Statistical Analyses

Normality of all variables was examined using histograms, Q-Q plots, and Shapiro-Wilk tests. Homoscedasticity was examined using Levene, Brown-Forsythe (BF), or Bartlett's tests (Ramsey and Schafer, 2002). Sampling did not occur evenly among all years and only 28% of telemetered turtles remained ($N = 16$) by 2012 (Fig. 2.6);

sampling in 2009 only occurred in August and November and sampling in 2012 only occurred in April, May, and June. Variables were compared between years with similar sampling intensity (2011 and 2012), between sexes, and among seasons (for home range, movement rates, and habitat selection) or months (for habitat characteristics). Home ranges and movement rates were compared among seasons because they are calculated from two points sometimes temporally separated by several months. Selection ratios were compared among seasons to increase sample size, power, and ensure model convergence. Variables that were non-normal, heteroscedastic, had unequal group sample sizes, or a combination thereof were examined using non-parametric tests. Kruskal-Wallis tests (KW), linear regression (LR), Mann-Whitney U-tests (MWU), Pearson's chi-square tests (PX), Spearman's rank correlation coefficients (SR), or Wilcoxon signed-rank tests (WS) were used for statistical comparisons. Median values are compared and displayed in text for KW, MWU, and WS tests. Multiple comparisons following KW tests were completed with pairwise Wilcoxon rank-sum tests or Dunn's multiple comparisons tests (movement rate comparisons; Jaeger, et al. 2005) with Bonferroni's confidence interval adjustment (Ramsey and Schafer, 2002). Selection ratios with 90% simultaneous Bonferroni confidence intervals were calculated, using SST habitat data and availability data derived from ArcMap, and compared among years and among seasons for each habitat comparison to identify preference (ratio significantly > 1) or avoidance (ratio < 1) of habitats and substrate types using program R v3.0.1 and package adehabitat (Manly et al., 2002; Calenge, 2006; Rogers and White, 2006; R Development Core, 2013). Selection ratios are reported in the results for all habitat use analyses. All analyses were conducted

in R v3.0.1 or SigmaPlot v11 (Systat Software, San Jose, CA); statistical significance level for all analyses was $\alpha = 0.05$.

Results

Movement and Home Range

Movement was highly diverse among individuals, between sexes, and among seasons. Median weekly movement rates (hereafter movement rates) calculated for 46 females and 11 males were not statistically different in 2010 and 2011 (MWU; $W = 121213$, $P = 0.44$). Movement rates varied between sexes (MWU; $W = 333$, $P < 0.001$) and among seasons (KW; $\chi^2 = 134.13$, $df = 3$, $P < 0.001$; Fig. 2.7). Female movement rates varied highly in all seasons, were highest in the summer (0.3 km/wk, range 0–143.1 km/wk), lowest in the winter (0.0 km/wk, range 0–3.0 km/wk), and were not different in spring and autumn (Table 2.4). Male movement rates were most highly varied in summer (0.1 km/wk, range 0–68.5 km/wk), highest in autumn (0.1 km/wk, 0–1.4 km/wk), and lowest in winter (0.0 km/wk, 0–0.1 km/wk); median spring, summer, and autumn movement rates were similar and movement rates in winter were not significantly different from those in spring. Female median and maximum movement rates were higher than male median and maximum movement rates during each season and were especially higher during spring and summer. However, male median and maximum movement rates were higher than female median and maximum movement rates in winter (Table 4). Median upstream and downstream movements were not significantly different from each other overall (MWU; $W = 305878$, $P = 0.92$), in years 2010 and 2011 ($W = 74546$ and 31209 , $P = 0.83$ and 0.98), for females or males (MWU; $W = 34282$ and

39168, $P = 0.79$ and 0.78), or in spring, summer, autumn, or winter (MWU; $W = 13728$, 96437, 5916, and 2301; $P = 0.23$, 0.34 , 0.77 , and 0.87). Diel movements averaged 6.5 km (range 0.9–12.7 km) observed over a mean movement period of 9.21 h (range 1.2–17.8 h). The fastest diel movement (8.2 km upstream over 4.9 hours = 1.7 km/h) was by a female during summer.

Turtle movements were variable, but most SSTs moved between and inhabited different areas in the active (May–September) and overwintering periods (October, November, and April) each year. Most SSTs remained close to their original trapping locations whereas some made large movements up or downstream, or both, away from their origin from spring through autumn of each year (Fig. 2.8 and 2.9). Ten turtles (8 female, 2 male) moved more than ten kilometers (range 10.4–86.8 km) from May through July, but typically immediately before or after peak streamflow (Fig. 2.10). The majority of SSTs (81%, $N = 42$) generally made reciprocal movements upstream and downstream, or vice versa, each year from May through July and August through September (Fig. 2.10).

Number of SSTs found in tributaries, ephemeral side channels, and inundated floodplains (i.e., lateral habitats) generally increased from spring to summer and decreased thereafter in 2010 and 2011 (Fig. 2.11). Number of SSTs in lateral habitats in 2010 increased in May (17%), peaked in June (76%), and decreased in July (18%) and August (2%). However, number of SSTs in lateral habitats in 2011 increased from zero and peaked in May (76%) and decreased to zero after June (50%), July (14.5%), and August (2%). Number of SSTs in lateral habitats was positively related to discharge (LR; $P < 0.001$, $R^2 = 0.69$; Fig. 2.12). Mean movement from main channel areas to reach these

lateral habitats was 2.24 km by water (range 0.02–54.59 km). Mean absolute distance from the main channel into 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 (19%, $N = 8$). Median distance between active period areas and hibernacula (3.43 km; range 0.02–23.27 km) was not different between years 2010 and 2011 (MWU; $W = 517$, $P = 0.92$) or between males and females (MWU; $W = 177$, $P = 0.33$).

Linear home range and AHR of both females and males were highly variable among individuals and different among seasons (Fig. 2.13). Eighty-eight percent ($N = 51$) of SSTs were located on both sides of the river and only seven (12%, $N = 6$ female and 1 male) were found exclusively on one side of the river (justifying the use of mean-channel width to estimate AHR). Median LHR and AHR were not significantly different between years 2010 and 2011 ($W = 1254$ and 1131 , $P = 0.94$ and 0.98) or between males and females (MWU; $W = 231$ and 251 , $P = 0.67$ and 0.98). Median LHR was 6.98 km (range 0.85–86.85) and median AHR was 1.01 km^2 (range 0.08–16.95 km^2). Median LHR and AHR were both significantly different among seasons (KW; $\chi^2 = 72.22$ and 74.25 , $df = 3$, $P < 0.001$), but trends were similar between the two home range estimators. Median LHR in each season differed from all other seasons, but median AHR in spring was similar to median AHR in autumn (Fig. 2.13). Median LHR and AHR were largest in the summer (4.99 km and 0.73 km^2) and smallest in the winter (0.02 km and 0.01 km^2). Median summer LHR and AHR were 3 to 249 and 3 to 73 times larger than median LHR and AHR during any other season. No correlation existed between monitoring duration and LHR (SR; $\rho = 0.05$, $P = 0.71$) and weak correlation existed between total number of

telemetry fixes and LHR (SR; $\rho = 0.24$, $P = 0.07$). No correlation existed between monitoring duration and total number of telemetry fixes and AHR (SR; $\rho = 0.07$ and 0.08 , $P = 0.62$ and 0.54). Positive correlation existed between CCL and AHR for all SSTs pooled (SR; $\rho = 0.25$, $P = 0.02$) and nearly significant positive correlation existed between CCL and LHR (SR; $\rho = 0.31$, $P = 0.06$). However, no correlation existed between CCL and LHR or AHR of males (SR; $\rho = 0.31$ and 0.44 , $P = 0.34$ and 0.17), but CCL and LHR and CCL and AHR were positively correlated (SR; $\rho = 0.41$ and 0.44 , $P < 0.01$).

Interannual Site Fidelity and Aggregation

Individual SSTs inhabited and showed fidelity to different habitats in active (May–August) and overwintering (October, November, and April) periods among years. Thirty-four telemetered SSTs (60%) were observed inhabiting at least one tributary from May through July of 2010 through 2012 and about half (53%, $N = 18$) of these inhabited a tributary in consecutive years. Thirteen SSTs (72%) inhabited the same tributary in consecutive years and two (11%) occurred in the same tributary in three consecutive years; three SSTs (17%) inhabited different tributaries in consecutive years. Two tributaries (Bullwhacker and Cow Creek) were inhabited in May through July of all three years (2010, 2011, and 2012).

Forty-one turtles were observed for more than one year of overwintering; nineteen were observed for two years, and twenty-two for three years. Turtles overwintered an average of 1.7 km (range 0.006–25.0 km) from their previous hibernacula in consecutive years. Fifty-eight percent ($N = 11$) of SSTs observed for two years overwintered less than

1 km from their previous hibernacula in consecutive years (range 0.01–7.7 km); 1 SST (5%) overwintered within 1 km, 3 SSTs (17%) overwintered within 0.5 km, 1 SST (5%) overwintered within 0.1 km, and 6 SSTs (33%) overwintered within 0.05 km of their previous hibernacula. Sixty-eight percent of SSTs observed for three years ($N = 15$) overwintered less than 1 km from their 2009 hibernacula in 2010 (range 0.006–25.9); 4 SSTs (8%) overwintered within 0.5 km, 3 SSTs (14%) overwintered within 0.1 km, and 8 SSTs (36%) overwintered within 0.05 km of their previous hibernacula. Fifty-nine percent ($N = 13$) of SSTs observed for three years overwintered less than 1 km from their 2010 hibernacula in 2011 (range 0.01–22.69 km); 2 SSTs (18%) overwintered within 1 km, 2 SSTs (9%) overwintered within 0.5 km, 3 SSTs (14%) overwintered within 0.1 km, and 4 SSTs (18%) overwintered within 0.05 km. More than half of SSTs (54%, $N = 29$) observed for two or three years overwintered within 100 m (range 6–498 m) of their previous hibernacula in consecutive years.

Telemetered SSTs aggregated in different areas and at different times of the year (Fig. 2.14). Some SSTs were initially trapped together when transmitters were attached; however, the proportion of SSTs aggregating with SSTs they were not trapped with was higher (69%) than the proportion aggregating with SSTs they were trapped with (2%). The proportion of SSTs aggregating with SSTs with which they were and were not trapped was 39%.

Median aggregation size was 2 and ranged from 2 to 6 SSTs. Telemetered SSTs also aggregated with non-telemetered SSTs and these aggregations were observed to exceed 30 turtles in tributaries. Ninety-two aggregations of two or more telemetered SSTs were observed from October 2009 through June 2012. Double or triple detections

of the same groups of turtles were accounted for when they occurred in the overwintering period (i.e., October, or November, or both, and April) and in tributaries (May–August). Only one of the multiple related aggregations was used, reducing the number of unique aggregations to 66. We located unique aggregations at hibernacula (36%, $N = 24$), in braided main channels (near islands; 27%, $n=18$), in near-shore main channels (21%, $N = 14$), and in tributaries (15%, $N = 10$).

Turtles aggregated in different habitats at different times of the year, but the respective habitats were generally used at the same time of the year among years. Turtles generally aggregated in hibernacula in the winter (November through April), in braided main channels (near islands) and tributaries during the spring (May and June), in nearshore main channels in summer (August and September), and then back in hibernacula in the winter. However, the progression of these events was slightly different among years (Fig. 2.14). Ten aggregations were observed at hibernacula in October 2009 and six remained until April 2010. Eleven aggregations were observed at hibernacula in November 2010 and four remained until April 2011. Ten and four aggregations were observed in tributaries in May or June 2010 and 2011; two and one aggregations remained in a unique tributary from May through June 2010 and 2011. Only one aggregation was observed in a tributary in June 2012. Thirteen aggregations were observed in braided main channel habitats in 2010, seven were observed in 2011, and one was observed in 2012. One braided main channel aggregation remained from June through July of 2010 and another remained from May through June of 2011. Twelve aggregations were observed in main channel habitats in 2010, six were observed in 2011, and one was observed in 2012 from May through August. Main channel aggregations did

not persist in a unique location for a month or longer. Decreasing number of each type of aggregation from 2009–2012 is probably mostly attributable to attrition of telemetered turtles throughout these years.

Interannual fidelity of SST aggregations existed for 11 sites in four different habitat types (Fig. 2.14). Five different hibernacula had interannual aggregation occupation. One hibernaculum had interannual aggregation in 2010, 2011, and 2012, two in 2009 and 2010, and two in 2010 and 2011. Two tributaries had interannual aggregation occupation in late spring and early summer; Bullwhacker Creek was occupied in 2010, 2011, and 2012 and Cow Creek in 2010 and 2011. Two braided main channels had interannual aggregation occupation in mid to late summer, both in 2010 and 2011, in island complexes downstream of a tributary. One main-channel area was inhabited by a SST aggregation among years in late summer 2010 and 2011.

Longitudinal Distribution and Habitat Selection

Longitudinal distribution of turtles was similar among years and different among seasons. Longitudinal distribution of SSTs in 2010, 2011, and 2012 were similar (PX; $\chi^2 = 98.58, 39, \text{ and } 25.19$; $df = 90, 30, \text{ and } 27$; $P = 0.25, 0.12, \text{ and } 0.56$) and were similar to the initial tagging distribution (PX; $\chi^2 = 94.25, 88.29, \text{ and } 27.62$; $df = 80, 72, \text{ and } 24$; $P = 0.13, 0.09, \text{ and } 0.28$). Longitudinal distribution in the spring and summer were similar to the initial tagging distribution (PX; $\chi^2 = 95.88 \text{ and } 104.0$, $df = 88$, $P = 0.27 \text{ and } 0.12$) when turtles were widely distributed throughout the study site and also concentrated in tributaries (Fig. 2.15). However, the distribution of SSTs shifted significantly from the original tagging distribution during autumn and winter (PX; $\chi^2 = 78 \text{ and } 91$, $df = 56 \text{ and }$

64, $P = 0.03$ and 0.01) when turtles were less widely distributed and not found above rkm 3,170 or below rkm 3,090.

Habitat selection trends of telemetered SSTs were similar among years for each habitat classification and substrate comparison. High variation among individual SSTs caused wide selection-ratio confidence intervals that overlapped preference (> 1), no preference (1), avoidance (< 1), or a combination thereof. Strong annual selection was observed in substrate and bend type (inside or outside) comparisons, but sparse evidence of annual selection was observed for geomorphic reach type or habitat unit (Fig. 2.16). Turtles avoided cobble and preferred fine substrates in 2010, 2011, and 2012 (cobble, < 0.2 , SE = 0.0–0.1; fine, > 3.4 , SE = 0.1–0.3). Selection was not observed for gravel substrate in 2010 (1.0, SE = 0.2), but gravel was moderately avoided in 2011 (0.6, SE = 0.1) and 2012 (0.7, SE = 0.4). Turtles avoided inside bends and preferred outside bends in 2010 (inside, 0.6, SE = 0.1; outside, 1.3, SE = 0.1), but showed only moderate avoidance of inside bends and moderate preference for outside bends in 2011 (inside, 0.9, SE = 0.1; outside, 1.1, SE = 0.1). We were unable to calculate estimates, or obtained very wide confidence intervals, or both for several 2012 habitat selection comparisons and we attributed this to low sample sizes (e.g., 0 observations for riffles and bends without islands in 2012) in certain habitat categories.

Strong seasonal preference was observed in substrate and bend type (inside or outside) comparisons, but little evidence of seasonal selection was observed for geomorphic reach type or habitat unit (Fig. 2.17). The highest preference was for outside bends (1.5 and 1.4, SE = 0.1 and 0.2) and the greatest avoidance was for inside bends in the autumn and winter (0.5 and 0.6, SE = 0.1 and 0.2, respectively). Fine substrate was

preferred (>2.8 , $SE = 0.1-0.2$) and cobble substrate was avoided (<0.2 , $SE = 0.0-0.1$) in all seasons. Moderate preference was observed for riffles in the spring (1.6 , $SE = 0.5$), but moderate avoidance of riffles was observed in autumn (0.6 , $SE = 0.3$). Moderate preference was observed for bends with islands (1.5 , $SE = 0.3$) whereas moderate avoidance was observed for straight reaches without islands in the spring (0.6 , $SE = 0.2$). Gravel substrate was also moderately preferred in the summer and autumn (1.3 and 1.9 , $SE = 0.3$ and 0.4), but moderately avoided in the spring and winter (0.3 and 0.2 , $SE = 0.2$ and 0.2).

Microhabitat Characteristics

Microhabitat characteristics at SST point locations did not differ between sexes (MWU; distance to shore, $W = 19777$, $P = 0.53$; depth, $W = 26059$, $P = 0.77$; difference between thalweg and point location depth, $W = 17784$, $P = 0.21$; velocity, $W = 9585$, $P = 0.09$; bottom velocity, $W = 9899$, $P = 0.23$; difference between temperature in main channel and lateral habitats, $W = 393$, $P = 0.54$), but occasionally varied among years and months. Habitat characteristics of locations occupied were generally similar within active (May–August) and overwintering (October, November, and April) periods, but were different between active and overwintering periods.

Median distance to shore (DTS) did not vary between years 2010 and 2011 (MWU; $W = 38861$, $P = 0.43$), but did vary among months (KW; $\chi^2 = 216.77$, $df = 6$, $P < 0.001$; Fig. 2.18). Distance to shore was highest in October (14.0 m; range $4.0-44.0$ m) and similar to DTS in November (14.0 m; range $5.0-27.0$ m) and April (13.7 m).

Distance to shore was lowest in May (2.0 m; range 0.0–47.5 m) and was not different from DTS in June (1.5 m), July (1.2 m), or August (2.0 m).

Median depth at point locations (depth) did not vary between years 2010 and 2011 ($W = 3886$, $P = 0.43$), but did vary among months (KW; $\chi^2 = 346.84$, $df = 6$, $P < 0.001$; Fig. 2.19) and was highest in November (2.3 m; range 1.2–3.3 m). Depth in November was different from depth in all other months and depth in October (1.9 m) was similar to depth in April (1.7 m). Depth was lowest in July (0.5 m; range 0.0–2.8 m) and was not different from depth in May (0.5 m), June (0.5 m), or August (0.6 m). Depth at point locations also varied by habitat type (KW; $\chi^2 = 53.29$, $df = 4$, $P < 0.001$; Fig. 2.20), was highest in main channel habitats (0.8 m; range 0–3.4 m), and lowest in tributaries (0.4 m; range 0–1.7 m). Depth in main channel habitats was different from depth in all other habitat types except in inundated floodplain habitats (0.7 m; range 0.3–2.2 m).

Depth at SST point locations was shallower than median depth in the adjacent river thalweg (thalweg depth; WS; $V = 0$, $P < 0.001$; Fig. 21). Median thalweg depth was 2.6 m (range 0.1–7.0 m) and was 3.2 times higher than point location median depth (0.80 m; range 0–4.2 m). Median difference between thalweg depth and location depth (delta depth) was 1.4 m (range 0.0–5.7 m) and varied between years 2010 and 2011 (MWU; $W = 13082$, $P < 0.001$). Delta depth in 2011 was 2.1 m (range 0–5.7 m) and was 2.5 times higher than the delta depth in 2010 (0.9 m; range 0.0–4.5 m). Delta depth also varied by month (KW; $\chi^2 = 166.94$, $df = 6$, $P < 0.001$; Fig. 2.21). Delta depth was lowest (more similar to thalweg depth) in November (0.4 m; range 0.1–1.7 m) and was similar to delta depth in October (0.5 m; range 0–3.1 m) and April (0.7 m; range 0–2.7 m). Delta depth was highest (less similar to thalweg depth) in May (3.7 m, 0–5.7 m) and was different

from delta depth in June (1.3 m; range 0–4.7 m), July (2.3 m; range 0–5.5 m) and August (1.5 m; range 0–3.7 m).

Median column water velocity at point locations (velocity) varied between 2010 and 2011 (MWU; $W = 15604$, $P = 0.04$) and was higher in 2011 (0.2 m/sec; range 0–1.5 m/sec) than in 2010 (0.11; range 0.0–1.3). Velocity varied among months (KW; $\chi^2 = 119.82$, $df = 6$, $P < 0.001$; Fig. 2.22) and was highest in April (0.5 m/sec; range 0.1–1.0 m/sec). Velocity in April was similar to velocity in both October (0.4 m/sec) and November (0.5 m/sec). Velocity was lowest in May (0.0 m/sec; range 0.0–1.3 m/sec) and was similar to velocity in June (0.0 m/sec) and July (0.1 m/sec).

Median bottom velocity at point locations (bottom velocity) did not vary between 2010 and 2011 (MWU; $W = 16392$, $P = 0.20$). Bottom velocity varied among months (KW; $\chi^2 = 125.93$, $df = 6$, $P < 0.001$; Fig. 2.22) and was highest in April (0.46 m/sec, range 0.1–0.9 m/sec) and was statistically similar to bottom velocity in both October (0.3 m/sec) and November (0.4 m/sec). Bottom velocity was lowest in May (0.0 m/sec, range 0.0–1.2 m/sec) when it was similar to bottom velocity in June (0.0 m/sec), July (0.1 m/sec), August (0.1 m/sec), and October (0.3 m/sec).

Velocity and bottom velocity also varied by habitat type (KW; $\chi^2 = 128.64$ and 114.12 , $df = 4$, $P < 0.001$; Fig. 2.23), were highest in main channel habitats (0.3 and 0.2 m/sec; range 0.0–1.7 and 0.0–1.6 m/sec), and lowest in tributaries (0.0 m/sec; range 0.0–0.5 and 0.0–0.5 m/sec) and backwaters (0.0 m/sec; range 0.0–0.2 and 0.0–0.1 m/sec). Velocity and bottom velocity in main channel habitats were different from velocity and bottom velocity in all other habitat types except side channels (0.1 and 0.1 m/sec; range 0.0–1.0 and 0.0–0.8 m/sec).

Velocity was lower than median mean-column velocity in the adjacent thalweg (thalweg velocity; WS; $V = 98$, $P < 0.001$; Fig. 2.24). Median thalweg velocity was 1.4 m/sec (range 0.0–3.0 m/sec) and was 5.6 times higher than median velocity (0.2 m/sec; range 0.0–1.7 m/sec). Median difference between thalweg velocity and velocity (delta velocity) was 1.1 m/sec (range -0.5–3.0 m/sec) and varied among months (KW; $\chi^2 = 98.94$, $df = 5$, $P < 0.001$; Fig. 2.24). Delta velocity was lowest in November (0.36 m/sec; range 0.1–0.8 m/sec) when similar to delta velocity in April (0.4 m/sec; range 0.0–1.1 m/sec). Delta velocity was highest in July (1.6 m/sec; range 0.1–2.9 m/sec) and was similar to delta velocity in May (1.5 m/sec) and June (1.4 m/sec). No thalweg velocity measurements were made in October because of velocity meter malfunctions. Comparisons between years could not be made because thalweg velocity measurements did not begin until April 2011.

Median water temperature in lateral habitats (lateral temperature) was higher than median temperature in the adjacent main channel (main temperature) when SSTs inhabited lateral habitats (WS; $V = 78.5$, $P < 0.001$; Fig. 2.25). Lateral temperature was 17.9 °C (range 12.9–35.4 °C) and was 1.2 times higher than main temperature (15.1 °C; range 12.8–24.3 °C). The median difference between lateral and main temperatures (delta temperature) was 1.1 °C (range -0.2–17.4 °C) and did not vary between years ($W = 498$, $P = 0.10$), but did vary by month (KW; $\chi^2 = 6.78$, $df = 2$, $P < 0.05$). Delta temperature was highest in June (1.9 °C; range 0–17.4 °C) and lowest in May (0.5 °C; range -0.2–9.3 °C). Delta temperature was similar between July (1.1 °C; range -0.1–2.3 °C) and June, and May and July.

Percent of SSTs that were active (# of SSTs that moved in 24 h or less / # located) in October, November, or April was weakly and positively related to average water temperature (LR; $F = 12.21$, $df = 1$ and 3 , $P = 0.04$, $R^2 = 0.80$; Fig. 2.26). Percent active SSTs was highest in October 2010 (53%) when average water temperature was 7.8 °C and was lowest in November 2010 (5%) when average water temperature was 3.3 °C.

Ice Dynamics

River geomorphology 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.

Ice conditions differed in the two winters. The winter of 2010–2011 was colder, had more precipitation, and had ice cover for more days than winter 2011–2012. Only a single major freeze event, and a single major thaw event, occurred in 2010–2011 whereas three major freezes and thaws occurred in 2011–2012 based on photographic evidence and gauge height data (Fig. 2.27). Complete ice cover at camera locations averaged 95 days (range 24–126 days) in 2010–2011 and 29 days (range 4–88 days) in 2011–2012. Photographs revealed the creation and destruction of ice jams and fluctuations in the gauge height revealed large variation in discharge and river stage during freeze and after breakup events (Fig. 2.27).

Ice formation and breakup differed at hibernacula and control reaches. In hibernacula, frazil ice aggregated and created border ice and eventually spanned the

width of the river. Subsequent flows of frazil ice were often overtopped existing ice at hibernacula. In control reaches, anchor ice formed on riffles and island boundaries and subsequent frazil ice flows were often forced under the initial ice layer.

Breakup of ice appeared to be primarily due to melting at hibernacula (thermal breakup; sensu Beltaos, 2003) whereas mechanical breakup of ice commonly occurred at control reaches. The thalweg normally melted first at hibernacula, and then large sections of thermally-degraded border ice broke off and were slowly carried away by main channel flows. Only one small ice jam was observed at hibernacula, in 2010–2011, and it was upstream and on the opposite bank from the hibernaculum location.

At control reaches, adjacent upstream tributaries contributed melt water that overtopped main channel ice, creating ice jams that subsequently broke and quickly cleared the reach downstream. Flows of ice from upstream, following the initial breakup, often grounded on riffles and islands near control sites creating other ice jams. A total of seven ice jams was observed in or adjacent to the main channel thalweg at control sites. Five ice jams occurred in 2010–2011 and two ice jams occurred in 2011–2012. Ice jams and flows produced considerable riverbed and riparian scour, most often at riffles, river constrictions, and upstream points of islands. Some islands were completely covered and scoured by ice in 2011.

Mortality

Two male turtles (code 81 and 67) were found dead; one turtle died in October 2009, 43 days after capture, and another died in July 2011, 688 days after initial capture. The first was located on a main channel shoreline by a fisherman and had died of

unknown causes. The second was found in a tributary underneath about 10–15 cm of dried silt, and may have died when the mudflat it inhabited dried and prevented its return to the main channel; this male was a particularly small individual. Five shed tags were found on or near shorelines tangled in dry vegetation or mudflats. Eighteen tags were located in mudflats or under large boulders, but they were never recovered and were concluded to be shed after six months of immobility during the active period. These tags may have been shed because of malfunctioning attachments or entanglement in vegetation or substrate.

Discussion

Our study was the first to describe SST movements and habitat use in a large river-floodplain ecosystem in the northwestern portion of the range of the species. Biological function and environmental conditions (e.g., streamflow and temperature) strongly influenced spatiotemporal movement and habitat of SSTs in this large river-floodplain ecosystem. The fundamental periods in the annual cycle of SSTs in this ecosystem were runoff, nesting, post-nesting, and hibernation periods and SST behavior differs among these periods.

Turtles dispersed from main-stem hibernacula as water temperature and streamflow increased above those that inhibit SST motor function ($< 5^{\circ}\text{C}$; Jackson et al., 2001; Ultsch, 2006; Jackson and Ultsch, 2010) during the runoff period. Thus, rising temperature is probably the initial environmental cue in this period to initiate movement; as poikilotherms, turtles are reliant on temperature for physical activity and metabolism.

Coincident with increasing and peaking streamflow in the runoff period, we observed that most turtles moved out of mainstem hibernacula into inundated lateral habitats such as tributary confluences, floodplains, and backwaters. In 2011, when streamflow had an annual exceedance probability of 4–10%, we observed a higher proportion of telemetered turtles in lateral habitats. These habitats were typically near-shore with shallow depth, slow to no water velocity, fine substrates, and higher water temperatures than in the mainstem. Such areas seem to be important during this period because some turtles moved considerable distances, aggregated, and showed interannual fidelity to particular tributary confluences.

Turtles may occupy lateral habitats to avoid peak flows and displacement, 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; MacCulloch and Secoy, 1983; Galat et al., 1998). However, displacement may be relatively unimportant given that SSTs are highly adapted to lotic conditions; moreover, the closely related smooth softshell, *Apalone mutica*, readily returned upstream following displacement (Plummer and Shirer, 1975). We observed higher temperature in lateral habitats and turtles that aggregated there may have been seeking higher temperature to facilitate egg development, metabolism, and growth. Moreover, turtles occupying warm lateral habits could thermoregulate in warm refuges without increasing their predation risk by basking on land. Prey fish densities can be high in lateral habitats in large river-floodplain ecosystems, particularly during this period, and may provide a reliable seasonal food source to expedite SST growth (Gibbons and Semlitsch, 1982; Iverson, 1991; Galat et al., 1998). Turtles may also locate and exploit influxes in carrion; we

located SSTs directly under partially submerged white-tailed deer (*Odocoileus virginianus*) carcasses on three separate occasions, two of which were in tributary confluences. Lateral habitats could also provide an opportunity for mating because SSTs aggregated there preceding nesting (Moll and Moll, 2004; Chapter 3). Lateral habitats were probably also preferred because they were generally dominated by fine substrates and SSTs often bury beneath submerged substrates (Graham and Graham, 1991 and 1997). We frequently pinpointed telemetered turtles and found them buried in 5-10 cm of fine or mixed (gravel and sand) substrate in shallow water where they could extend their neck and reach the water surface. Spiny softshell turtles probably sit and wait under water, partially or entirely buried in substrate, to ambush prey swimming near them (Moll and Moll, 2004).

Riffles and braided reaches moderately preferred during the runoff period generally occurred downstream of tributaries; therefore, SSTs may have just passed through and briefly inhabited riffles and braided reaches when moving to and from tributary confluences. However, riffles and braided reaches are complex, provide heterogeneous habitats, and probably provide similar benefits to SSTs as lateral habitats do; complex braided habitats may also provide adequate nesting habitats.

During the nesting period (late June and July, Chapter 3), streamflow decreased from peak and water temperatures continued to increase. As river stage decreased, lateral habitats dried, and turtles occupying them dispersed. Tributaries were mostly dry by late July and most turtles had moved back to the main stem. More terrestrial habitats, including nesting beaches (Chapter 3), were exposed and braided habitats became more complex. Female turtle movements (distance and rate) was higher than that of males in

all seasons, but was especially so during the nesting period. This trend was similar to SSTs in Lake Champlain in Canada (Galois et al., 2002), but converse to SSTs in a small Arkansas stream when males moved more than females (Plummer et al., 1997). However, results of our study are biased towards females because we intentionally telemetered more female turtles to study SST nesting ecology. Female movements made before and after peak streamflow were probably associated with nest-site selection because many nests were located within the study site in 2011 and 2012 (Chapter 3). Furthermore, female SST movement rates may increase proximate to peak streamflow to facilitate arrival at nesting habitat as it becomes exposed with receding streamflow (Chapter 3). During the 2011 flood event, we observed females along shorelines at known nesting habitats prior to the recession of river stage and exposure of nesting beaches. Thus, increasing-to-peak and decreasing-from-peak streamflow may cue nesting-related movements. However, large movements by both sexes could be exploratory or temporally irregular movements (“extrapopulational movements” sensu Gibbons et al., 1990) in search of mates, food, or shelter (Gibbons et al., 1990; Moll and Moll, 2004).

During the nesting period, most turtles occupied and aggregated in braided reaches and near shorelines of islands or riverbanks with shallow depth, slow to no water velocity, and warmer temperature relative to the main channel thalweg. Turtles probably moved into braided reaches because islands generally provided heterogeneous habitats that included shallow water and basking habitats (rocks, logs, and shorelines with sparse vegetation; Chapter 3) to forage and thermoregulate. Moreover, braided reaches also provide nesting habitats (sand or sand and gravel shorelines with scant vegetation, particularly on islands; Chapter 3) for females to oviposit. Large, ostensibly

reproductively active females, were staging outside known nesting areas that were typically islands with mixed gravel and sand substrates, which may explain why gravel substrates were moderately preferred during the nesting period.

Streamflow decreased and stabilized at base flow and water temperatures decreased during the post-nesting period (late July–September). Lateral habitats became dry and aquatic mainstem and braided habitats became more heterogeneous. Most SSTs moved out of braided reaches and into nearshore mainstem habitats. Nearly all SSTs moved towards hibernacula before temperatures decreased below thermal limits for SST activity ($< 5^{\circ}\text{C}$; Jackson et al., 2001; Ultsch, 2006; Jackson and Ultsch, 2010).

Decreasing temperatures may therefore initiate movement to hibernacula. Migration of riverine turtles to aquatic hibernacula has also been reported for *A. spinifera* in Vermont and Quebec (Graham and Graham, 1997; Galois et. al, 2002), *Chrysemys picta* in southeastern Michigan (Sexton, 1959), *C. marmorata* in northern California (Reese, 1996), and *Emydoidea blandingii* in Massachusetts (Butler and Graham, 1995). Female movement rates decreased in this period, suggesting that movement for nest-site selection is more intense than movement to hibernacula. Male movement rates were higher in the post-nesting period than in any other period. Higher male movement in this period is probably related to searching for optimal hibernacula, but could also be attributed to locating suitable mates within optimal hibernacula. Males of other lentic turtle species also made long-range movements that were attributed to increased female encounter rates and mating events (Morreale et al., 1984; Gibbons, 1986; Tuberville et al, 1996). Areas inhabited during the post-nesting period were generally near-shore with shallow depth and slow to no water velocity. However, habitat characteristics during this period were

sometimes transitional and more similar to overwintering habitats that were generally between the thalweg and shoreline with moderate depth and water velocity.

The lowest river discharge and water temperatures occurred in the overwintering period (October–April) when ice covered the majority of the river for most of the period. Most turtles moved from near shore mainstem and braided habitats into main stem hibernacula, or were already in hibernacula. Aggregation during this period suggests that hibernacula provide opportunities to mate immediately before or after thaw, provide specific characteristics facilitating overwinter survival, or are limited throughout the study site (Kuchling, 1999; Bodie and Semlitsch, 2000; Moll and Moll, 2004; Ultsch, 2006; Ernst and Lovitch, 2009). The active period in the extreme northern range of the species is truncated. Aggregation can localize mate searching and reduce mating-related movements occasionally made by males (Morreale et al., 1984; Gibbons, 1986; Tuberville et al, 1996; Kuchling, 1999; Bodie and Semlitsch, 2000; Moll and Moll, 2004; Ernst and Lovitch, 2009). Immediate post-thaw movement (as we observed to lateral habitats) or reliance on sperm storage would need to occur to ensure annual reproduction if aggregation and mating at hibernacula did not occur. A truncated active period may be another factor, along with scarcity of mates, selecting for the sperm storage mechanism in turtles (Gist and Jones, 1989).

Hibernacula were similar to those of other populations of SSTs in the northern range of the species—usually in outside bends of main channel reaches without islands, between shore and river thalweg, and with ample depth and water velocity (Graham and Graham, 1997; Galois et al., 2002). Turtles remain in a state of metabolic depression for up to six months during this period and habitat characteristics at hibernacula ostensibly

facilitate survival (Ultsch, 2006). Spiny softshell turtles are one of the most anoxia intolerant turtles (Reese et al., 2003) but are capable of acquiring all metabolic oxygen demands directly from well-oxygenated water (Jackson et al., 2001). As a consequence, moderate water velocity is probably the major determinant in the distribution of hibernacula of anoxia-intolerant species such as SSTs (Ultsch, 2006). Moderate velocity would provide adequate dissolved oxygen for SSTs without displacing them. High velocity and river stage changes during ice formation and breakup could displace hibernating SSTs if low water temperatures restricted locomotory activity ($< 5^{\circ}\text{C}$; Jackson et al., 2001; Ultsch, 2006; Jackson and Ultsch, 2010). Turtles may therefore anchor or bury in substrate to avoid displacement (Graham and Graham, 1991), which may explain why friable substrates were preferred during this period. However, we speculate that complete burial in fine substrates may reduce oxygen uptake during hibernation.

Winter distribution and choice of hibernacula may be influenced by riverine ice dynamics. Ice formation and breakup and scour differed at camera-monitored hibernacula and control sites. Ice melted gradually at hibernacula without forming ice jams in contrast to control sites where ice broke up frequently, jammed, and scoured the substrate. Moreover, hibernacula may have provided protection from deep ice scour because they were relatively deep. At control sites, the riverbed and any SSTs overwintering would be vulnerable to displacement, freezing, or scour because shallow depth would not be adequate for ice to drift without scouring the substrate. Riffles and other shallow water habitats were avoided during overwintering; SSTs may occupy deeper depths to avoid freezing and deep ice scour (Scrimgeour et al., 1994; Ultsch, 2006). Fish also 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; Mitro and Zale, 2002; Karchesky and Bennett, 2004; Muhlfeld and Marotz, 2005).

Differences in ice dynamics between years (number of days of ice cover and number of thaws and ice jams) were probably a result of colder temperatures and higher precipitation in winter 2010–2011 as compared to 2011–2012. More freeze and breakup events could increase the chance of ice scour; however, more ice jams occurred in the colder year. Ice jams are probably more related to the magnitude of the freeze, which influences ice thickness and percent ice cover, rather than the number of freeze and thaw events. Climate change will undoubtedly continue to influence future temperature and precipitation patterns and thus the severity of ice dynamics that influence SST distribution.

Riverine turtles are seasonally or ontogenetically dependent on various habitats in river-floodplain ecosystems throughout their life cycle (Bodie and Semlitsch, 2000; Anderson et al., 2002; Moll and Moll, 2004; Ernst and Lovitch, 2009). Spiny softshell turtles in a large-floodplain ecosystem at the northern extent of their range experienced high and variable streamflow, indeterminate timing of habitat availability, often cold and prolonged winters, and sometimes powerful ice dynamics. Possibly limited and spatiotemporally separated fundamental habitats necessitated movement, aggregation, and fidelity of SSTs to occupy habitats that provided specific resources needed to complete life history processes, as do other riverine turtles (Gibbons et al., 1990; Graham and Graham, 1997; Bodie, 2001; Galois et al., 2002; Moll and Moll 2004).

Conservation Implications

This was the first study to investigate the natural history and ecology of SSTs in the Missouri River in Montana. This population could be especially sensitive to various forms of disturbance because it is disjunct from the nearest downstream SST populations by over 200 km and a dam and reservoir, is at the extreme northern extent of the range of the species, has a truncated active period, and individuals within the population make seasonal movements for nesting and overwintering. Changes to the already quasi-natural flow regime, habitat alteration, or increasing human activities could affect SST populations by creating asynchrony between environmental cues and movement, reducing or eliminating critical habitat, reducing population abundance, or a combination thereof. The persistence of a population could be imperiled in only a few years because of the annual loss of reproductively active females in addition to natural mortality (Congdon et al., 1993, 1994; Garber and Burger, 1995). Disjunct populations such as this one are especially vulnerable to extirpation because of limited possibilities for recolonization.

Spiny softshell turtles have inhabited the Missouri and Mississippi rivers for millions of years (Parmley, 1992; Holman and Andrews, 1994). Their life-history strategy is probably dependent on local environmental conditions, similar to other species there (Wildhaber et al., 2011), evolving their life-history strategies in direct response to natural flow regimes (Bunn and Arthington, 2002). Changes to peak streamflow timing, duration, and magnitude could influence SST movement, habitat selection, and survival by altering seasonal temperatures, altering the availability and suitability of habitats, reducing sinuosity and habitat heterogeneity, or altering ice dynamics and locations of ice scour. The installation of new dams could also negatively influence SST populations by

further dividing the Missouri River population and increasing the chances of a genetic bottleneck. Dams or channelization or both could decrease habitat heterogeneity and alter, change the locations of, or eliminate shallow-water habitat used by SSTs in the summer for feeding and reproduction and deep-water hibernacula used for overwintering (Plummer et al., 1997; Barko and Briggler, 2006). Dams could reduce the ability of SSTs to colonize new areas and range termination can occur when optimal habitats become reduced in size or number because turtle dispersal abilities over large adverse stretches typically are not adequate to colonize new optimal patches (Shively and Jackson, 1985). However, other anthropogenic influences such as human presence may also influence SST distribution and persistence in the Missouri River in Montana.

Hunting, fishing, camping, and river floating on kayaks, canoes, and motorized boats are the most common land uses within the study site and the presence of humans in relatively pristine habitat can be as detrimental to turtles as habitat degradation (Garber and Burger, 1995). Recreation within the study site is largely limited to non-motorized traffic during the nesting period, but all motorized traffic is allowed during autumn. Basking and nesting are important for SST thermoregulation, incubation, and reproduction and could be influenced by river recreation because of the wary nature of this species while on land (Bolton, 2007). Increased boat traffic near heavily used basking and nesting habitats could cause SSTs to abandon heavily used basking and nesting habitats. This could decrease opportunities for behavioral thermoregulation, which may be important for egg development, or cause SSTs to move further distances to find secluded habitats, which is energetically costly. These disturbances eventually led to limitations on recreation near critical nesting sites in Lake Erie because female SSTs

would not return to cover abandoned nests and this often led to nest failure (Bolton, 2007). Traumatic injuries caused by recreational activities, such as boating or fishing, have also been documented; SSTs are exceptionally susceptible to propeller injury because of their affinity for shallow water (e.g., water depth < 1.5 m; Gibbons et al., 2001; Moll and Moll, 2004; Galois and Ouellet, 2007). We documented no boat-induced injuries, but anglers frequently hooked SSTs, which were usually cut free leaving hooks in their mouths or, less commonly, killed.

We suggest two forms of management to reduce negative influences on SST populations and three areas for future research to increase our understanding of their ecology in the Missouri River in Montana. First, maintaining near-natural streamflow with a single peak would preserve possible movement cues, promote sinuosity and habitat heterogeneity, provide SSTs access to shallow lateral habitats in the summer, reduce the possibility of nest inundation by late flows, and maintain diverse habitats fundamental for SST feeding, mating, nesting, and overwintering. Second, public outreach and restrictions on floater (e.g., kayaks, canoes, and rafts) and motorboat activity could reduce possible negative influences by keeping traffic away from nesting sites and reducing the chance of propeller injury, nest abandonment, and increased mortality. Additionally, signs at popular angling locations could be used to suggest that anglers free SSTs that are inadvertently hooked.

Estimation of population abundance and population viability analyses may be important next steps in understanding SST ecology on the Missouri River in Montana because they are unknown there. Moreover, genetic analyses would determine if Missouri River populations are experiencing a genetic bottleneck that could negatively influence

the survival of these disjunct SST populations. Sparse data exists for river-floodplain ecosystem managers to base management decisions on nongame wildlife, such as turtles (Galat et al., 1998). The continued survival of SSTs in the Missouri River in Montana is largely dependent on furthering our understanding of the ecology of the species there. This will aid in protecting populations and critical habitats and managing anthropogenic effects.

Acknowledgments

Funding for this project was provided by PPL Montana, USFWS, MTFWP, and the Bureau of Reclamation. This study was conducted under the auspices of Montana State University Institutional Animal Care and Use protocols #2009–19 and #2012–24, two MTFWP scientific collection permits (#2009–056 and #2010–050), and a USFWS special use permit (#10–012). We thank M. Plummer from Harding University, J. Chaffin and J. Peters from the U.S. Bureau of Land Management, L. Hanauska-Brown from Montana Fish, Wildlife & Parks, and D. Trimpe and J. Kucera from the U.S. Bureau of Reclamation for logistical support. We thank J. Rotella, S. Leathe, and E. Kenison for comments on this manuscript. We also thank A. Dood, C. Jensen, C. Manning, M. Mayfield, D. Moore, A. Reinhold, R. Richards, T. Ritter, and Z. Wenderott for invaluable logistical support and assistance with data collection or analysis. We also thank the Lewistown, Montana, USFWS and MTFWP offices and employees for shuttling vehicles and other logistical support; specific thanks to J. Dillum, R. Potts, and J. Fox. The Montana Cooperative Fishery Research Unit is jointly sponsored by the U.S. Geological Survey, Montana Fish, Wildlife & Parks, Montana State University, and the U.S. Fish

and Wildlife Service. The use of trade names or products does not constitute endorsement by the U.S. Government.

Tables

Table 2.1. Missouri River discharge summary statistics from USGS gaging station 06115200 on the Missouri River at the Fred Robinson Bridge near Landusky, Montana, for water years 2010–2012 and the average at this site (1934–2012).

Variable	Water year			
	2010	2011	2012	Average
Annual median flow (m ³ /sec)	201.3	261.9	195.4	193.1
Standard deviation	164.3	361.9	81.2	113.2
Maximum daily mean flow (m ³ /sec, date)	945.8 (6/20)	2,019.0 (6/11)	512.5 (6/11)	3,851.1 (6/6/1953)
Minimum daily mean flow (m ³ /sec, date)	138.5 (12/9)	139.3 (2/2)	96.3 (1/20)	34.5 (12/13/1936)
Annual runoff (million acre-ft)	6.8	10.7	6.0	6.5

Table 2.2. Numbers of *Apalone spinifera* fitted with radio transmitters (Fitted), numbers that became undetectable or were unconfirmed shed transmitters (Lost), and numbers of confirmed shed transmitters (Shed) by year. Sample size denotes number of active transmitters at the end of each year.

Year	Fitted	Lost	Shed	Dead	Sample size
2009	54	0	0	1	53
2010	4	4	7	0	46
2011	0	10	13	1	22
2012	0	19	3	0	0
Total	58	33	23	2	

Table 2.3. Means and standard deviations of mass, curved carapace length (CCL), curved carapace width (CCW), monitoring period, and number of point locations of 46 female and 11 male telemetered *Apalone spinifera* in the Missouri River in Montana from 2009 through 2012. Number of point locations includes the total number of times each turtle was located by hand fixes and remote station fixes.

	Females		Males		Pooled	
	Mean	SD	Mean	SD	Mean	SD
Mass (g)	2597.8	721.0	540.7	123.8	2207.7	1041.1
CCL (mm)	320.6	36.3	180.3	9.2	294.0	64.5
CCW (mm)	264.9	21.9	160.9	7.8	245.1	45.7
Period (d)	748.8	292.1	600.5	294.0	720.7	295.8
Locations (n)	25.7	17.1	16.2	10.1	16.2	16.4

Table 2.4. Minimum, maximum, median, and standard deviation of total weekly movement rates (km/week) by sex and season of telemetered *Apalone spinifera* in the Missouri River in Montana from 2009 through 2012. Pooled weekly movement rates were significantly different between sexes. Letters indicate significant differences in median movement among seasons; seasons with the same letter are not significantly different.

Variable	Period	N turtles	n obs.	Min	Max	Median	SD
Female movement (km/week)	Pooled	46	1082	0.00	143.07	0.13	10.36
	Spring ^a	44	224	0.00	128.38	0.06	10.33
	Summer ^b	46	635	0.00	143.07	0.31	12.03
	Autumn ^a	45	156	0.00	9.14	0.06	1.18
	Winter ^c	38	67	0.00	3.02	0.00	0.37
Male movement (km/week)	Pooled	11	187	0.00	68.54	0.06	5.55
	Spring ^{a,b}	9	35	0.00	1.03	0.05	0.26
	Summer ^a	11	109	0.00	68.54	0.08	7.33
	Autumn ^a	11	33	0.00	1.45	0.09	0.34
	Winter ^b	8	10	0.00	0.05	0.00	0.02

Figures

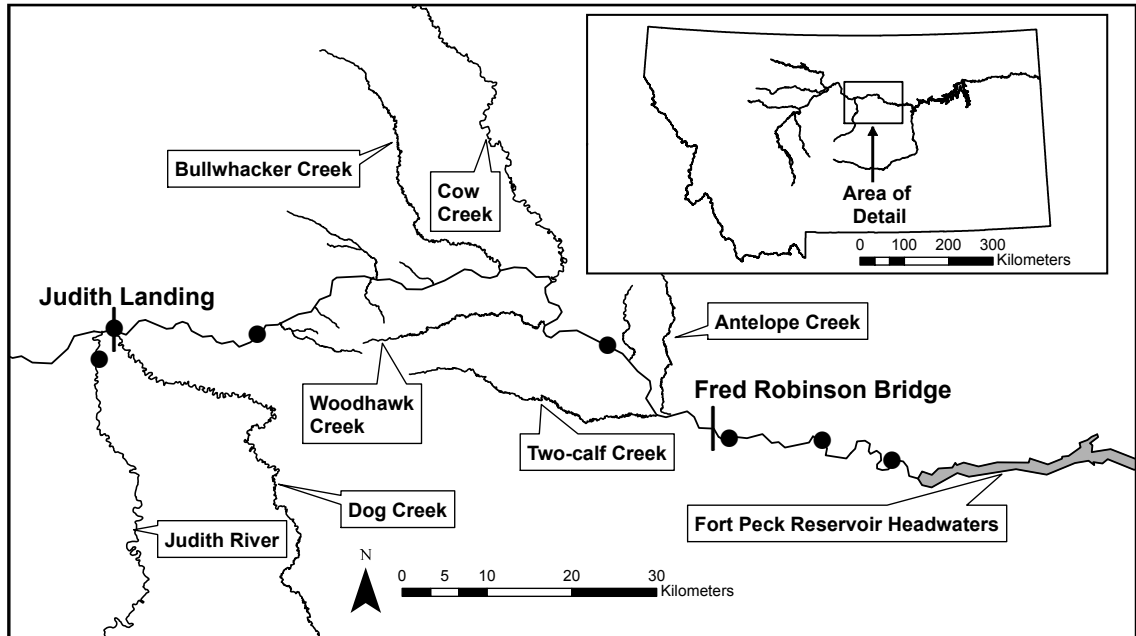


Figure 2.1. Study site on the Missouri River, Montana, including major tributaries inhabited by telemetered *Apalone spinifera*. Black circles represent remote telemetry station locations and solid lines perpendicular to the river represent bridges.

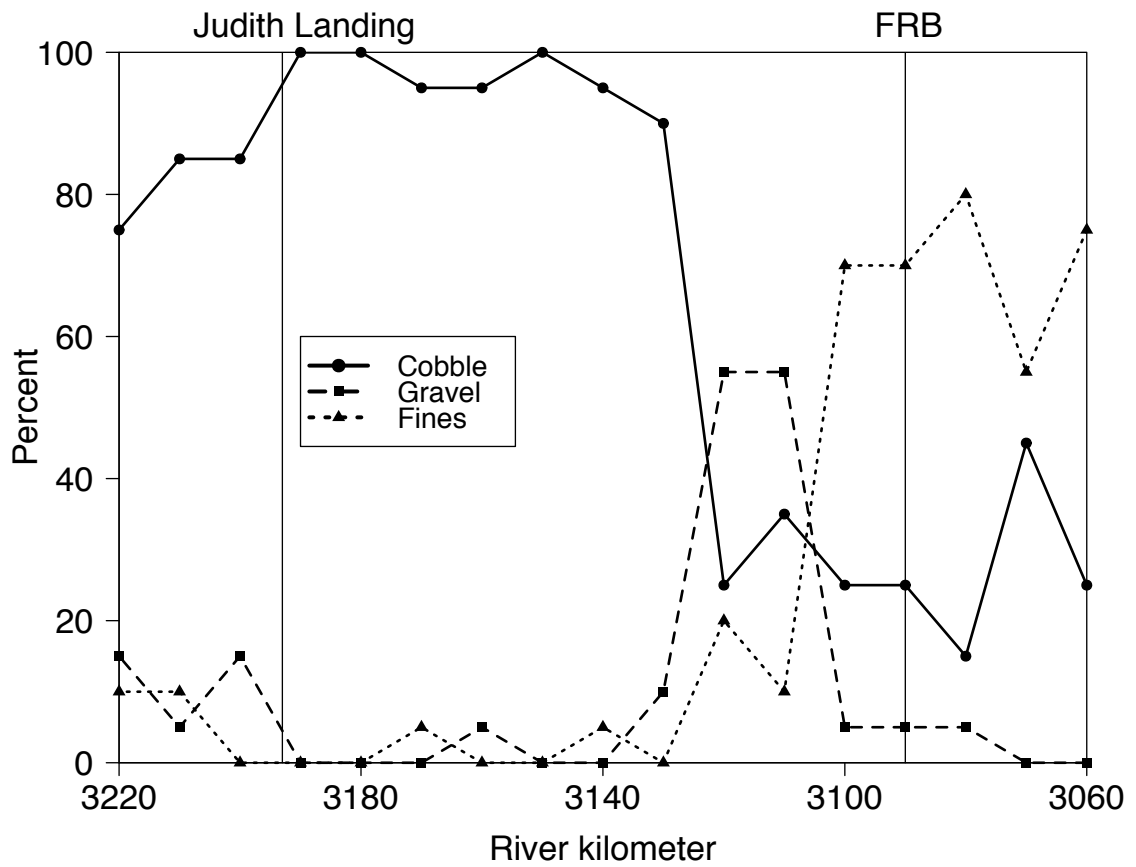


Figure 2.2. Distribution of substrate types in the Missouri River, Montana, upstream of Fort Peck Reservoir (Richards et al., 2012). Vertical lines represent the locations of the Judith River confluence (Judith Landing) and Fred Robinson Bridge (FRB). River kilometer is the distance from the confluence with the Mississippi River.

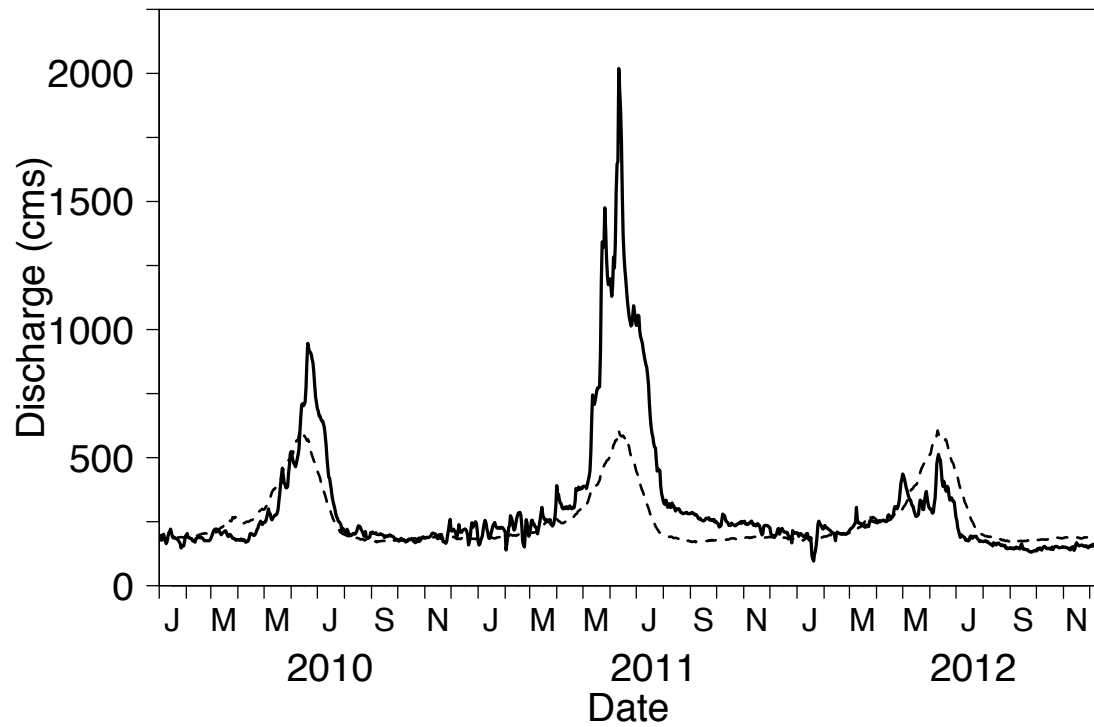


Figure 2.3. Average (1934–2012; dashed line) and January 2010 through November 2012 (solid line) mean daily discharges in the Missouri River, Montana, at the Fred Robinson Bridge near Landusky, Montana.

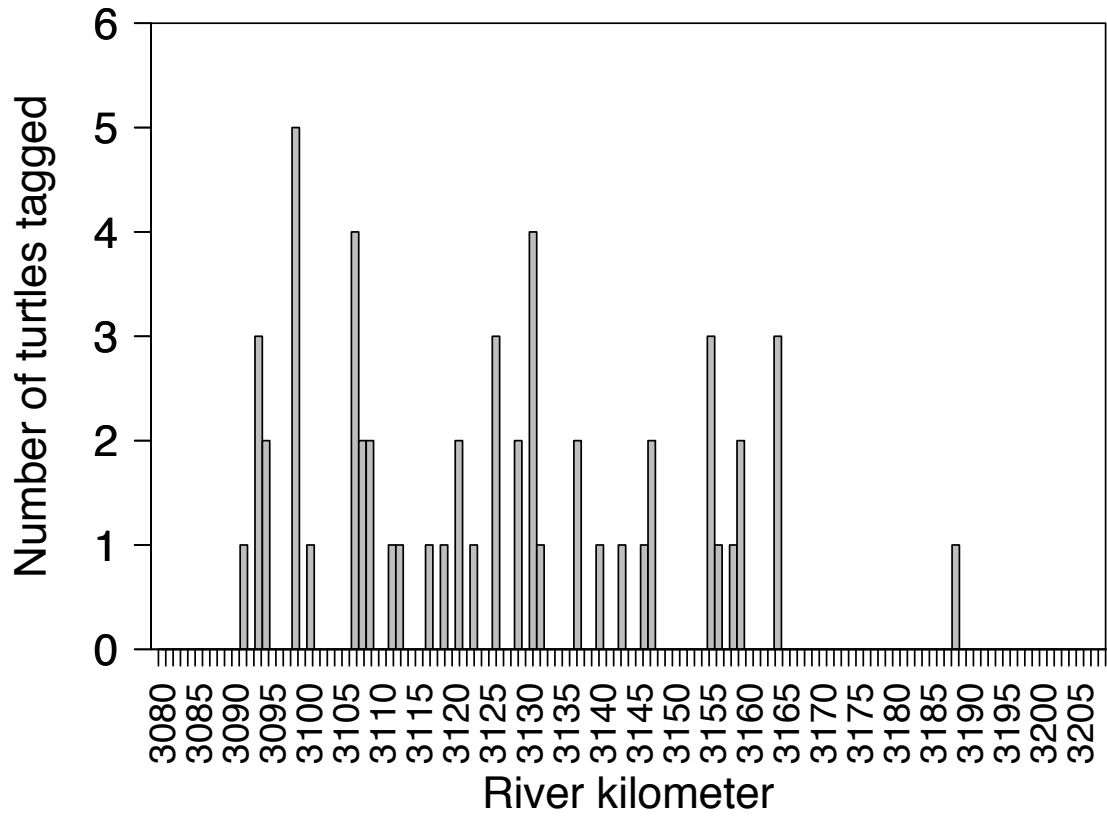


Figure 2.4. Initial distribution of telemetered *Apalone spinifera* in the Missouri River in Montana in August 2009.

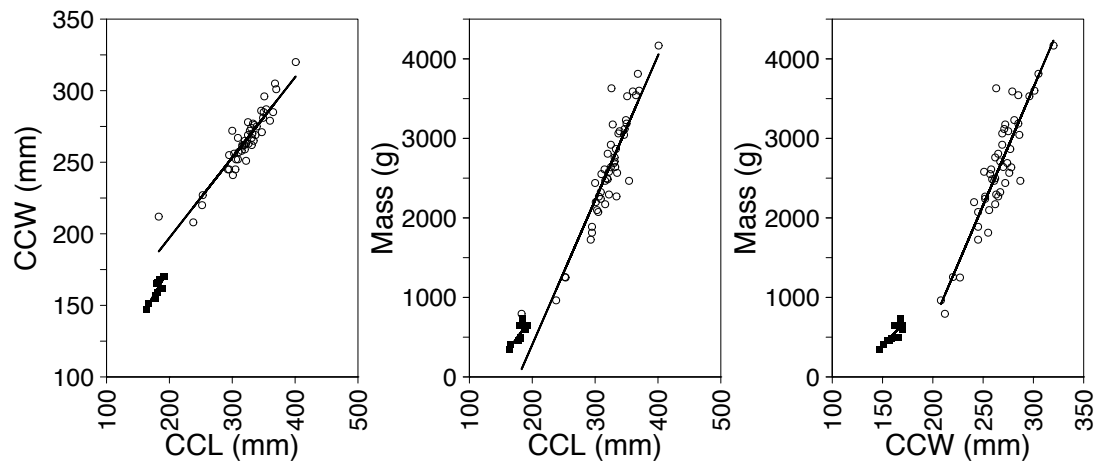


Figure 2.5. Relationships among curved carapace width (CCW), curved carapace length (CCL), and mass of 11 adult male (solid squares and solid line) and 47 female (open circles and solid line) telemetered *Apalone spinifera* in the Missouri River, Montana.

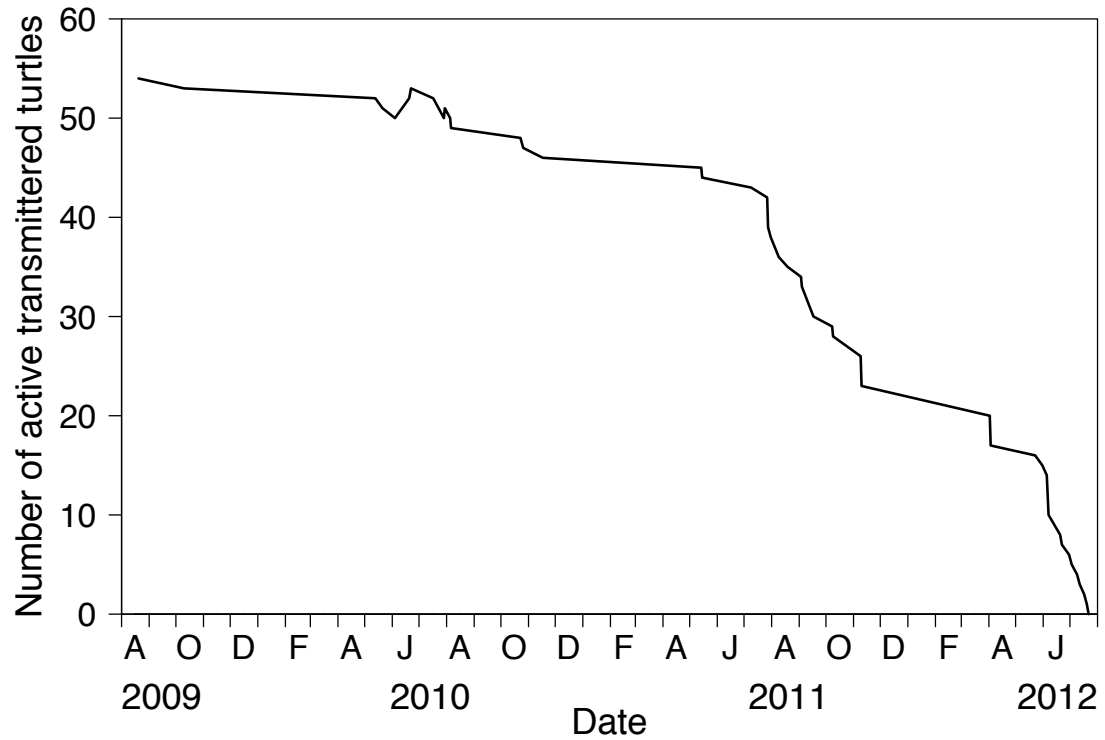


Figure 2.6. Number of active telemetered *Apalone spinifera* (i.e., have not shed transmitters, been lost because of weakened signals, or died) in the Missouri River, Montana, from August 2009 through July 2012. Fifty-four turtles were telemetered in August 2009 and the increases in June and July 2010 were because of additional sampling.

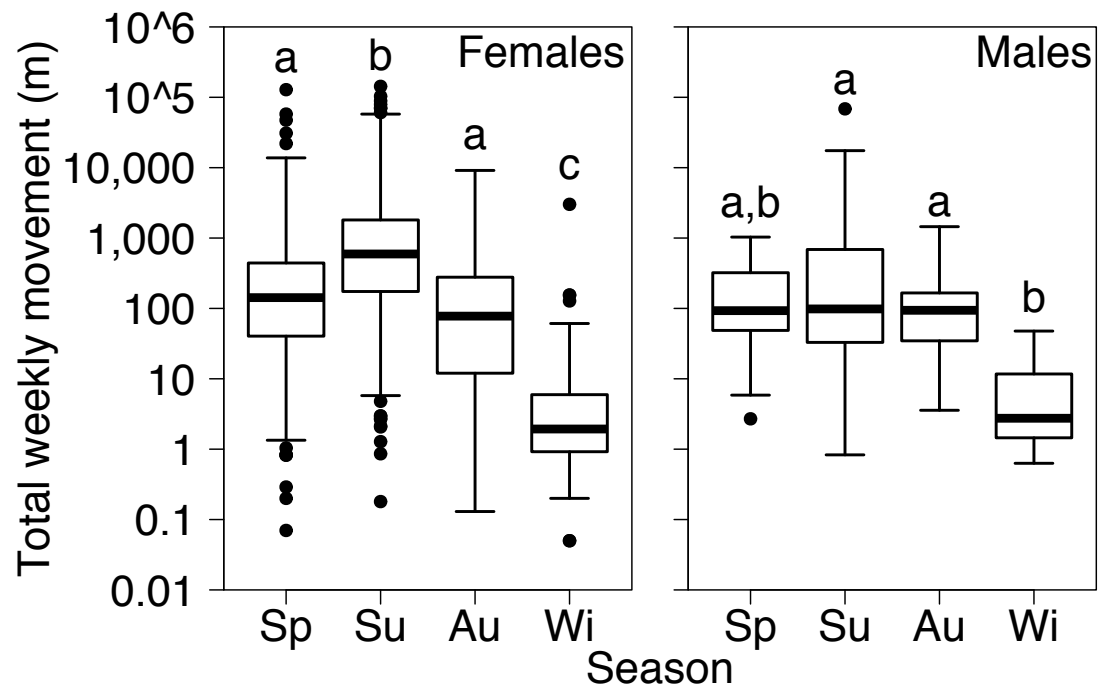


Figure 2.7. Log-normal median weekly movements of 47 female and 11 male telemetered *Apalone spinifera* in the Missouri River, Montana, from 2009 through 2012 by season. Total weekly movement (y-axis) was back-transformed for clarity. Letters above bars indicate significant differences in median total weekly movement rates among seasons; seasons with the same letter are not significantly different.

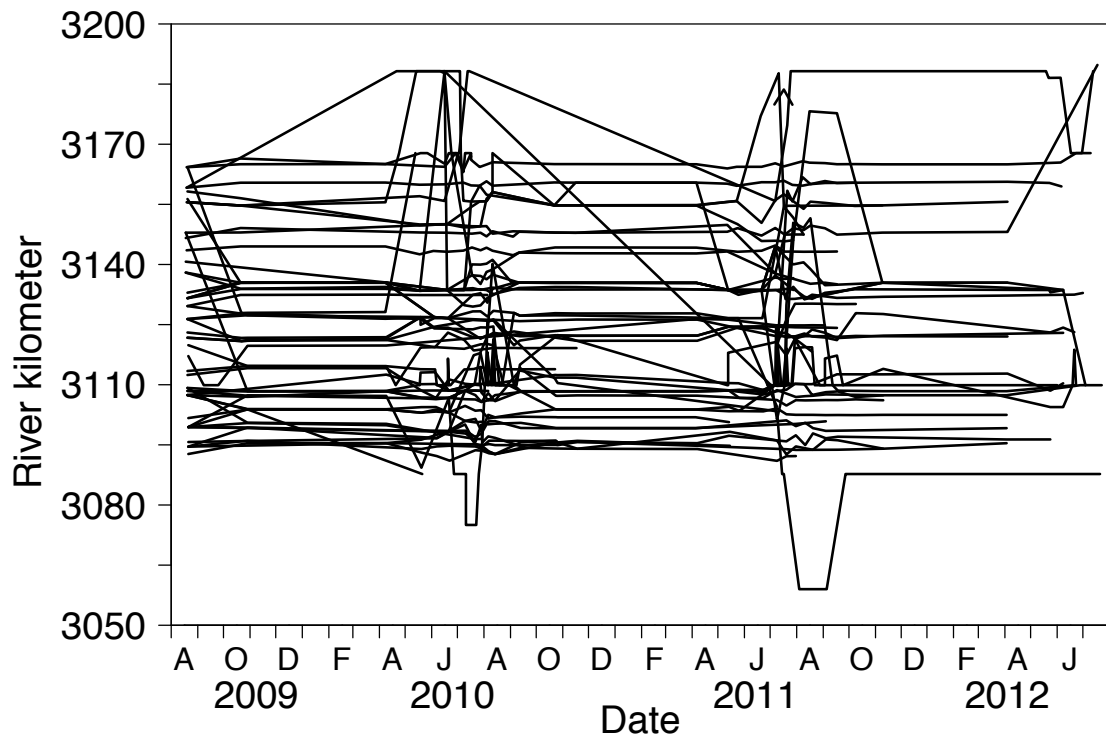


Figure 2.8. Movement patterns of 11 male and 47 female telemetered *Apalone spinifera* on the Missouri River, Montana, from 2009 through 2012. Lines represent movements of individual telemetered turtles. River kilometer is the distance from the confluence with the Mississippi River.

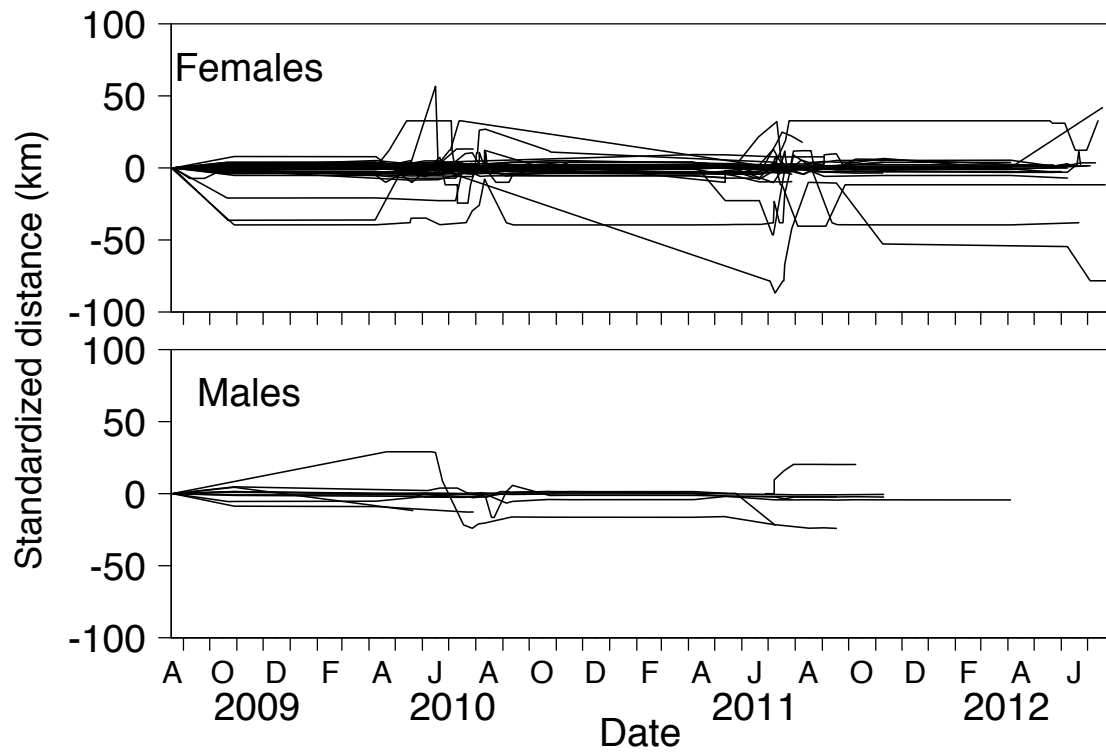


Figure 2.9. River-kilometer-standardized movements of 11 male and 47 female telemetered *Apalone spinifera* on the Missouri River, Montana, from 2009 through 2012. The river kilometer of the first annual location of each turtle is standardized to zero. Positive values indicate upstream movement and negative values indicate downstream movement.

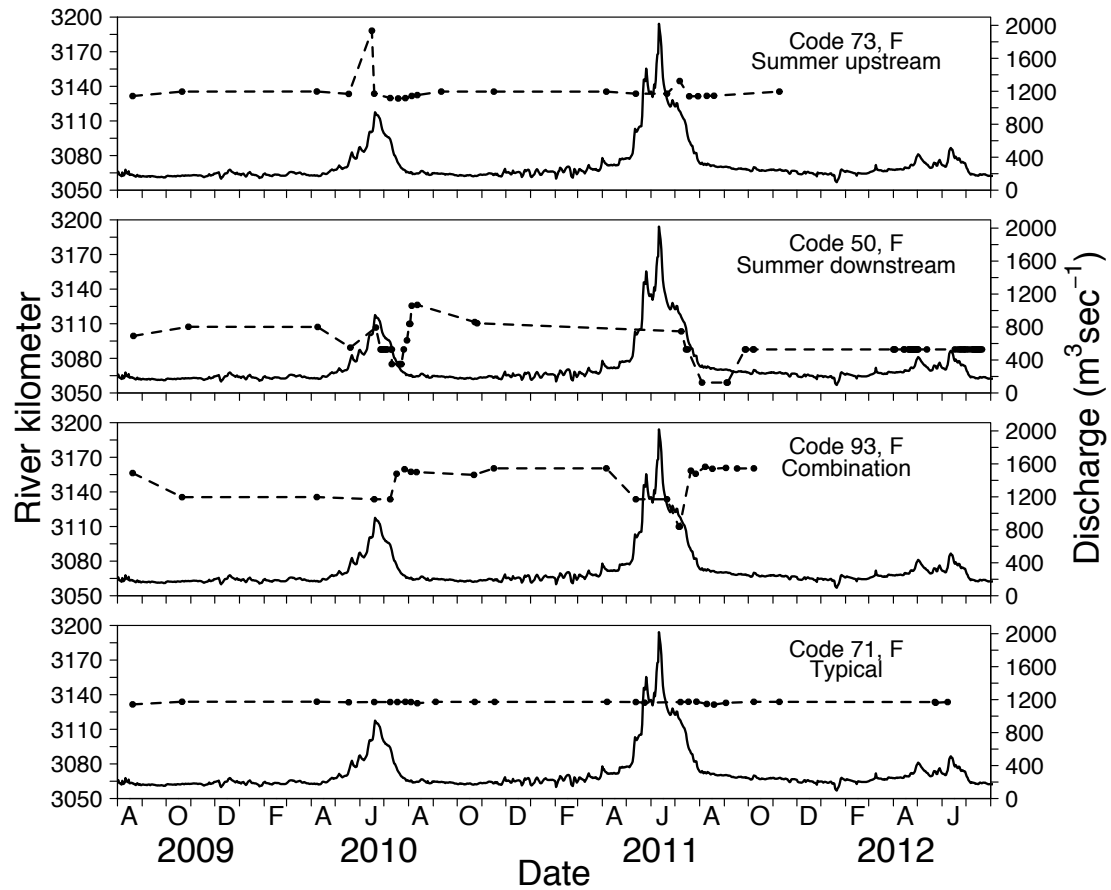


Figure 2.10. Individual movement plots for four female *Apalone spinifera* in the Missouri River, Montana, from 2009 through 2011 displaying four common movement trends. The first (top) plot represents a turtle that moved upstream during the summer and downstream in the winter each year. The second plot represents one that moved downstream in the summer and upstream for the winter. The third plot represents one that did a combination of the two scenarios. The fourth plot (bottom) represents the most typical, small scale, turtle movement; this female moved downstream each summer, but only about 0.5–2 km.

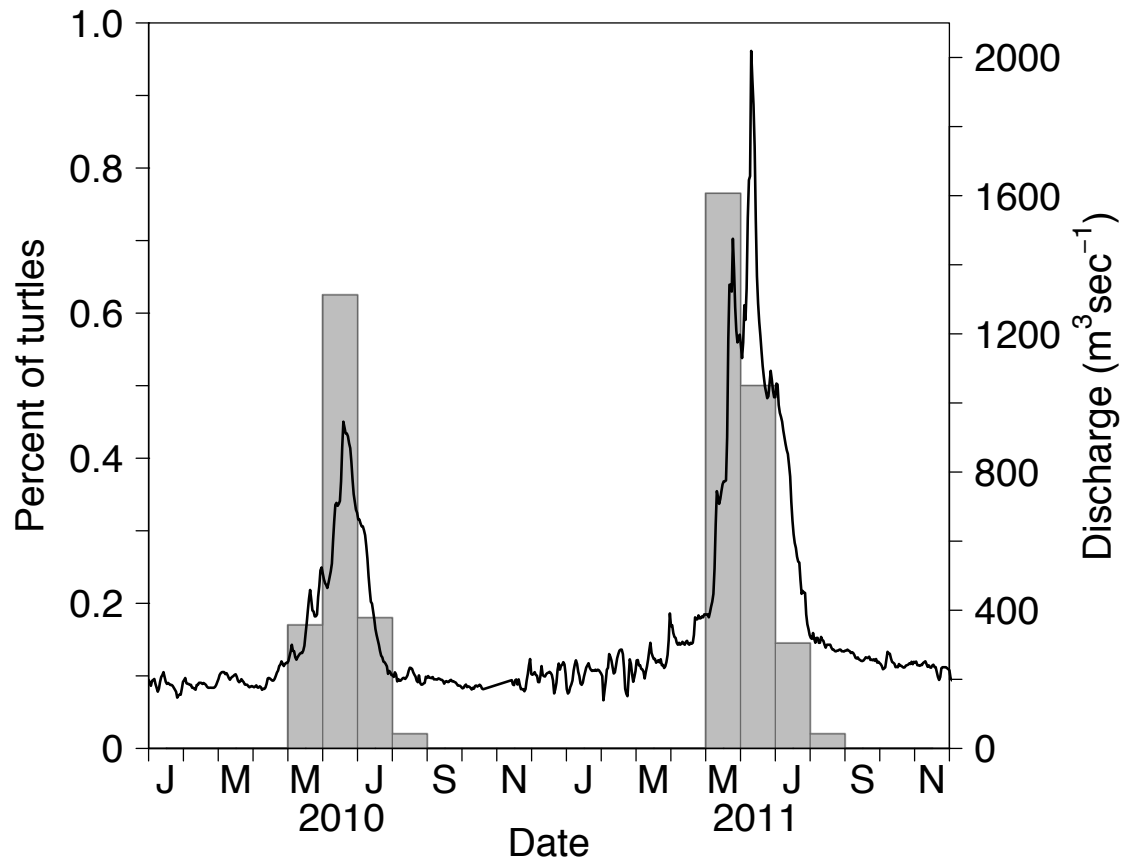


Figure 2.11. Temporal patterns of the percent of telemetered *Apalone spinifera* (N = 58; 11 male and 47 female) in lateral habitats (i.e., tributaries, ephemeral side channels, and floodplain) in the Missouri River, Montana, from 2010 through 2011.

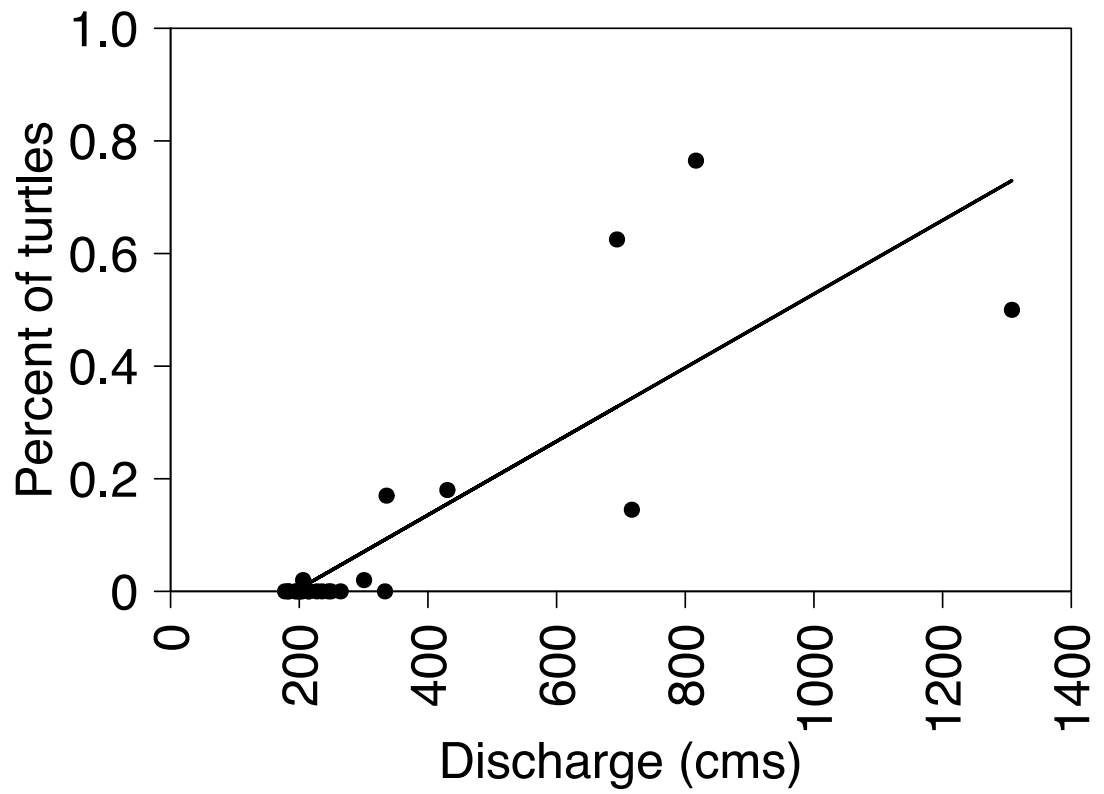


Figure 2.12. Relationship between the percent of telemetered *Apalone spinifera* (N = 58; 11 male and 47 female) in lateral habitats (i.e., tributaries, ephemeral side channels, and floodplain) and discharge in the Missouri River, Montana, from 2010 through 2011.

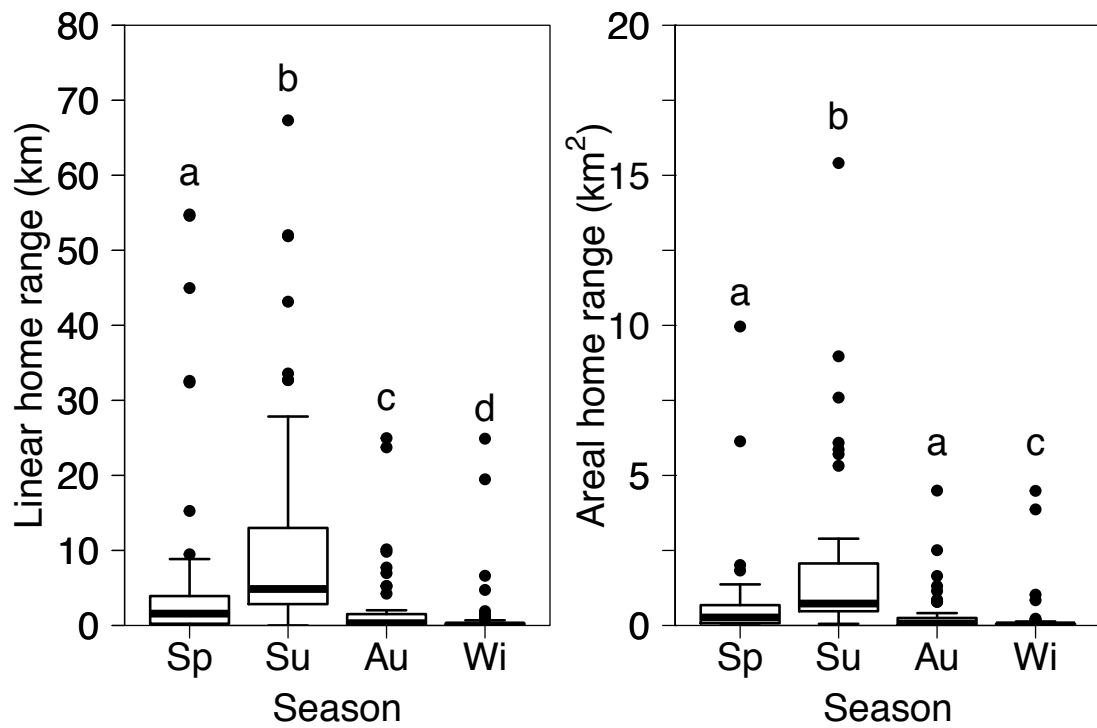


Figure 2.13. Mean linear and areal home ranges (km and km², respectively) of 11 male and 47 female telemetered *Apalone spinifera* in the Missouri River, Montana, by season. Sp = spring, Su = summer, Au = autumn, and Wi = winter. Letters above bars indicate significant differences in median LHR and AHR among seasons; median home ranges with the same letter are not significantly different.

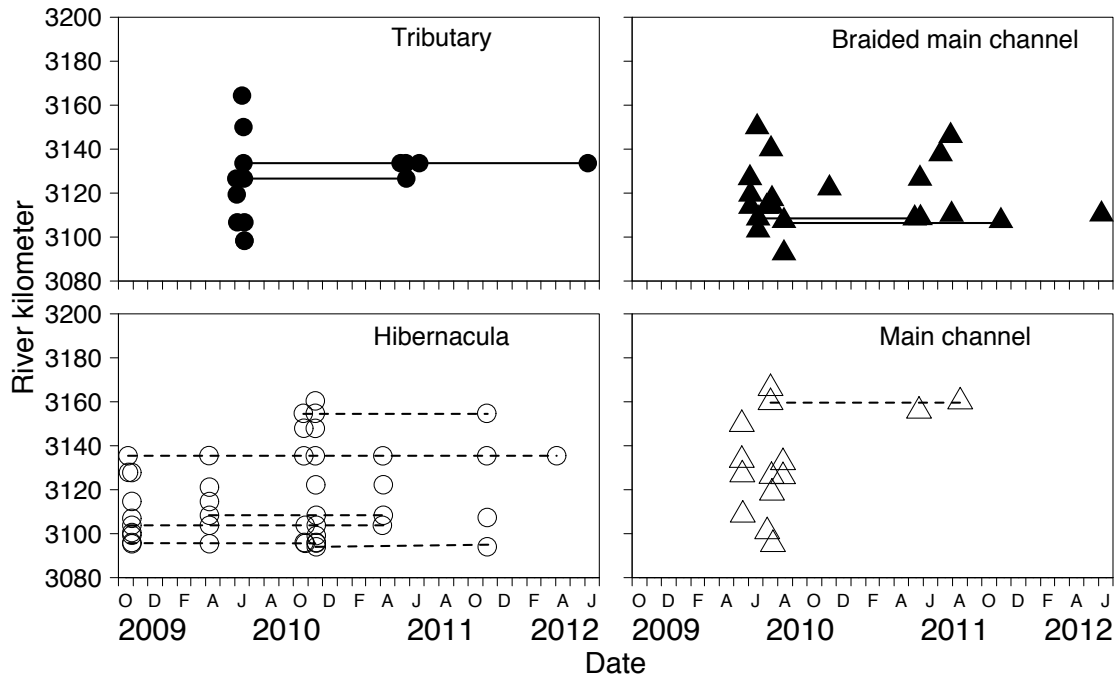


Figure 2.14. Aggregations of 2 or more telemetered *Apalone spinifera* in the Missouri River, Montana from 2009 through 2010 in four different habitat types. Closed circles represent aggregations in tributaries, closed triangles represent aggregations in a braided main channel habitat, open circles represent aggregations in the main channel at hibernacula, and open triangles represent other aggregations in the main channel. Lines connecting points represent interannual fidelity among years.

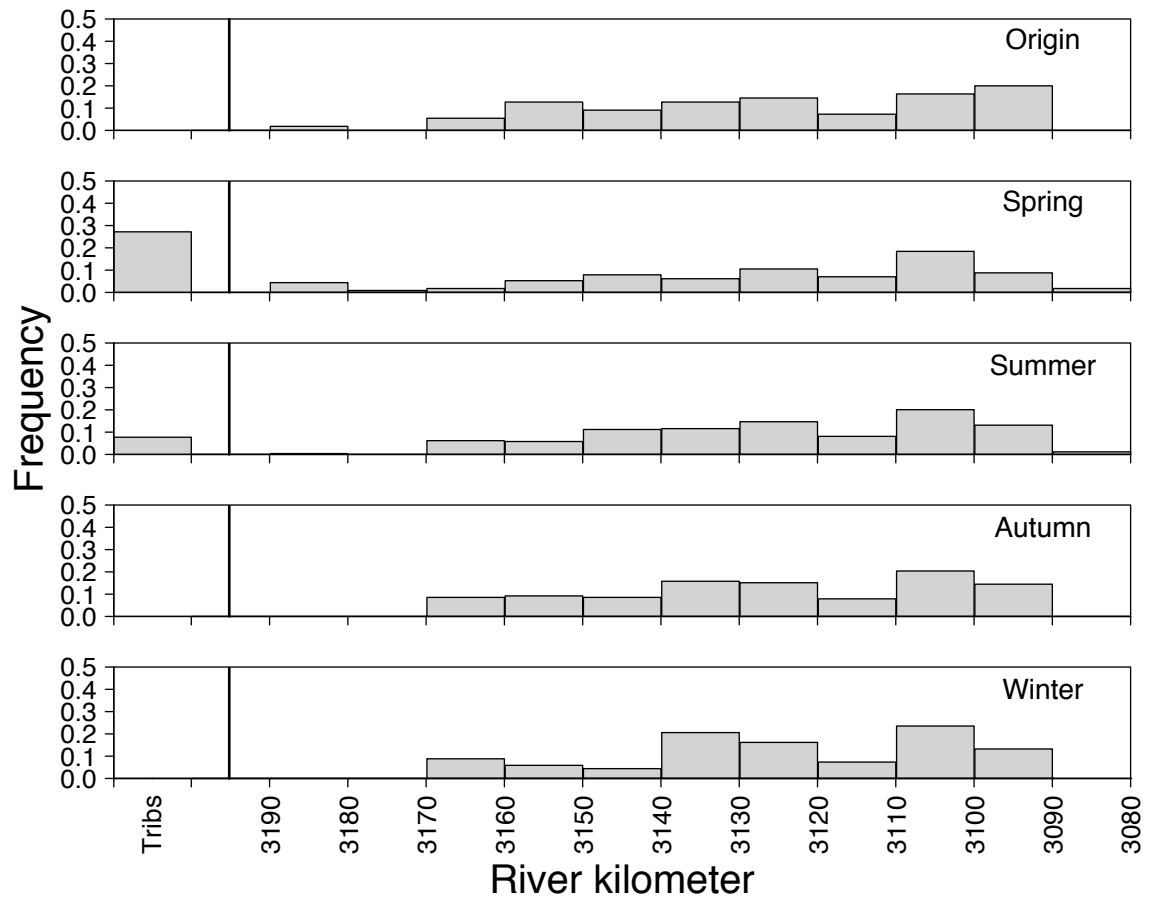


Figure 2.15. Initial tagging (i.e., origin) and seasonal frequency distributions of 11 male and 47 female telemetered *Apalone spinifera* on the Missouri River, Montana, from 2009 through 2012 categorized by 10-kilometer river sections. Tributaries have been pooled into a single bin (TRIB) and the horizontal line in each plot represents an empty bin to separate tributaries and main channel bins.

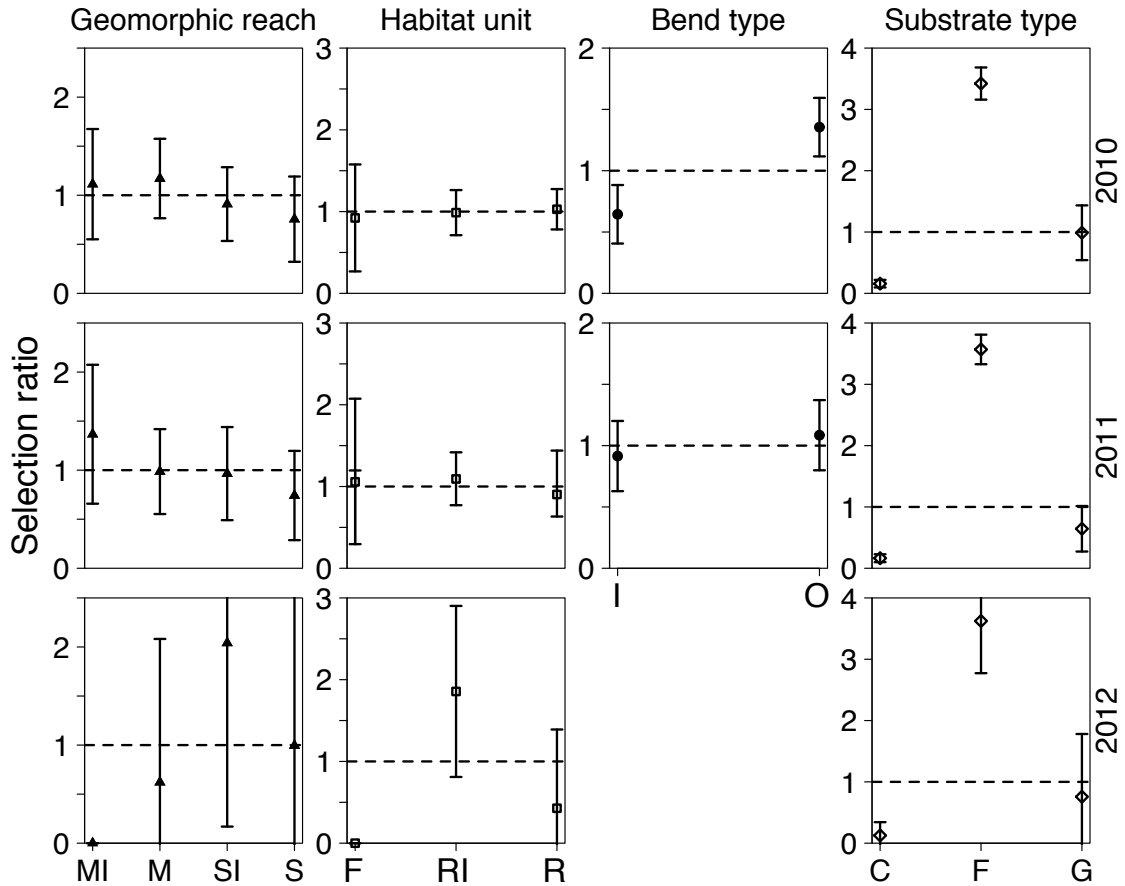


Figure 2.16. Annual habitat-type selection by telemetered *Apalone spinifera* on the Missouri River, Montana, from 2010 through 2012 for four habitat type comparisons. For geomorphic reach type (closed triangles): MI = meander with islands, M = meander without islands, SI = straight reach with islands, and S = straight reach without islands. For habitat unit (open squares): F = riffle, RI = run with islands, and R = run without islands. For bend type (closed circles): I = inside bend and O = outside bend. For substrate type (open diamonds): C = cobble, F = fines, and G = gravel. The dashed line represents a selection ratio of 1 (i.e., no preference), values less than zero indicate a reach is used less than expected (avoidance), and values greater than zero indicate a reach is used more than expected (preference). Error bars describe 90% Bonferroni confidence intervals. Note the different scales for each habitat type comparison.

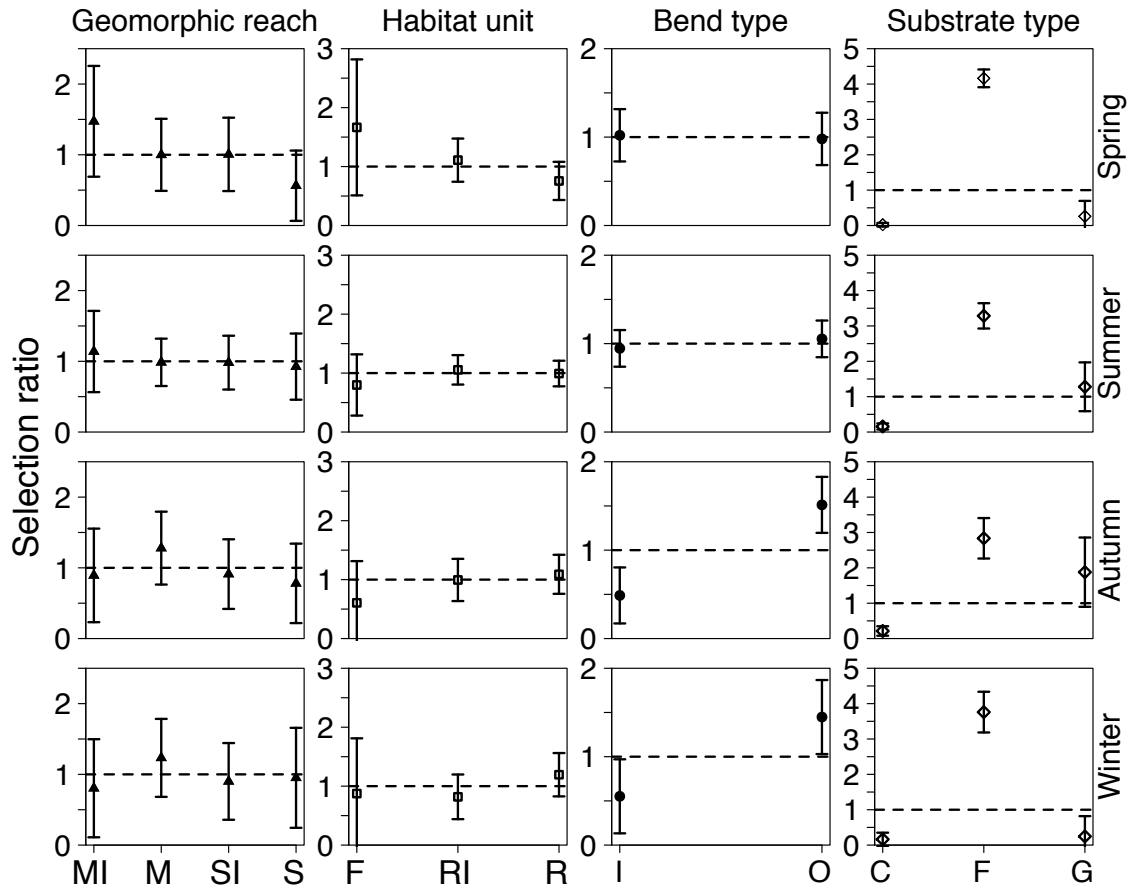


Figure 2.17. Seasonal habitat-type selection by telemetered *Apalone spinifera* on the Missouri River, Montana, from 2010 through 2012 for four habitat type comparisons. For geomorphic reach type (closed triangles): MI = meander with islands, M = meander without islands, SI = straight reach with islands, and S = straight reach without islands. For habitat unit (open squares): F = riffle, RI = run with islands, and R = run without islands. For bend type (closed circles): I = inside bend and O = outside bend. For substrate type (open diamonds): C = cobble, F = fines, and G = gravel. The dashed line represents a selection ratio of 1 (i.e., no preference), values less than zero indicate a reach is used less than expected (avoidance), and values greater than zero indicate a reach is used more than expected (preference). Error bars describe 90% Bonferroni confidence intervals. Note the different scales for each habitat type comparison.

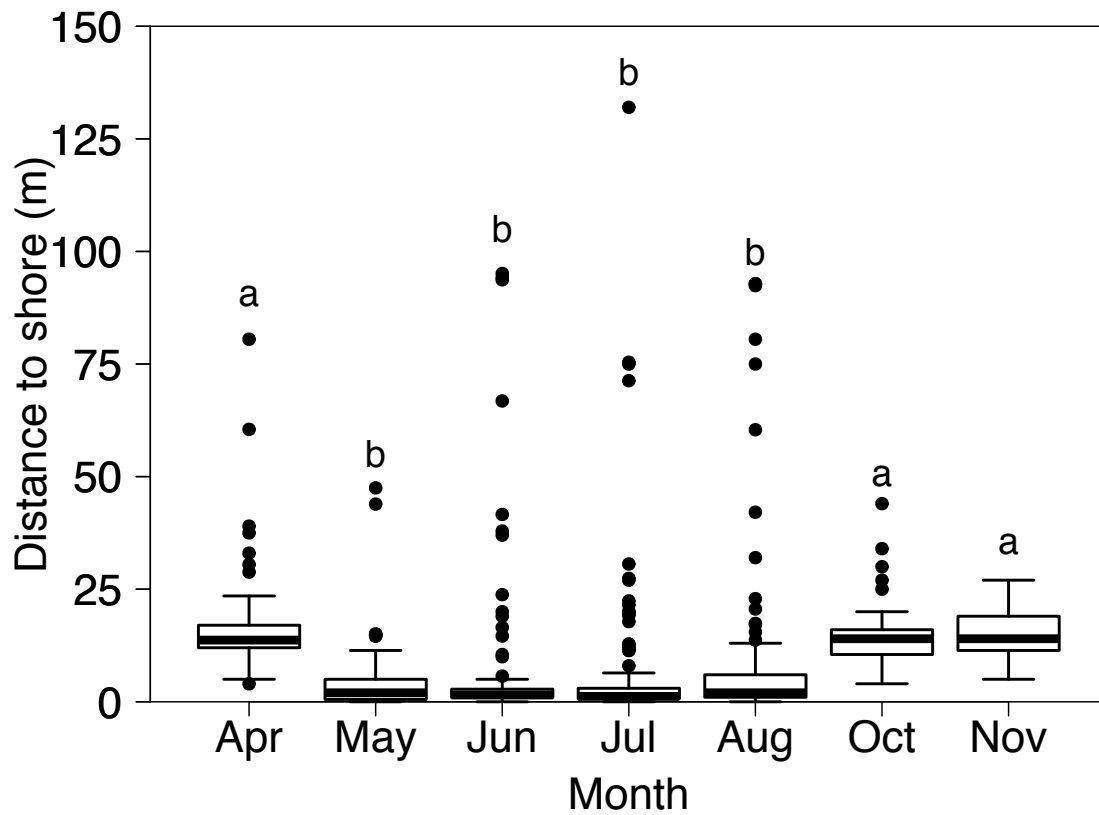


Figure 2.18. Median distance to shore from point locations of 11 male and 47 female telemetered *Apalone spinifera* from April through November on the Missouri River, Montana, from 2009 through 2012. Letters above bars indicate significant differences in median distances to shore among months; distances with the same letter are not significantly different.

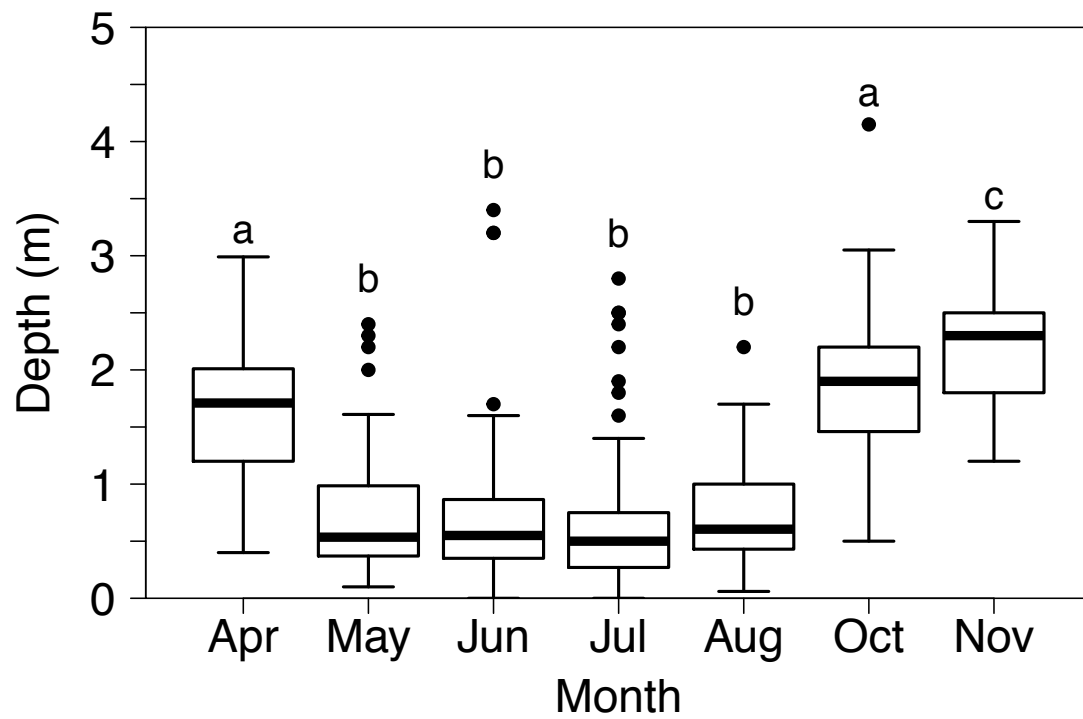


Figure 2.19. Median water depths at point locations of 11 male and 47 female *Apalone spinifera* from April through November on the Missouri River, Montana, from 2009 through 2012. Letters above bars indicate significant differences in median water depth among months; depths with the same letter are not significantly different.

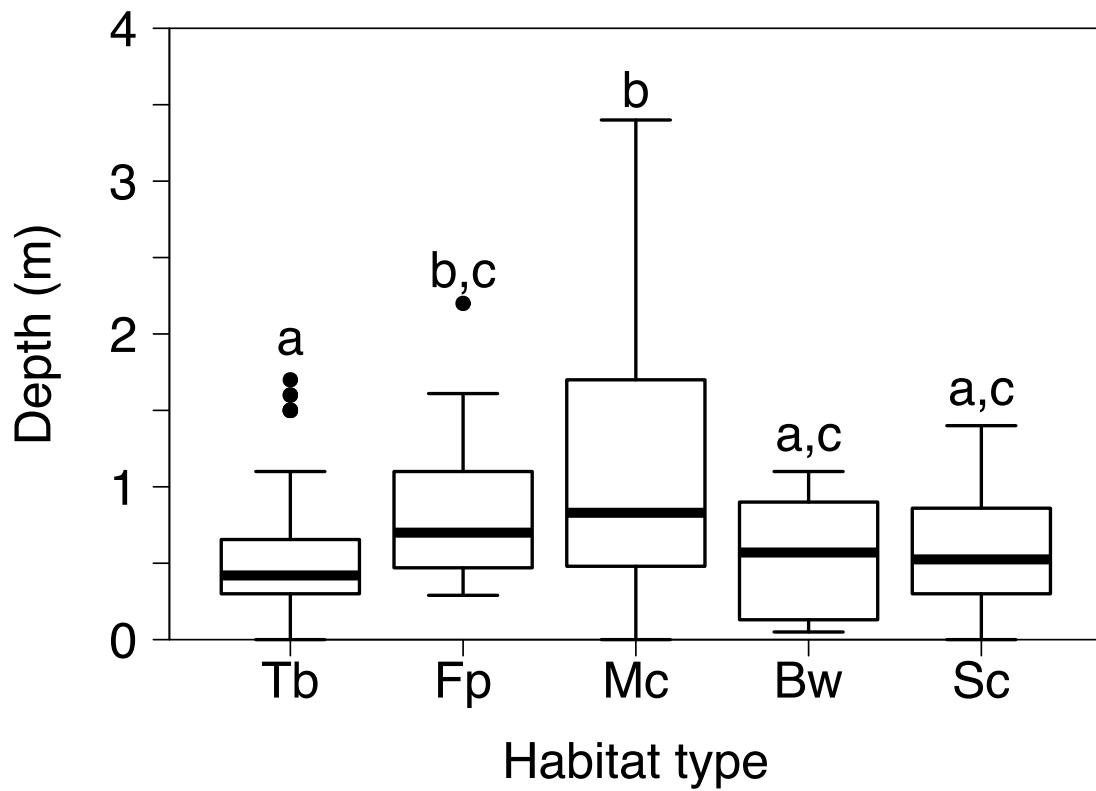


Figure 2.20. Medians water depth at point locations of 11 male and 47 female *Apalone spinifera* by habitat type (Tb = tributaries, Fp = floodplain, Mc = main channel, Bw = backwaters, Sc = side channel) on the Missouri River, Montana, from 2009 through 2012. Letters above bars indicate significant differences in median water depth among habitat types; depths with the same letter are not significantly different.

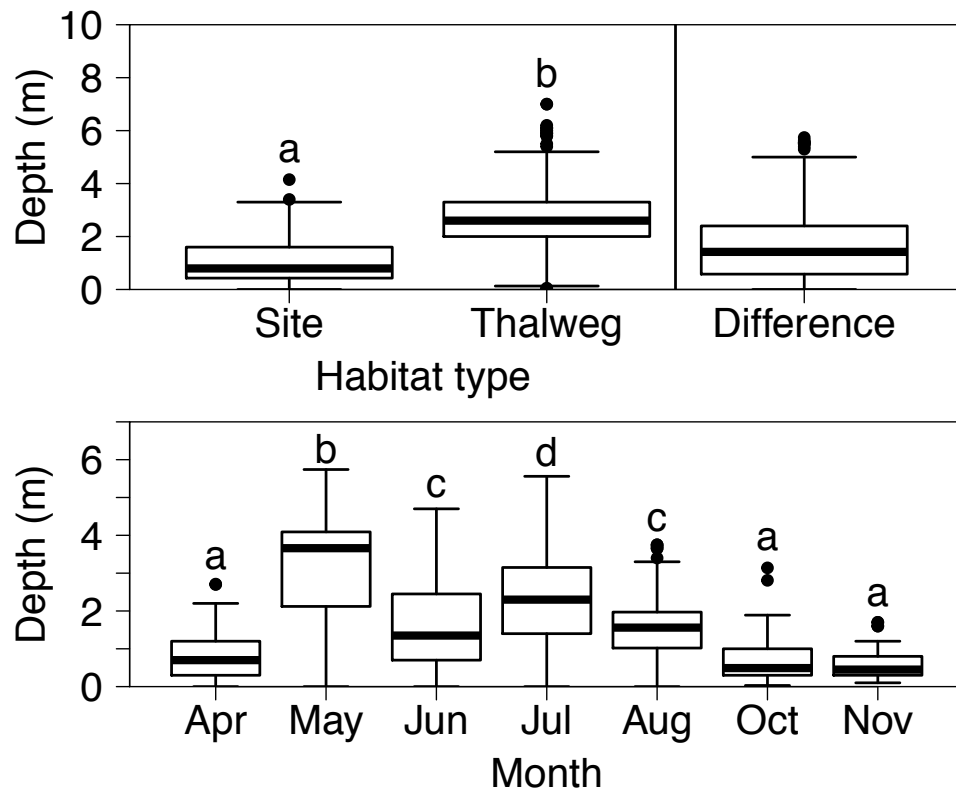


Figure 2.21. Top: median water depths at point locations and in the immediate thalweg and the difference between depths at these locations of 11 male and 47 female *Apalone spinifera* from April through November on the Missouri River, Montana, from 2009 through 2012. Bottom: median differences between depths in the immediate thalweg and at point locations from 2009 through 2012 by month. Letters above bars indicate significant differences in median difference between depths between habitat types (top) or among months (bottom); depths with the same letter are not significantly different.

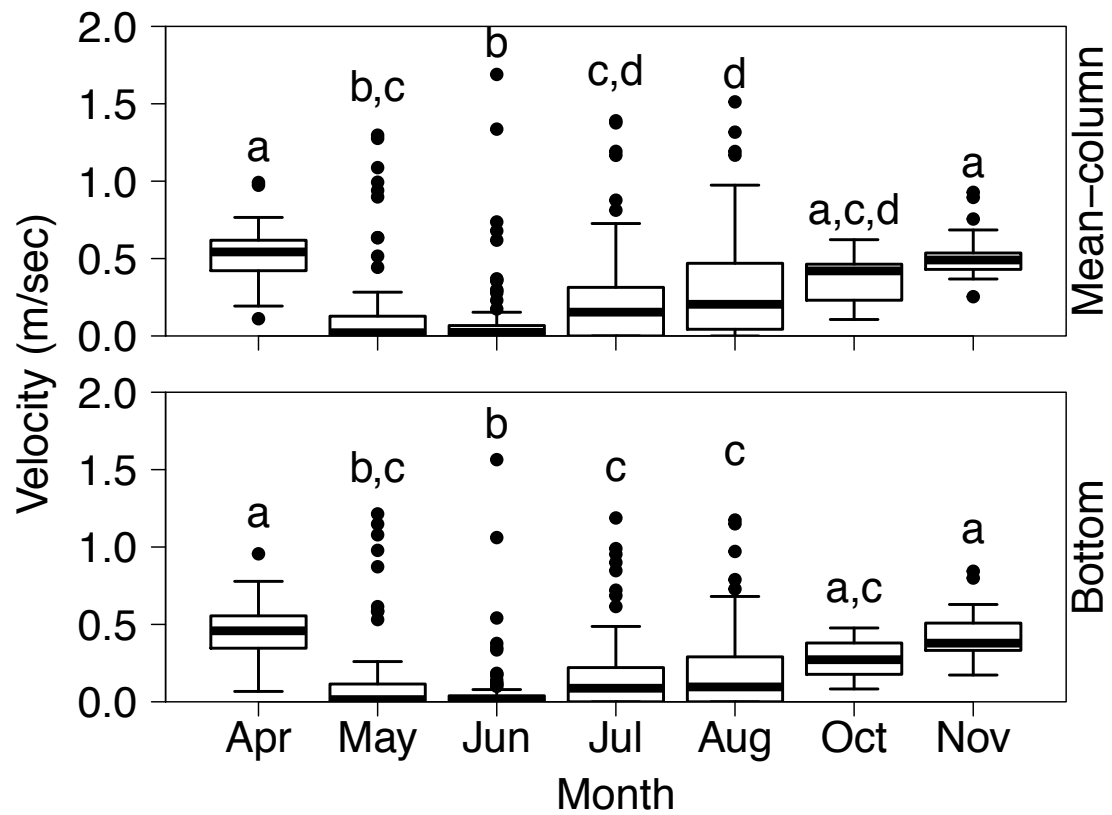


Figure 2.22. Median mean-column (top) and bottom (bottom) water velocities at point locations of 11 male and 47 female *Apalone spinifera* from April through November on the Missouri River, Montana, from 2009 through 2012. Letters above bars indicate significant differences in median water velocity among months; velocities with the same letter are not significantly different.

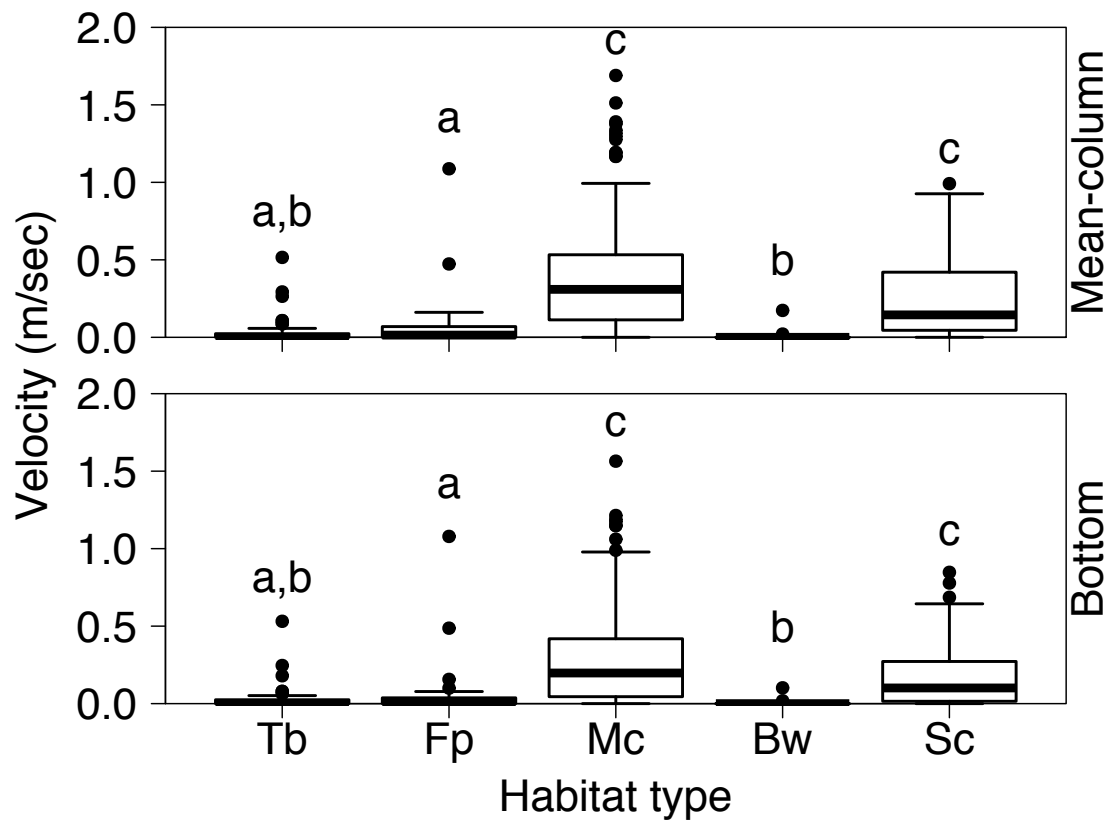


Figure 2.23. Median mean-column (top) and bottom (bottom) water velocities at point locations of 11 male and 47 female *Apalone spinifera* by habitat type (Tb = tributaries, Fp = floodplains, Mc = main channel, Bw = backwaters, Sc = side channels) on the Missouri River, Montana, from 2009 through 2012. Letters above bars indicate significant differences in median water velocity among habitat types; velocities with the same letter are not significantly different.

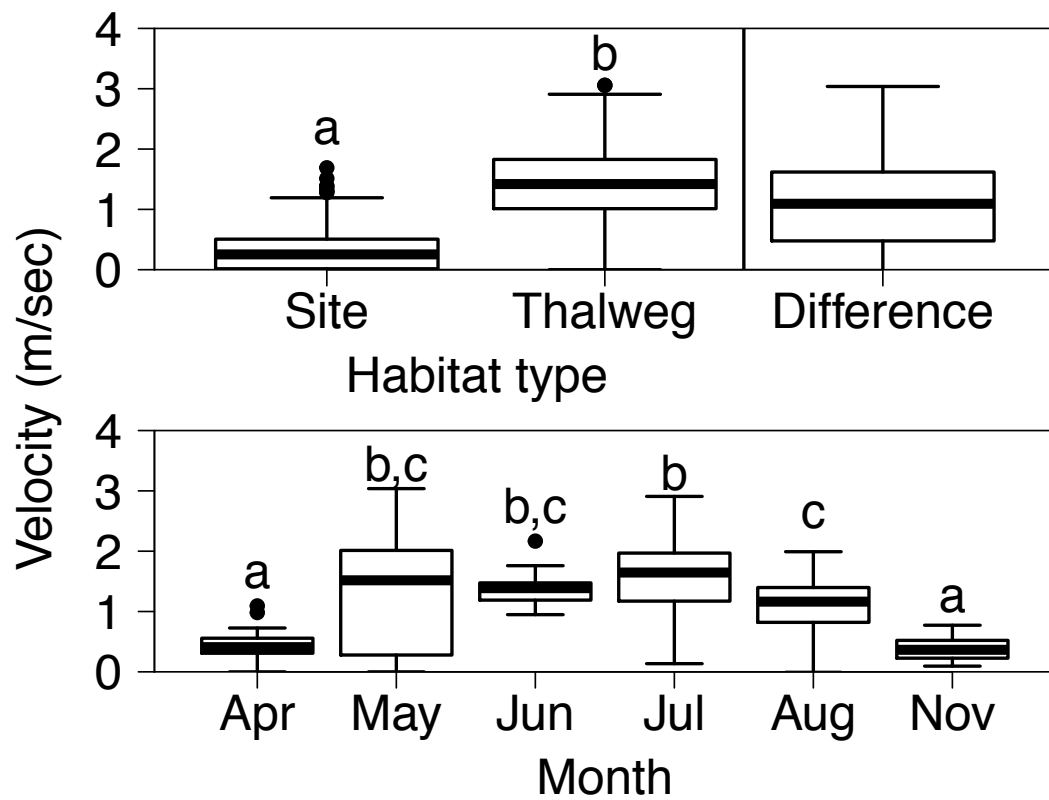


Figure 2.24. Top: median mean-column water velocities at point locations, median mean-column water velocities in the immediate thalweg, and median differences between the two of 11 male and 47 female *Apalone spinifera* from April through August and November on the Missouri River, Montana, from 2011 through 2012. Bottom: median differences between mean-column water velocities in the immediate thalweg and point locations from 2010 through 2012 by month. Letters above bars indicate significant differences in median relative water velocities between habitat types (top) and among months (bottom); velocities with the same letter are not significantly different.

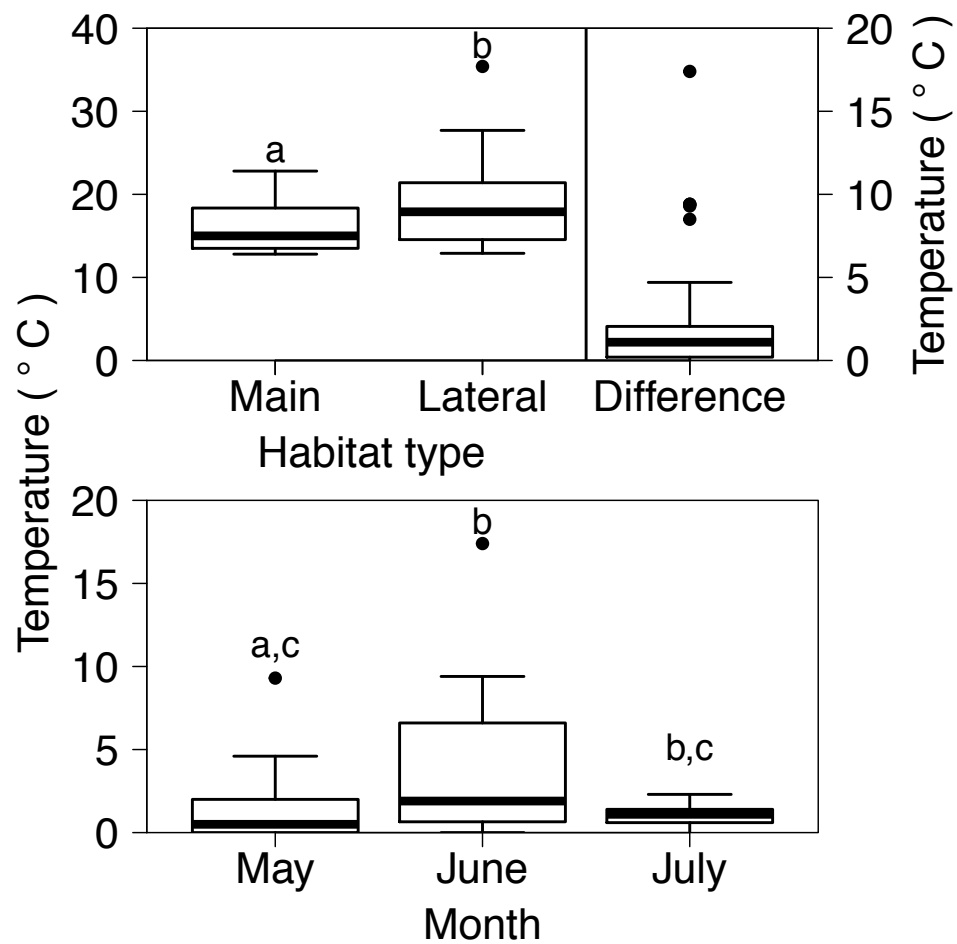


Figure 2.25. Top: median temperatures, in degrees Celsius, in main channel and lateral habitats and the median differences between temperatures in the two habitat types in the Missouri River, Montana, in May, June, and July of 2011 and 2012. Bottom: median differences between temperatures in main channel and lateral habitats in the Missouri River, Montana, in May, June, and July of 2011 and 2012. Letters above bars indicate significant differences in median differences between temperatures in main and lateral habitats among months; temperatures with the same letter are not significantly different.

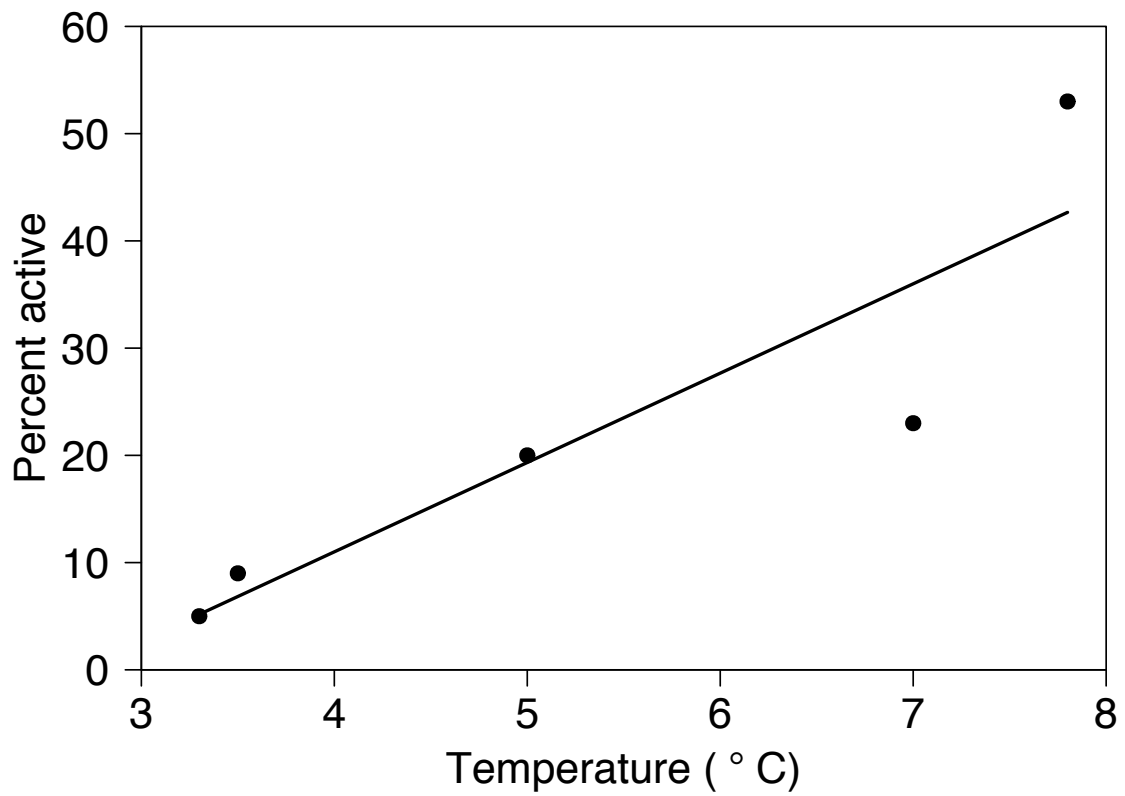


Figure 2.26. Relationship between percent of active (had moved within 24 h of being located) telemetered *Apalone spinifera* and temperatures during October and November winter excursions on the Missouri River, Montana, in 2009, 2010, and 2011.

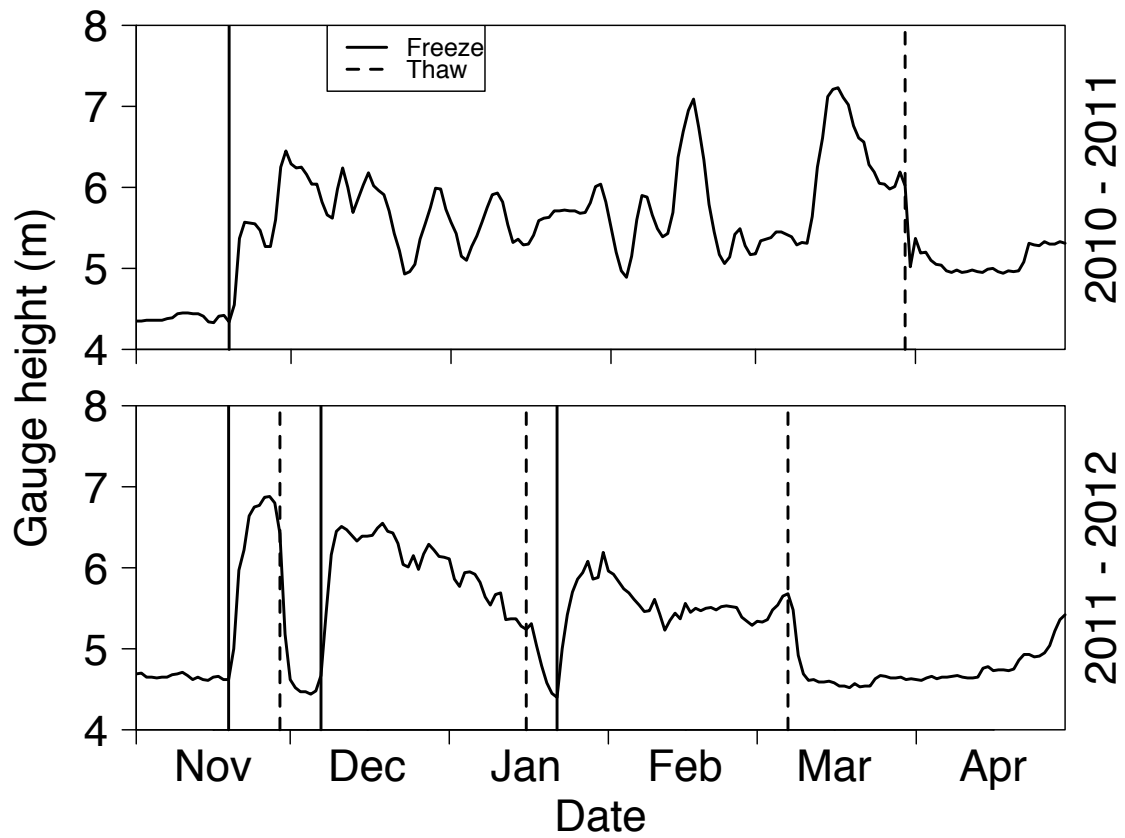


Figure 2.27. Gauge height on the Missouri River at the Fred Robinson Bridge near Landusky, Montana, in the overwintering period from November through April 2010 through 2011 (top) and 2011 through 2012 (bottom). Solid lines represent the beginning of major freeze events in which ice completely covered the river and dashed lines represent major thaw events when ice no longer completely covered the river.

Literature Cited

- Anderson, R. V., M. L. Gutierrez, and M. A. Romano. 2002. Turtle habitat use in a reach of the upper Mississippi River. *Journal of Freshwater Ecology* 17:171–177.
- Barko, V. A., and J. T. Briggler. 2006. Midland smooth softshell (*Apalone mutica*) and spiny softshell (*Apalone spinifera*) turtles in the middle Mississippi River: habitat associations, population structure, and implications for conservation. *Chelonian Conservation and Biology* 5:225–231.
- Bellgraph, B. J., C. S. Guy, W. M. Gardner, and S. A. Leathe. 2008. Competition potential between saugers and walleyes in nonnative sympatry. *Transactions of the American Fisheries Society* 137:790–800.
- Beltaos, S. 2003. Threshold between mechanical and thermal breakup of river ice cover. *Cold Regions Science and Technology* 37:1–113.
- Bodie, J. R. 2001. Stream and riparian management for freshwater turtles. *Journal of Environmental Management* 62:443–455.
- Bodie, J. R., and R. D. Semlitsch. 2000. Spatial and temporal use of floodplain habitats by lentic and lotic species of aquatic turtles. *Oecologia* 122:138–146.
- Bolton, R. M. 2007. Effects of anthropogenic disturbance, nest-site selection, and dipteran infestation on spiny softshells (*Apalone spinifera*). M.S. Thesis, The University of Guelph, Ontario, Canada.
- Bowen, Z. H., K. D. Bovee, and T. J. Waddle. 2003. Effects of flow regulation on shallow-water habitat dynamics and floodplain connectivity. *Transactions of the American Fisheries Society* 132:809–823.
- Bramblett, R. G., and R. G. White. 2001. Habitat use and movements of pallid and shovelnose sturgeon in the Yellowstone and Missouri Rivers in Montana and North Dakota. *Transactions of the American Fisheries Society* 130:1006–1025.
- Brinson, M. M., A. E. Lugo, and S. Brown. 1981. Primary productivity, decomposition and consumer activity in freshwater wetlands. *Annual Review of Ecology and Systematics* 12:123–161.
- Bunn, S. E., and A. H. Arthington. 2002. Basic principles and ecological consequences of altered flow regimes for aquatic biodiversity. *Environmental Management* 30:492–507.

- Butler, B. O., and T. E. Graham. 1995. Early post-emergent behavior and habitat selection in hatchling Blanding's turtles, *Emydoidea blandingii*, in Massachusetts. *Chelonian Conservation Biology* 1:187–196.
- Congdon, J. D., A. E. Dunham, and R. C. Van Loben Sels. 1993. Delayed sexual maturity and demographics of Blanding's turtles (*Emydoidea blandingii*): implications for conservation and management of long-lived organisms. *Conservation Biology* 7:826–833.
- Congdon, J. D., A. E. Dunham, and R. C. Van Loben Sels. 1994. Demographics of common snapping turtles (*Chelydra serpentina*): implications for conservation and management of long-lived organisms. *Integrative and Comparative Biology* 34:397.
- Dood, A. R., B. Schmitz, V. Riggs, N. McClenning, M. Jaeger, D. Fuller, R. Rauscher, S. Leathe, D. Moore, J. Dullum, J. Ensign, S. Story, and M. Backes. 2009. Relative abundance of spiny softshell turtles (*Apalone spinifera*) on the Missouri and Yellowstone rivers in Montana, Final Report. Montana Fish, Wildlife & Parks, Helena, Montana.
- Ernst, C. H., and J. E. Lovich. 2009. Turtles of the United States and Canada. The Johns Hopkins University Press, Baltimore, Maryland.
- Funk, J. L., and J. W. Robinson. 1974. Changes in the channel of the lower Missouri River and effects on fish and wildlife. Missouri Department of Conservation, Aquatic Series 11, Jefferson City, Missouri.
- Galat, D. L., C. R. Berry, W. M. Gardner, J. C. Hendrickson, G. E. Mestl, G. J. Power, C. Stone, and M. R. Winston. 2005. Spatiotemporal patterns and changes in Missouri River fishes. *American Fisheries Society Symposium* 45:249–291.
- Galat, D. L., L. H. Fredrickson, D. D. Humburg, K. J. Bataille, J. R. Bodie, J. Dohrenwend, J. R. Jones, M. E. Knowlton, J. Mazourek, A. C. McColpin, R. B. Renken, and R. D. Semlitsch. 1998. Flooding to restore connectivity of regulated, large-river wetlands. *BioScience* 48:721–733.
- Galois, P., M. Léveillé, L. Bouthillier, C. Daigle, and S. Parren. 2002. Movement patterns, activity, and home range of the eastern spiny softshell turtle (*Apalone spinifera*) in northern Lake Champlain, Québec, Vermont. *Journal of Herpetology* 36:402–411.
- Galois, P., and M. Ouellet. 2007. Traumatic injuries in eastern spiny softshell turtles (*Apalone spinifera*) due to recreational activities in the northern Lake Champlain basin. *Chelonian Conservation and Biology* 6:288–293.

- Garber, S. D., and J. Burger. 1995. A 20-yr study documenting the relationship between turtle decline and human recreation. *Ecological Applications* 5:1151–1162.
- Gardner, W. M., and C. B. Jensen. 2011. Upper Missouri River basin pallid sturgeon study 2005–2010 final report. United States Bureau of Reclamation, Montana Department of Fish, Wildlife & Parks, Helena, Montana.
- Gibbons, J. W. 1986. Movement patterns among turtle populations: applicability to management of the desert tortoise. *Herpetologica* 42:104–113.
- Gibbons, J. W., and R. D. Semlitsch. 1982. Survivorship and longevity of a long-lived vertebrate species; how long do turtles live? *Journal of Animal Ecology* 51:523–527.
- Gibbons, J. W., J. L. Greene, and J. D. Congdon. 1990. Temporal and spatial movement patterns of sliders and other turtles, pp. 201–215. *In: Life History and Ecology of the Slider Turtle*. J. W. Gibbons (ed.). Smithsonian Institution Press, Washington D.C.
- Gibbons, J. W., J. E. Lovich, A. D. Tucker, N. N. FitzSimmons, and J. L. Greene. 2001. Demographic and ecological factors affecting conservation and management of the diamondback terrapin (*Malaclemys terrapin*) in South Carolina. *Chelonian Conservation and Biology* 4:66–74.
- Graham, T. E., and A. A. Graham. 1991. *Trionyx Spiniferus Spiniferus* (Eastern Spiny Softshell). Burying behavior. *Herpetological Review* 22:56–57.
- Graham, T. E., and A. A. Graham. 1997. Ecology of the eastern spiny softshell, *Apalone spinifera spinifera*, in the Lamoille River, Vermont. *Chelonian Conservation and Biology* 2:363–369.
- Gregory, P.T. 1982. Reptilian hibernation, pp. 53–154. *In: Biology of the Reptilia*. Gans, C., and Pough, F. H. (eds.). Vol. 13, Physiology D. New York: Academic Press.
- Hesse, L. W., J. C. Schmulbach, J. M. Carr, K. D. Keenlyne, D. G. Unkenholz, J. W. Robinson, and G. E. Mestl. 1989. Missouri River fishery resources in relation to past, present, and future stresses. Pp. 352–371 *In* D. P. Dodge (Ed.), *Proceedings of the International Large River Symposium*. Canadian Special Publication of Fisheries Aquatic Science 106.
- Holman, J. A., and K. D. Andrews. 1994. North American Quaternary cold-tolerant turtles: distributional adaptations and constraints. *Boreas* 23:44–52.
- Hynes, H. B. N. 1970. *The ecology of running waters*. University of Toronto Press, Ontario, Canada.

- Iverson, J. B. 1991. Patterns of survivorship in turtles (Order Testudines). *Canadian Journal of Zoology* 69:385–391.
- Jackson, D. C., and G. R. Ultsch. 2010. Physiology of hibernation under the ice by turtles and frogs. *Journal of Experimental Zoology* 313A:311–327.
- Jackson, D. C., C. E. Crocker, and G. R. Ultsch. 2001. Mechanisms of homeostasis during long-term diving and anoxia in turtles. *Zoology* 103:150–156.
- Jaeger, M. E., A. V. Zale, T. E. McMahon, and B. J. Schmitz. 2005. Seasonal movements, habitat use, aggregation, exploitation, and entrainment of saugers in the lower Yellowstone River: an empirical assessment of factors affecting population recovery. *North American Journal of Fisheries Management* 25:1550–1568.
- Karchesky, C. M., and D. H. Bennett. 2004. Winter habitat use by adult largemouth bass in the Pend Oreille River, Idaho. *North American Journal of Fisheries Management* 24:577–585.
- Litzgus, J. D., and T. A. Mousseau. 2004. Home range and seasonal activity of southern spotted turtles (*Clemmys guttata*): implications for management. *Copeia* 2004:804–817.
- Maxell, B. A. 2013. Montana animal species of concern report. Montana natural heritage Program and Montana Fish, Wildlife, and Parks. Retrieved on 8/19/2013 from <http://mtnhp.org/SpeciesOfConcern/?AorP=a>
- MacCulloch, R. D., and D. M. Secoy. 1983. Movement in a river population *Chrysemys picta belli* in southern Saskatchewan. *Journal of Herpetology* 17:283–285.
- Mitro, M. G., and A. V. Zale. 2002. Seasonal survival, movement, and habitat use of age-0 rainbow trout in the Henrys Fork of the Snake River, Idaho. *Transactions of the American Fisheries Society* 131:271–286.
- Moll, E. O., and J. M. Legler. 1971. The life history of a neotropical slider turtle, *Pseudemys scripta* (Schoepff), in Panama. *Los Angeles County Museum Science Bulletin* 11:1–102.
- Moll, D., and E. O. Moll. 2004. The ecology, exploitation, and conservation of river turtles. Oxford University Press, New York.
- Morreale, S. J., J. W. Gibbons, and J. D. Congdon. 1984. Significance of activity and movement in the yellow-bellied slider turtle (*Pseudemys scripta*). *Canadian Journal of Zoology* 62:1038–1042.

- Muhlfeld, C. C., and B. M. Marotz. 2005. Seasonal movement and habitat use by subadult bull trout in the upper Flathead River system, Montana. *North American Journal of Fisheries Management* 25:797–810.
- Parmley, D. 1992. Turtles from the late Hemphillian (latest Miocene) of Knox County, Nebraska. *Texas Journal of Science* 44:339–348.
- Pegg, M. A., C. L. Pierce, and A. Roy. 2003. Hydrological alteration along the Missouri River basin: a time series approach. *Aquatic Sciences* 65:63–72.
- Plummer, M. V., and J. C. Burnley. 1997. Behavior, hibernacula, and thermal relations of softshell turtles (*Trionyx spiniferus*) overwintering in a small stream. *Chelonian Conservation and Biology* 2:489–493.
- Plummer, M. V., and H. W. Shirer. 1975. Movement patterns in a river population of the softshell turtle, *Trionyx muticus*. *University of Kansas Natural History Museum Occasional Papers* 43:1–26.
- Plummer, M. V., N. E. Mills, and S. L. Allen. 1997. Activity, habitat, and movement patterns of softshell turtles (*Trionyx spiniferus*) in a small stream. *Chelonian Conservation and Biology* 2:514–520.
- R Core Team. 2013. R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. URL <http://www.R-project.org/>.
- Ramey, M. P., S. M. Beck, and D. W. Reiser. 1993. Determination of flushing flow needs – Madison and upper Missouri rivers. Supplemental Report. Prepared by R2 Resource Consultants for Montana Power Company. Butte, Montana.
- Ramsey, F. L., and D. W. Schafer. 2002. *The Statistical Sleuth, A course in Methods of Data Analysis*. Second Edition. Duxbury Press, Belmont, California.
- Reese, D. A. 1996. Comparative demography and habitat use of western pond turtles in northern California: the effects of damming and related alterations. PhD dissertation, University of California, Berkley.
- Reese, S. A., D. C. Jackson, and G. R. Ultsch. 2003. Hibernation in freshwater turtles: softshell turtles (*Apalone spinifera*) are the most intolerant of anoxia among North American species. *Journal of Comparative Physiology B: Biochemical, Systemic, and Environmental Physiology* 173:263–268.
- Richards, R. R. 2012. Movement of *Scaphirhynchus* species in the Missouri River above Fort Peck reservoir, Montana. M.Sc. Thesis, Montana State University, Bozeman.

- Rogers, K. B., and G. C. White. 2007. Analysis of movement and habitat use from telemetry data, pp. 625–676. *In*: Analysis and interpretation of freshwater fisheries data. C.S. Guy, and M.L. Brown (eds). American Fisheries Society, Bethesda, Maryland.
- Sanford, J. P. 2007. Dam regulation effects on sand bar migration on the Missouri River: Southeastern South Dakota. M.A. Thesis, The University of Montana, Missoula.
- Scrimgeour, G. J., T. D. Prowse, J. M. Culp, and P. A. Chambers. 1994. Ecological effects of river ice break-up: a review and perspective. *Freshwater Biology* 32:261–275.
- Sexton, O. J. 1959. Spatial and temporal movements of a population of the painted turtle, *Chrysemys picta marginate* (Agassiz). *Ecological Monographs* 29:113–140.
- Shively, S. H., and J. F. Jackson. 1985. Factors limiting the upstream distribution of the Sabine map turtle. *American Midland Naturalist* 114:292–303.
- Swales, S., R. B. Lauzier, and C. D. Levings. 1986. Winter habitat preferences of juvenile salmonids in two interior rivers in British Columbia. *Canadian Journal of Zoology* 64:1506–1514.
- Ultsch, G.R. 2006. The ecology of overwintering among turtles: where turtles overwinter and its consequences. *Biological Reviews* 81:339–367.
- USHR (United States House of Representatives). 1976. Designation of Missouri River segment as a Wild and Scenic River. USHR, Subcommittee on National Parks and Recreation Report, Washington, D.C.
- Vuke, S. M., K. W. Porter, J. D. Lonn, and D. A. Lopez. 2007. Geologic map of Montana. Montana Bureau of Mines and Geology. Geologic Map 62B, 1:500,000.
- Werner, J. K., B. A. Maxell, P. Hendricks, and D. L. Flath. 2004. Amphibians and reptiles of Montana. Mountain Press, Missoula, Montana.
- White, G. C., and R. A. Garrott. 1990. Analysis of wildlife radio-tracking data. Academic Press, San Diego, California.
- Wildhaber, M. L., A. J. DeLonay, D. M. Papouilas, D. L. Galat, R. B. Jacobsen, D. G. Simpkins, P. J. Braaten, C. E. Korschgen, and M. J. Mac. 2011. Identifying structural elements needed for development of a predictive life-history model for pallid and shovelnose sturgeons. *Journal Applied Ichthyology* 27:462–469.

CHAPTER THREE

NESTING ECOLOGY OF THE TURTLE *APALONE SPINIFERA*
IN A LARGE RIVER-FLOODPLAIN ECOSYSTEM

Contributions of Authors and Co-Authors

Manuscript in Chapter 3

Author: Brian J. Tornabene

Contributions: Conceived the study, collected and analyzed data, interpreted analyses, and authored the manuscript

Co-author: Robert G. Bramblett

Contributions: Conceived the study, obtained funding, collected data, and assisted with study design and interpretation of analyses. Discussed results and implications and edited the manuscript.

Co-author: Stephen A. Leathe

Contributions: Conceived the study, obtained funding, collected data, and discussed results and implications.

Co-author: Alexander V. Zale

Contributions: Assisted with study design and interpretation of analyses. Discussed results and implications and edited the manuscript.

Manuscript Information Page

Brian J. Tornabene, Robert G. Bramblett, Stephen A. Leathe, Alexander V. Zale
Herpetologica

Status of Manuscript:

- ☒ Prepared for submission to a peer-reviewed journal
- ☐ Officially submitted to a peer-review journal
- ☐ Accepted by a peer-reviewed journal
- ☐ Published in a peer-reviewed journal

Published by The Herpetologists' League

Abstract

The nesting ecology of spiny softshell turtles in Montana, where they are at the northern extent of their range and a state Species of Concern, is poorly known. We used visual surveys, observation from shore-based blinds, and remote cameras to document nesting and emergence timing, behavior, and habitat in a 101-kilometer reach of the Missouri River. A large flood event occurred during 2011 that submerged riparian habitats into late July and produced substantial riparian scour; median average discharge and runoff in 2011 were 1.3 and 1.6 times higher than average. We located 25 nests in 2011 and 97 in 2012. Nesting followed annual peak river stage, and mostly occurred in the afternoon when temperatures were 25–30° C and no humans were present. Nesting and emergence occurred 20 and 24 d later in 2011 than in 2012, but incubation periods between years were similar. Longitudinal distribution of nests was more restricted in 2011 than in 2012 and nest distribution was more similar to the distribution of islands in 2012. Nearly all nests were in mixed-gravel substrates, only 9% were in pure sand, and vegetative cover at nest sites was sparse. Median distance of nests to the water's edge was 10.6 m and median nest elevation was 0.7 m; these microhabitat characteristics of nests during the emergence period were typically greater than those during the nesting period (15.8 m and 0.8 m). Habitat characteristics at basking sites were generally opposite and more diverse than at nesting sites (0.3 m distance to shore and 0.1 m elevation). Proportion of nests found on island and mainland habitats were similar in 2011, but 90% of nests were on islands in 2012. Predation occurred on 46 nests; mainland nests incurred three times higher predation rates than island nests. Only 36% of

nests were successful in 2011, but 60% were successful in 2012. Substrate temperatures in simulated nests during the incubation period differed little between depths, but were about 4 °C higher in mixed gravel than pure sand substrates. Potential freezing episodes penetrated to 20 cm and occurred at all depths and varied among them; duration was generally longer in sand substrates, and minimum temperatures were general cooler in mixed gravel substrates. Mixed gravel substrates may be pivotal for ensuring that turtle eggs acquire adequate degree-days for successful incubation in their extreme northern range. Flooding in 2011 probably decreased nesting effort and success by reducing habitat availability and delaying the onset of nesting, thereby prematurely ending incubation because of low temperatures. However, flood events maintain and create nesting habitats by clearing vegetation and depositing substrates. Premature termination of incubation and the ostensible inability of *Apalone spinifera* hatchlings to overwintering in the nest suggest that the northern range of this species is probably limited by successful incubation and emergence before winter each year.

Key words: River turtle; Spiny softshell turtle; Emergence; Incubation; Egg predation; Microhabitat; Nest success; Substrate temperature; Northern range; Flood; Missouri River; Riparian scour; Remote cameras; Temperature loggers

Introduction

Spiny softshell turtles (herein SSTs or turtles) have inhabited the Missouri and Mississippi rivers for thousands of years (Parmley, 1992; Holman and Andrews, 1994) therefore their life-history strategies are influenced by local environmental conditions, natural streamflow patterns, and disturbance events such as flood pulses similar to other

species occupying river-floodplains (Kuchling, 1999; Bunn and Arthington, 2002; Moll and Moll, 2004). However, scarce information exists concerning the ecology of SSTs in river-floodplain ecosystems despite being the most widespread species of the genus *Apalone* in North America (Webb, 1962; 1973). Information about SSTs in Montana was limited to incidental presence records (Werner et al., 2004) and systematic sampling (Dood et al., 2009). Systematic sampling determined longitudinal distributions and relative abundances of SSTs in the Yellowstone and Missouri rivers in Montana from 2004–2008 (Dood et al., 2009). The disjunct population of SSTs in the Missouri River in Montana is probably the most vulnerable population to declines or extirpation because it is separated from downstream populations by Fort Peck Dam, is influenced by upstream dam regulation, individuals in the population move between different habitats in different seasons (Chapter 2), may be negatively influenced by river recreation (Bolton, 2007), and is at the northern range limit of the species (47° N).

The ecology of SSTs in the northern portion of their range has only been investigated in Lake Champlain in Quebec, Canada, and Vermont, USA (45° N; Graham and Graham, 1997, Galois et al., 2002). No nesting ecology studies have been conducted in a large river in the northwestern part of the range of SSTs. Turtles occupying the extreme northern portion of their range may have a truncated active season and fewer degree days available for incubation; nevertheless, temperature influences general timing and success of nests in temperate-region turtles (Kuchling, 1999). Moreover, populations in their northern range may have lower annual growth, delayed maturity, and lower relative clutch mass (Larsen and Gregory, 1989; Bobyn and Brooks, 1994).

Dams can influence riverine turtles by fragmenting populations, altering flood-pulse cycles, converting lotic to lentic habitats, and influencing timing and availability of habitats (Ward and Stanford, 1983; Moll and Moll, 2004). The installation of dams in lower reaches of the Missouri River has altered natural flow cycles (Ward and Stanford, 1983), influenced sandbar migration (Sanford, 2007), and influenced distribution and abundance of fish communities (Hesse et al., 1989; Bowen et al., 2003; Galat et al., 2005). Dams and channelization reduced islands and sand bars by 98% in a 740-km reach of the Lower Missouri River from 1879–1954 (Funk and Robinson, 1974). A reduction of these habitats, commonly basked and nested upon by riverine turtles, could decrease annual nesting success and fitness (Moll and Moll, 2004; Barko and Briggler, 2006). Moreover, if extirpation occurs, dams and reservoirs could obstruct recolonization by downstream populations.

The influences of a variable hydrograph, a truncated active season, and recreation on the nesting ecology of SSTs in a large river-floodplain ecosystem are not known. A fundamental requisite for management and conservation is a more complete understanding of the relationships between life history characteristics of a species and anthropogenic and natural factors. Our objective was to document SST nesting ecology and habitats in relation to natural and anthropogenic factors in a large river-floodplain ecosystem in the Missouri River above Fort Peck Reservoir.

Materials and Methods

Study Site

Our study was conducted on 101 river kilometers (rkm) of the Missouri River above Fort Peck reservoir in central Montana extending from the Judith River confluence (rkm 3,194; measured from the confluence with the Mississippi River) downstream to the Fred Robinson Bridge (rkm 3,093; Fig. 3.1). We selected this reach because catch rates of SSTs were highest here during systematic sampling surveys conducted on the Missouri and Yellowstone rivers from 2004 through 2008 by Montana Fish, Wildlife and Parks (MTFWP), PPL Montana, and the U.S. Fish and Wildlife Service (USFWS; Dood et al., 2009).

The study reach is part of a designated Wild and Scenic River and is located within the Charles M. Russell National Wildlife Refuge and the Upper Missouri River Breaks National Monument (USHR, 1976). This area was mapped and explored by the Lewis and Clark Expedition in 1805 and it remains to be one of the most pristine and secluded places in Montana. Canyons of eroding bluffs of Judith and Fox Hills sandstone surround the river and transition to diminished slopes of Bearpaw shale about 10 km upstream of the Fred Robinson Bridge (Vuke et al., 2007).

Channel-bottom and shoreline substrates are dominated by gravel, cobble, sand, occasional boulders, or a combination thereof in the upper reaches of the study site, but transition to predominately sand about 10 rkm above the Fred Robinson Bridge (Fig. 3.2; Richards, 2012). Numerous ephemeral tributaries enter the study site, but the Judith River is the only perennial tributary; the Judith River is about 200 km in length and enters the

Missouri River at the upstream terminus of the study site. The six largest ephemeral tributaries within the study site are Antelope, Bullwhacker, Cow, Dog, Two Calf, and Woodhawk creeks. The creeks generally flow from April through June, range in length from about 30 to 70 km, range in width from about 5 to 20 m, are less than about 2 m deep, and are dominated near their confluences by silt and sand substrates with occasional gravel and cobble deposits.

Several regulated hydroelectric dams affect the hydrology of the Missouri River in our study area, but three dams (Canyon Ferry, Gibson Dam on the Sun River, and Tiber Dam on the Marias River) operated by the U.S. Bureau of Reclamation ostensibly have the most influence on streamflow and habitat. Peak flows in spring have been reduced to 70–80% of natural flows and base flows in autumn and winter have been increased downstream of these dams (Ramey et al., 1993; Gardner and Jensen, 2011). However, our study area is considerably less hydrologically altered than downstream reaches that have been converted to lentic settings, are highly flow-altered, channelized, or a combination thereof (Pegg et al. 2003; Galat et al., 2005; Sanford, 2007).

Missouri River average mean daily discharge (i.e., 1932–2012) and mean daily discharge for years 2010 through 2012 were calculated from daily discharge data obtained from the United States Geological Survey (USGS) flow gauge at the Fred Robinson Bridge near Landusky, Montana. Discharge during our study was highly variable (Fig. 3.3). Annual median flow, maximum daily mean flow, and annual runoff were intermediate in 2010, high in 2011, and low in 2012 compared to the 79-year average (Table 3.1). Median annual flow differed among years 2010 through 2012 (KWU; $\chi^2 = 219.02$, $df = 2$, $P < 0.001$) and was 1.3 times greater in 2011 than in 2010,

2012, and compared to the 79-year average. Annual runoff in 2011 was 1.6 and 1.8 times higher and maximum daily mean flow in 2011 was 2.1 and 3.9 times higher than in 2010 and 2012. Maximum daily mean flow (herein, peak flow) occurred on 11 June in 2011 and 2012, but occurred 9 d later on 20 June in 2010.

Describing Nesting Timing and Behavior

Potential spiny softshell turtle (herein, SST) nesting habitats were defined as areas with accessible shorelines (slope $< 45^\circ$), sparse vegetation ($< 50\%$ cover), and friable substrates dominated by sand or mixes of gravel and sand (Ernst and Lovitch, 2009; Bolton et al., 2008; Bolton, 2007; Graham and Graham, 1997; Plummer et al., 1997). Three techniques were used to locate nests and observe nesting behavior in 2011 and 2012: (1) observing potential nesting habitat from a distance with a blind and spotting scope, (2) extensive visual surveys of all potential nesting habitats, and (3) placing remote cameras at potential nesting habitats (only in 2012). Nests were also located when unknown nests were depredated, evinced by dug out holes, or when hatchlings emerged which creating characteristic exit holes.

We observed female SSTs from a distance when they were spotted on land near putative nesting locations. Nesting behaviors were observed unobtrusively from the opposite shoreline using binoculars or a portable blind and spotting scope and general behaviors were documented (e.g., actions and times and duration on land) along with reactions to passing motorized and non-motorized boat traffic. We conducted visual searches of all potential nesting habitats throughout the study site from May through September throughout the study site in 2011 and 2012. Nest locations were evinced by

following distinctive tracks of adult or hatchling SSTs in the sand, finding characteristic depressions in the substrate, finding eggshells and fragments, or a combination of the three (Bolton, 2007). Aggregations were defined as 2 or more nests within 50 m of each other. Macro and microhabitat characteristics were documented at each nest when they were located and after predation occurred or after hatchlings emerged because discharge and river stage height could differ considerably between these periods (see below). The beginning and end of the nesting and emergence period were defined as date of first and last observation or sign of nesting and emergence within each year.

We placed one of two types of remote cameras (10 Reconyx PC800 Hyperfire Professional IR; Reconyx, Inc., Holmen, WI; <http://www.reconyx.com>; and 4 Moultrie Game Spy I-65; EBSCO Industries, Inc., Birmingham, AL; <http://www.moultriefeeders.com>) on 9 potential or known nesting sites to photograph and describe the behaviors of nesting SSTs. Reconyx cameras took photographs every 5 min from about 16 June to 19 July 2012 at 7 locations. Moultrie cameras took photographs every hour at 2 locations, but 2 Moultrie cameras were overlapped at each of these locations to obtain a photograph every 30 min. Remote trail cameras at nesting sites had wide views of the nesting beaches, adjacent shorelines, and river channels. Each picture ($n = 90,380$) was individually entered into a database and coded for time, date, temperature, number of SSTs on shoreline (basking), number of SSTs exhibiting nesting behavior (> 1 m from shoreline and nest searching, digging, or laying eggs), lunar phase, and number of boats (i.e., motor or non-motorboat) in view using Timelapse Image Analysis software v. 1.1.0.17 (Bolton, 2007; Greenberg and Godin, 2012).

Describing Nesting,
Emergence, and Basking Habitats

We recorded microhabitat characteristics at nesting and emergence habitats in 2011 and 2012. We also recorded microhabitat characteristics at basking sites in May through August of 2010 and from May through June and August through September, before and after the nesting period, in 2011. We recorded location, habitat type, seral stage of nesting islands, channel type, substrate type, distance from shore, depth at shore, slope, elevation of nest above water level (i.e., nest elevation), percent vegetative cover, maximum vegetation height, and depth to top of egg chamber (i.e., egg chamber depth). We measured potential nesting area on islands nested on in 2012 using a metric measuring wheel and calculated area of irregular polygons using Brahmagupta's formula. We traced the outline of islands from 2011 aerial imagery of the study site and calculated area of islands nested on in 2012 in ArcMap 10.1 (ESRI, Redlands, CA; <http://www.esri.com>). We calculated nest density (nests/m²) by dividing the number of nests at each site by their respective potential nesting area (m²). Latitude and longitude location of SST nests were recorded using a hand held Geographic Positioning System (Garmin GPS eTrex Legend, $\pm$ 15 m; Garmin Ltd., Olathe, KS; <http://www.garmin.com>) projected onto 5-m orthoimagery and converted to river kilometer (rkm) using ArcMap version 10.1. General nest locations were marked with two rebar, each about 30 cm from the nests, and a small rock cairn was used to mark the approximate center of the nest. Habitat type was described as either island or mainland. Seral stage of nesting islands was described as bare, mature, or pioneer for islands nested on in 2012. Bare islands had no vegetation and were almost entirely inundated during peak streamflow. Pioneer

islands had patches of willow (*Salix* spp.) and cottonwood thickets (*Populus deltoides*) and were not entirely inundated during peak streamflow. Mature islands had stands of mature cottonwoods (> about 0.5 m diameter at breast height) and typically had only shorelines inundated during peak flow. Channel type was defined based on the geomorphology of the adjacent bank as alluvial, bluff, cut bank, or slope. Alluvial banks were within the geomorphic floodplain, usually at inside bends, and where deposition occurred. Bluffs were steep cliffs that reached high above the geomorphic floodplain, often to the top of the river canyon, and were resistant to river erosion. Cut banks were within or just above the geomorphic floodplain, usually at outside bends, where erosion and undercutting of the riverbank occurred. Slopes were bluffs that had eroded considerably from the top of the canyon down and declined gradually. Substrate was defined as predominantly boulder, clay, gravel, log, sand, or silt. Distance from nest or basking turtle to shore was measured using a metric measuring wheel. Elevation above water surface and riverbank slope were measured using a clinometer and a 2-m long and 2.5-cm diameter PVC pipe with 5-cm increment measurements denoted (habitat pole). If no discernable tracks remained, riverbank slope was measured at the suspected entrance immediate to nests, which was determined by accessibility (slope < 45°) and vegetation cover (< 50% cover). Depth at shore was measured 0.5 m from the shoreline using a boat-mounted depth sounder (Eagle Cuda 350; NAVICO, Catoosa, OK) or habitat pole. We visually estimated percent vegetative cover, and measured maximum vegetation height with a habitat pole. We measured depth to the top of the nests using a metric ruler after careful digging to verify presence of eggs. We documented animal (e.g., cattle, avian, or

mammal) and human track, and if the turtle abandoned the nesting or basking site and why.

Describing Incubation Period and Emergence Timing and Behavior

Nests located during the nesting period were checked at least every other week to document disturbance, predation, or emergence and to remeasure habitat characteristics upon emergence, predation, or both. Incubation periods were calculated for nests with known nesting and emergence dates by subtracting the earliest possible nesting Julian date from the earliest possible emergence Julian date, and subtracting the latest possible nesting Julian date from the latest possible emergence Julian date, and calculating an average incubation period for each nest because nests were not always immediately detected. Emergence rate was defined as the number of nests that successfully emerged divided by the total number of nests minus the number depredated in each year and total success rate was defined as the number of nests that successfully emerged divided by the total number of nests in each year. We placed remote cameras (Reconyx PC800 Hyperfire Professional IR; Reconyx, Inc., Holmen, WI) on ten individual nests from August through September of 2012, following the nesting period, to monitor predation and emergence timing and behavior. Each camera took a picture every 5 min, was pointed nearly straight down on a single nest, and had a narrow view. Emergence was documented when the nest opened, hatchlings were in view, new hatchling tracks appeared, or a combination thereof. Each picture ($n = 198,297$) was scanned through and photographs containing disturbance (predation or emergence), new hatchling tracks, or hatchlings were individually entered into a database and coded for time, date, temperature,

lunar phase, number of SST hatchlings or tracks, time elapsed since previous emergence, and time elapsed since first emergence from each individual nest.

We estimated the number of unknown (not located) nests and an abundance estimate for nests within the study site in both years. We estimated the number of unknown nests (N_2) by relating the number of known nests (N_1) and number of known nests depredated (P_1) to unknown nests that were depredated (found because of predation; P_2) as follows (sensu Burger, 1976; Tinkle et al., 1981):

$$\frac{P_1}{N_1} = \frac{P_2}{N_2}$$

where P_1 = predation on known nests

P_2 = predation on unknown nests

N_1 = total known nests

N_2 = total unknown nests

and abundance estimate for nests = $N_1 + N_2$.

Incubation and Overwintering Temperatures

We described ambient substrate temperatures in simulated nests throughout the incubation period among different depths and between different substrate types in 2012 using buried temperature loggers (Onset HOBO TidbiT v2 Temperature Data Logger; Onset Computer Corporation, Bourne, MA). Temperature loggers were buried at 3 different depths (5, 12.5, and 20 cm) inside three simulated nests in sand and three simulated nests in mixed gravel. The simulated nests in sand and mixed substrates were across the river from each other, about 200 m apart, and had similar vegetative cover

qualities to limit temperature variation due to spatial location and vegetative cover.

Temperature loggers in each simulated nest were tied to a 1-m long piece of 1.2-cm wide rebar, which was hammered 0.9 m into the substrate in front of each simulated nest, using tie-able metal fishing leader (Tyger Leader; Tyger Leader Sporting, Ironwood, MI).

Temperature loggers were deployed on 16 June 2012, recorded temperature every 10 min, and were retrieved on 30 September of 2012. The mixed gravel site was struck by lightning on 18 June 2012 at 2020 h and shut down the 5 cm depth temperature logger in 1 simulated nest, the 12.5 cm depth temperature loggers in 2 simulated nests, and the 20 cm depth temperature logger in 1 simulated nest.

We documented overwintering substrate temperatures inside simulated nests to determine whether SST hatchlings could overwinter inside the nest and emerge the next spring. We deployed temperature loggers in the same location and following the same design as above with three simulated nests per two substrate types and three depths per simulated nest. Temperature loggers were deployed on 9 November 2010, recorded temperature every 10 min, and were retrieved on 1 June 2012. We characterized frequency, duration, and minimum temperatures of potential freezing episodes (PFEs), which were defined as a distinct progression of soil temperatures less than -0.55°C , the estimated point at which turtle tissues reach their equilibrium freezing point, for each depth of each substrate type (Costanzo et al., 1995; Churchill and Storey, 1992a and 1992b).

Statistical Analyses

We examined normality of all variables using histograms, Q-Q plots, and Shapiro-Wilk tests and homoscedasticity was examined using Levene, Brown-Forsyth, or Bartlett's tests. Microhabitat variables were compared between years 2011 and 2012 for nesting and emergence sites, between pooled nesting and pooled emergence sites, and between pooled basking and pooled nesting sites using Mann-Whitney U-tests (MWU). We used linear regression (LR) to investigate the relationships between incubation period and nesting date, nest site area and number of nests, and total island area and number of nests. We examined the differences in temperature throughout the incubation period between substrates and among depths using nested mixed effects models (NMEM) fit by restricted maximum likelihood because of our interest in variation between depths and substrate types; these models are robust to missing values and allowed us to account for spatial autocorrelation, if it occurred. We investigated autocorrelation with autocorrelation and partial autocorrelation function plots and initially selected an appropriate model by comparing saturated, candidate, and autoregressive models fit by maximum likelihood with analysis of variance tests (ANOVA) and negative log-likelihood values (Zuur et al., 2009). Median frequency, duration, and minimum temperatures for PFEs were compared among depths within substrate types using Kruskal Wallis tests (KWU) and between substrates at each depth using MWUs. Multiple comparisons following Kruskal-Wallis tests were completed with pairwise Wilcoxon rank-sum tests with Bonferroni's confidence interval adjustment. All analyses were conducted in R v3.0.2 (R Core Team, 2013) and statistical significance level for all analyses was $\alpha = 0.05$.

Results

Nesting Timing and Behavior, and Recreation

Timing of nesting, length of the nesting period, and number of nests located were different between 2011 and 2012; however, SSTs nested after peak discharge in both years (Fig. 3.4 and Table 3.2). The beginning and end of the nesting period were defined as date of first and last observation or sign of nesting within each year. We located 25 nests in 2011 and 97 in 2012. Detection of nests did not differ between years because all main channel and islands shorelines were surveyed for nests in both years. However, detection of nests may have differed between substrate types (mixed gravel and sand) because wind and other disturbances (e.g., human and animal) could quickly obscure SST tracks in sand, whereas SST tracks in gravel were largely unaffected by these disturbances. Nesting began on 4 July in 2011 when river discharge was $1053.4 \text{ m}^3/\text{sec}$ and ended on 23 July (length, 17 d). Nesting began on 14 June in 2012 when discharge was about $455.9 \text{ m}^3/\text{sec}$ and ended on 7 July (length, 24 d). At the onset of nesting in 2011, discharge was 2.3 times higher and nesting began 20 d later than in 2012.

We documented 1 full nesting event (from start to finish) in 2011 and 7 in 2012 at 6 different locations by direct observation or using remote cameras ($n = 5$ and 3). The nesting process consisted of four major steps, sometimes directly following basking: (1) adult female SSTs appeared at the shoreline, walked inland, and searched for a nesting site while often probing the substrate with their tubular snout and digging with their front legs (test digs) at various locations; (2) SSTs began digging earnestly with their front legs; (3) SSTs moved forward and continued digging with their back legs; and (4) SSTs

lowered their posterior into the excavated chamber, oviposited eggs, buried eggs with alternating strokes of their back legs, and smoothed over the mound of substrate with their plastron as they moved back to the shoreline. Total duration of nesting, durations of each step, and number of test digs varied widely (Table 3.3). Nest searching (1) lasted an average of 22 min (range 10–82 min), digging with front legs (2) lasted an average of 17 min (range 5–25 min), digging with rear legs (3) lasted an average of 14 min (range 6–35 min), and oviposition lasted an average of 13 min (range 5–35 min); average total time for nesting was 66 min and ranged from 39 to 127 min. Average number of test digs was 2 and ranged from 0–3 test digs. One SST exhibited terrestrial burying behavior on a single occasion in 2012 wherein she rocked back and forth and flipped substrate over herself using her front legs after nesting. Troughs and track in substrate at nesting sites, ostensibly created by similar behaviors, were also documented at 3 other sites in 2012.

We documented 21 basking events associated with nesting and 13 nesting attempts, 3 of which were interrupted by direct human disturbance, while attempting to observe full nesting events. Basking events occurred directly before observations of nesting attempts and lasted an average of 34 min (range 13–60 min). Seven nesting attempts (54%) stopped after nest site searching (Step 1) and six (46%) stopped after digging with their front legs (Step 2).

We observed 3 interrupted nesting events. We interrupted two nesting events during observation from the opposite shoreline when we made accidental noise. One nesting event was interrupted 3 min into Step 1 and one was interrupted 18 min into Step 2. Upon hearing the noise, both SSTs craned their neck, looked in our direction, and then quickly moved back into water. One nesting event was abandoned 36 minutes into the

nesting process during Step 2, when a group of canoeists talked and floated closely by the nesting turtle. This turtle abruptly noticed the floaters, turned to face the shoreline, tumbled down the riverbank, and moved into the water. Average total time of interrupted nesting attempts was 43 min and ranged from 3 to 181 min. The first step averaged 34 min (range 3–181 min), the second step averaged 1 min (range 2–30 min), and the average number of test holes was 2 (range 1–4). Moreover, all basking events, separate from nesting events, documented (100%) were abandoned by SSTs when our motorboat first came into view.

All remote cameras documented nesting behavior and captured 482 instances of SSTs exhibiting nesting behavior under varied environmental conditions. Cameras also documented 208 instances of motorized or non-motorized (kayaks, canoes, or rafts) boat recreation during the nesting period in 2012. These are minimum estimates for nesting activity for nesting and recreation because all nest sites and river channels were not monitored throughout the study.

In 2012, nesting activity began two days before the installation of remote cameras and peaked on 19 June (26%, $n = 128$), decreased until 24 June, increased again until 27 June (7%, $n = 32$), and then occurred sporadically until 9 July (Fig. 3.5). Recreation activity had four peaks at 16 June (11%, $n = 22$), 26 June (11%, $n = 23$), 30 June (13%, $n = 26$), and 7 July (12%, $n = 24$). Diel timing of nesting was roughly bimodal, began at 0700 h, peaked at 1000 h and 1700 h with a decrease between, and ended at 2000 h (Fig. 3.6). Recreation activity had a uniform single peak from 1300 h to 1400 h, but was observed at all hours except 0000 h, 0200 h, 0500 h, and 2300 h. Recreation activity was comprised largely of non-motorboats (76%, $n = 159$; e.g., canoes, kayaks, and rafts), but

motorized boats were also observed (24%, $n = 53$). Nesting activity generally occurred when temperatures were 25–30 °C (54%, $n = 261$), when there was no precipitation (99%, $n = 479$), when there was 0–25 or 76–100% cloud cover (43 and 26%, $n = 208$ and 129), when no other animals were present on shore (90%, $n = 435$), when no humans were in view (99%, $n = 479$), and mostly during the waxing gibbous (60%, $n = 291$) lunar phase (Fig. 3.7).

Predation, Incubation Period, and Emergence Timing and Behavior

Nests were found depredated from 19 June through 17 September in 2011 and 14 August through 13 September in 2012; 34 nests were found because they were depredated. Depredation occurred a mean of 62 d after nesting (range 55–72 d, $n = 6$) in 2011 and 60 d (range 48–61 d, $n = 6$) in 2012; the duration between nesting and depredation was not different between years (MWU; $W = 22$, $P = 0.23$). Scat and track near nesting sites and depredated nests suggested that coyotes (*Canis latrans*) were the primary nest predator. An average of 3 nests were depredated at a nesting site, but this ranged from 1 to 9 nests per site. Depredation rates were similar in 2011 (40%, $n = 10$) and 2012 (37%, $n = 36$) and depredation was about three times higher at mainland nests (57% and 90%, $n = 8$ and 9) than at island nests (18% and 31%, $n = 2$ and 27) in both years.

Mean incubation period was 63 d (range 44–77 d, $n=10$) in 2011 and 58 d (range 36–76 d, $n = 24$) in 2012. Incubation period was not strongly related to nesting date in 2011 (LR; $df = 8$, $R^2 = 0.05$, $P = 0.50$), but was strongly related to nesting date in 2012

(LR; $df = 21$, $R^2 = 0.61$, $P < 0.001$). Nesting one day later was related to a 1-d decrease in incubation period in 2012 (Fig. 3.8).

Remote cameras documented emergence of hatchling SSTs from 9 of 10 monitored nests; 64 hatchling tracks and 10 hatchlings were observed for a total of 74 hatchlings evinced. Hatchlings emerged from 14 through 31 August 2012 and activity peaked at about 1900–2100 h (65%, $n = 48$) and 0200 h (15%, $n = 11$) when temperatures were 10–40 °C, but mostly when temperatures were 25–30 °C (53%, $n = 39$, Fig. 3.9). Hatchlings emerged alone or in small groups, all at once on only a single occasion, and mean group size was 2 and ranged from 1–6. A mean of 8 turtles emerged from each nest (range 1–17 hatchlings, tracks, or both). Probably not all hatchlings and tracks were observed because cameras captured photographs every 5 min; our estimated mean is therefore a mean of minima. Mean time between successive emergence events from the same nest was 10 min (range 0–140 min), but mean time from first emergence event from the same nest was 160 min (range 0–875 min). Most emergence events occurred as the moon was waxing into the full moon during waxing crescent (19%, $n = 14$), first quarter (23%, $n = 17$), waxing gibbous (26%, $n = 19$), full moon (8%, $n = 6$), and waning crescent (24%, $n = 18$) lunar phases.

Timing of emergence and length of the emergence period differed between years 2011 and 2012 (Fig. 3.4 and Table 3.4) and was later in 2011. Emergence began on 4 September and ended on 27 September (24 d) in 2011 and emergence began on 11 August and ended on 6 September (27 d) in 2012; emergence began 24 d later in 2011 than in 2012. Emergence and total success rates were different between years and were 1.6 times higher in 2012 (95 and 60%, $n = 58$) than in 2011 (60 and 36%, $n = 9$).

Nest Site Distribution, Aggregation,
Fidelity, and Macrohabitat Characteristics

Longitudinal distribution of nests was different between years 2011 and 2012 (PX; $\chi^2 = 59.18$, $df = 32$, $P < 0.01$; Fig. 3.10 and 3.11). Nesting sites (sites) were loosely defined as general and large (50–2000 m; Fig. 3.5) potential nesting beaches and nesting areas (areas) were loosely defined as smaller and more specific nesting beaches; multiple areas could often be located within a site, and were typically separated by about 50-100 m. Some of the same areas were used for nesting in both years; in 2011, nests were restricted to 6 reaches (10-km stretches of river) and 8 areas, but nests in 2012 were more widely distributed in 9 reaches and 15 areas (Fig. 3.10 and Table 3.4). Longitudinal distribution of nests was different than the longitudinal distribution of islands, but more closely resembled the distribution of islands in 2012 (PX: $\chi^2 = 92.48$, $df = 72$, $P = 0.05$) than in 2011 (PX: $\chi^2 = 55.09$, $df = 36$, $P = 0.02$). Five areas had nests in both years, but three areas used in 2011 were not nested at in 2012 and ten areas used in 2012 were not nested at in 2011.

Nests were aggregated in both years. Nearly half of nests in 2011 (48%, $n = 12$) were located at a single area in the upstream portion of the study site (Table 3.4) and we located more than 1 nest at 62% ($n = 5$) of sites in 2011. We also located more than 1 nest at 87% ($n = 13$) of sites in 2012 and 4 areas (27%) contained 10 or more nests (Table 3.4). Average number of nests per area was 3 (range 1–12) in 2011 and 5 in 2012 (range 1–15). About a third of nests were in aggregations in 2011 (32%) and 2012 (28%).

Nesting macrohabitats of SSTs were different, but channel and substrate types were similar, between years 2011 and 2012. Nearly half (44%, $n = 11$) of nests were

located on islands in 2011, but almost all nests were located on islands in 2012 (90%, $n = 87$). Seral stage of nesting islands was only described in 2012 and pioneer islands (70%, $n = 61$) were most often nested upon. However, mature (29%, $n = 25$) and bare islands (1%, $n = 1$) were also nested on. Number of nests at a nesting beach in 2012 was highly related to potential nesting area in 2012 (LR; $df = 11$, $R^2 = 0.75$, $P < 0.001$; Fig. 3.12 and Table 3.5), but was not related to total island area (LR; $df = 11$, $R^2 = 0.03$, $P = 0.54$) in 2012. Moreover, total island area was not related to potential nesting area in 2012 (LR; $df = 11$, $R^2 < 0.001$, $P = 0.96$).

Most SSTs nested in mixed sand and gravel substrates in 2011 and 2012 (84 and 93%, $n = 21$ and 90), but some also nested in sand (16 and 7%, $n = 4$ and 7). The majority of nests in 2011 and 2012 (60 and 91%, $n = 15$ and 88) were found on alluvial shorelines (Fig. 3.13). The remainder of SST nests was found on the toe of sloped shorelines in 2011 and 2012 (36 and 6%, $n = 9$ and 6), the toe of short bluffs in 2011 (4%, $n = 1$), and the edge of cut banks in 2012 (3%, $n = 3$).

Basking Site Distribution, Aggregation, Fidelity, and Macrohabitat Characteristics

Macrohabitat characteristics at basking sites differed from those at nesting sites and basking sites of SSTs were distributed widely. The majority of basking sites were on alluvial (46%, $n = 29$) and sloped (40%, $n = 25$) shorelines, but cut banks (13%, $n = 8$), and bluffs (1%, $n = 1$) were also used (Fig. 3.14). Substrate at basking sites was dominated by silt (32%, $n = 20$), clay (28%, $n = 18$), and sand (24%, $n = 15$) substrates. However, SSTs also were found basking on boulders (8%, $n = 5$), fallen logs (5%, $n = 3$), and gravel substrates (3%, $n = 2$). Basking sites were observed throughout the study site

except in the upper 20 and lower 5 km of the study site, and the highest numbers of basking sites occurred in rkm 3130-3125 (14%, $n = 10$), 3115-3110 (8%, $n = 6$), 3110-3105 (8%, $n = 6$), and 3105-3100 (10%, $n = 7$). Basking sites were on both mainland (54%, $n = 37$) and island shorelines (46%, $n = 32$).

Microhabitat Characteristics at Nest Sites and Basking Sites

During the nesting period, median distance to shore (distance), median percent vegetative cover (cover), and median maximum vegetative height (height) at nests were not different between 2011 and 2012 (MWU; $W = 166, 182$, and 174 ; $P = 0.21, 0.34$, and 0.25). Depth at shore immediate to nests (depth), slope, and nest elevation (elevation) were greater at nests during the nesting period in 2011 than in 2012 (MWU; $W = 0.84, 344$, and 266 ; $P < 0.01, 0.001, 0.05$; Fig. 3.15 and Table 3.6). Median depth during the 2011 nesting period was 0.10 m (range 0.05–0.33 m) and was 1.7 times greater than median depth during the 2012 nesting period (0.06 m, range 0.02–0.21 m). Median slope during the 2011 nesting period was 10° (range 0 – 26°) and was 10 times greater than slope during the 2012 nesting period (1° , range 0 – 5°). Median elevation at nests during the nesting period in 2011 was 0.8 m (range 0.2–1.9 m) and was 1.6 times greater than elevation in 2012 (0.5 m, range 0.2–1.4 m). Median egg chamber depth was only measured during the nesting period in 2012 and was 11.9 cm and ranged from 7.3 to 17.9 cm ($n = 24$), justifying our temperature logger deployment scheme of depths of 5, 7.5, and 20 cm.

During the emergence period, median distance, cover, and height at nests were not different between 2011 and 2012 (MWU; $W = 924, 792$, and 704 ; $P = 0.35, 0.90$, and

0.39). However, median depth, slope, and elevation at nests during the emergence period varied between years (MWU; $W = 1585, 1373, 1472, P < 0.001$; Fig. 3.16 and Table 3.6). Median depth during the emergence period in 2011 was 0.26 m (range 0.05–0.58 m) and was 8.7 times greater than median depth during the emergence period in 2012 (0.06 m, range 0.02–0.21 m). Median slope during the emergence period in 2011 was 10° (range $0\text{--}25^\circ$) and was more than 10 times greater than in 2012 (0° , range $0\text{--}27^\circ$). Median elevation in 2011 during the emergence period in 2011 was 2 m (range 1.1–2.2 m) and was 2.2 times greater than in 2012 (0.9 m, range 0.4–2.4 m).

All median microhabitat characteristics at nests varied between the nesting and emergence periods except cover and height, which only approached significance (MWU; $W = 1978$ and $1993, P = 0.11$ and 0.12 ; Fig. 3.17 and Table 3.7). Median distance during the nesting period (10.6 m, range 1.9–48.5 m) was 1.5 times less than during emergence period (15.8 m, range 3.9–56.7 m; MWU; $W = 1472, P < 0.001$). During the nesting period, median depth (0.07 m, range 0.02–0.33 m) was 1.7 times greater than during the emergence period (0.04 m, range 0.01–0.58 m; MWU; $W = 3116, P < 0.001$). Median slope during the nesting period (2° , range $0\text{--}26^\circ$) was more than 2 times greater than during the emergence period (0° , range $0\text{--}27^\circ$; MWU; $W = 912, P < 0.001$). Median elevation during the nesting period (0.7 m, range 0.2–1.9 m) was 1.3 times less than during the emergence period (0.7 m, range 0.4–2.4 m; MWU; $W = 912, P < 0.001$).

Microhabitat characteristics at basking sites were different than at nests during the nesting period (Fig. 3.18 and Table 3.8) with the exception of cover (MWU; $W = 1298.5, P = 0.86$). Median distance was about 35 times greater at nests (10.6 m, range 1.9–48.5 m) than median distance at basking sites (0.3 m, range 0–1.3 m; MWU; $W = 6832, P <$

0.001). Median depth at nests (0.1 m, range 0–0.3 m) was 2.3 times less than at basking sites (0.2 m, range 0–2 m; MWU; $W = 535.5$, $P < 0.001$). Median slope at nests (2° , range 0– 26°) was 7.5 times less than at basking sites (15° , range 0–58; MWU; $W = 746$, $P < 0.001$). Median elevation at nests (0.7 m, range 0.2–1.9 m) was 7 times greater than at basking sites (0.1 m, range 0–0.6 m; MWU; $W = 320$, $P < 0.001$). Median height at nests (0 cm, range 0–51 cm) was only slightly, but still significantly, different than at basking sites (0 cm, range 0–56 cm; MWU; $W = 1618$, $P = 0.02$).

Cattle activity (observed presence, tracks, sign, or scat) was only observed in 2012 at one nesting location. In this case, receding waters allowed cattle access to a heavily used nesting island (9% of nests located there in 2012, $n = 9$) where they disturbed substrate (hoof impressions) and grazed vegetation. However, no disturbance to known nests was documented; of the 9 nests located there, 7 were depredated and 2 successfully emerged. Cattle activity at basking sites was only documented once; a single SST was basking near numerous hoof impressions on a shoreline.

We estimated that 14 nests were not located in 2011 and 335 nests were not located in 2012. Thus, the population estimate for nests was 35 in 2011 and was 402 in 2012.

Incubation and Overwintering Nest Substrate Temperatures

Air temperatures in 2012 were generally average and warmer than average in April and May. The model, for incubation temperatures in simulated nests, with the most support had depths nested within individual simulated nests within substrate types (sand or gravel) per our original design. Substrate type was the mixed effect, of primary interest,

and depth and individual simulated nest were random effects. We accounted for temporal autocorrelation using an autoregressive AR(1) correlation structure ($\phi = 0.93$).

Substrate temperatures varied little among depths within holes or among holes of the same substrate, but varied between substrates (NMEM; $df = 4$, $t = -7.83$, $P = 0.001$; Fig. 3.19 and 3.20). Sand substrates were 4.3 °C (95% CI = 3.3–5.4 °C) cooler than mixed substrates in simulated nests. Substrate temperatures were more variable in simulated nests in sand compared to gravel substrate (BF; $F = 8.25$, $P < 0.01$). Moreover, variance in substrate temperatures of gravel and sand substrate types decreased with increasing depth (BF; $F = 478.14$, 810.52, and 1008.96; $P < 0.001$).

Potential freezing episodes (PFEs) were documented in both substrates types and at all depths, differed among depths within substrates, and differed between substrates within depths (Fig. 3.21 and 3.22, and Table 3.9) The most PFEs occurred at 5 cm depths in mixed gravel and sand substrate (63 and 39, range 48–66 and 29–41), but more PFEs occurred in mixed gravel substrates than in sand substrates at 5, 12.5 (21 and 15, range 21–22 and 9–16) and 20 cm (14 and 10, range 16–23 and 9–11).

Duration and minimum temperature of PFEs varied among depths within each substrate type. Median duration of PFEs in mixed gravel substrates was highest at 20 cm (41.8 h, range 0.2–351.0 h) and lowest at 12.5 cm (15.5 h, range 0.7–503.8 h) and did not differ between 5 and 12.5 cm or 10 and 20 cm (KW; $\chi^2 = 10.0$; $df = 2$, $P < 0.001$; Table 3.9). Median duration of PFEs in sand substrates was also highest at 20 cm (68.3 h, range 0.2–496.0 h), but lowest at 5 cm (17.0 h, range 0.3–444.8 h), and did not differ between 12.5 and 20 cm (KW; $\chi^2 = 21.13$; $df = 2$, $P < 0.001$). Median duration of PFEs only differed between mixed gravel and sand substrates at 12.5 cm soil depth where duration

was 3.12 times longer in sand substrates than in mixed substrates (MWU; $W = 889$, $P < 0.01$).

Median minimum temperature of PFEs in mixed gravel substrates was highest at 20 cm (-2.7°C , range -12.2 to -0.6°C) and lowest at 5 cm (-5.5°C , range -20.3 to -0.6°C) and did not differ between 12.5 (-3.3°C , range -15.1 to -0.6°C) and 20 cm depths (KW; $\chi^2 = 30.5$; $df = 2$, $P < 0.001$). Median minimum temperature of PFEs in sand substrates was highest at 20 cm (-2.33°C , range -7.4 to -0.6°C) and lowest at 5 cm depths (-3.8°C , range -15.3 to -0.6°C) and did not differ between 5 and 12.5 cm (-2.8°C , range -11.4 to -0.6°C) or 12.5 and 20 cm (KW; $\chi^2 = 12.57$; $df = 2$, $P < 0.001$). Median minimum temperature of PFEs only differed between mixed gravel and sand substrates at 5 cm substrate depth where minimum temperature was 1.3 times cooler in mixed than in sand substrates (MWU; $W = 7014$, $P < 0.01$).

Discussion

Nesting is a fundamental and vulnerable time in the life cycle of highly aquatic turtles. Annual nest success was influenced by the timing and magnitude of flood pulses and the truncated active season in this river-floodplain ecosystem at the extreme northern portion of the range of the species. Recreation may influence nesting behavior, nest sites had specific habitat characteristics that were influenced by streamflow and were probably related to nest success and fitness, and emergence was dependent on timing of nesting and temperature profiles.

Female SST movements towards nesting habitats occurred immediately before or after peak discharge and were probably most influenced by temporal changes in

streamflow (Chapter 2). Nesting occurred after streamflow decreased from peak and nesting activity decreased shortly thereafter. Thus, decreasing streamflow coupled with the exposure of nesting habitats probably initiated SST nesting similar to other riverine turtles (Pritchard and Trebbau, 1984; Vogt, 1997; Kuchling, 1999; Moll and Moll, 2004).

Recreation may influence SST timing of nesting and nest site distribution. Turtles were extremely wary on land, probably because they are highly lotic-adapted species, and abandoned basking and nesting efforts when they became aware of human presence. Moreover, peak diel recreational river traffic coincided with a decrease in the number of female SSTs exhibiting nesting behavior. This may result in turtles delaying nesting until human disturbance ceases, moving in an attempt to locate concealed habitats, or decreased nest success if SSTs are disturbed during oviposition. Similar disturbance eventually resulted in limitations on recreation near critical nesting sites in Lake Erie because female SSTs would not return to cover abandoned nests, which often resulted in nest failure (Bolton, 2007). However, decreases in nesting activity also coincided with, and could be related to, peak daily temperature. During diel temperature peaks, we observed substrate surface temperatures exceeding 40 °C. These temperatures probably limited the duration that SSTs could spend on exposed shorelines because the critical thermal maxima for SSTs is 41.5 °C (Hutchison et al. 1966), and SSTs heat faster than they cool (Smith et al. 1981). We also observed that females created troughs as described in other parts of the SSTs range (Bolton, 2007; Plummer and Doody, 2010); this behavior may have reduced the influence of hazardous temperatures (Plummer and Doody, 2010).

Basking substrates were more diverse than nesting substrates and SSTs primarily basked on shorelines. In contrast, Lindeman (2001) reported that SSTs primarily basked

on logs, braches and stumps. The differences in basking habitat may be attributable to the relative lack of large woody debris along shorelines in our study area. Moreover, basking habitats were always closer to the shoreline than nesting habitats, where they had the ability to quickly escape into water, and SSTs frequently basked while partially submerged. Basking activity peaked at about the onset of nesting and we commonly observed basking prior to nesting activity. Basking probably enhances metabolism and egg development (Kuchling, 1999) and pre-nesting basking behavior has been attributed to initiating the final development of eggs for oviposition for South American river turtles (Kuchling, 1999) and *Graptemys pseudogeographica* and *G. ouachitensis* in the Mississippi River (Vogt, 1980). However, turtles may also bask more frequently during pre-nesting when water temperatures are cooler than during post-nesting when water temperature are warmer.

Nesting habitats were most often on islands with alluvial banks, sparse vegetation, and gravel substrate. Nesting habitats were at higher elevations, but shallower slopes, than basking habitats. Shallow slopes probably allow SSTs easier access and higher elevations may reduce risk of inundation; duration of inundation decreased nest success in the closely related *Apalone mutica* (Plummer, 1976). However, shallower slopes may occur at nesting sites because of the associated scour that maintains and creates nesting habitats. In a near-average discharge year (2012), vegetation of nesting islands was of an earlier seral stage (sparse willow and cottonwood thickets) than in a high water year (2011). This is probably because most of the early seral stage islands were inundated in 2011 during the nesting period, and more early seral islands may have been available

following the 2011 flood event. Vegetation on islands may serve as a visual indicator of nesting habitat that turtles can observe from the river.

Converse to most riverine turtles, including SSTs (Doody 1996; Graham and Graham, 1997; Moll and Moll 2004), SST nesting occurred primarily in gravel substrates. Detection of nests may have been lower in sand opposed to mixed gravel substrates, but sand substrates for nesting were limited throughout the study site. Incubation temperatures in simulated nests in gravel substrates were warmer, acquired more degree-days for incubation, and were more consistent than in sand substrates. Thus, choosing gravel over sand substrates could be important in maximizing degree-days for incubation, and reducing negative effects of variable and extreme incubation temperatures (e.g., on physiology, morphology, and behavior; Miller et al., 1987; Packard et al., 1987; Packard and Packard, 1988; Janzen, 1993; Doody, 1999) in the northern range of the species. However, turtles may not have actively chosen gravel substrates because gravel substrates were the most available substrate type within the study area.

A combination of microhabitat characteristics probably influenced SST nest-site choice (Wood and Bjørndal, 2000; Hughes and Brooks, 2006) such that thermal and soil-moisture properties of the substrate maintain consistent thermal patterns and moderate moisture content. Nest-site choice and nest habitat characteristics ultimately influence nest survivorship, hatchling development, and fitness (Bull and Vogt, 1979; Janzen, 1993; Wilson, 1998) and turtles provide considerable parental investment by choosing nesting sites that increase hatchling survival (Resetarits, 1996; Weisrock and Janzen, 1999; Valenzuela, 2001; Kolbe and Janzen, 2002; Hughes and Brooks, 2006). Turtles were ostensibly selective about nest location given that we observed the highest female

movement rates during nesting (Chapter 2) and individual SSTs dug multiple test holes in various locations before choosing a nest site.

Emergence occurred about two months after nesting, similar to SSTs elsewhere (Doody, 1995; Ernst and Lovitch, 2009), when river discharge declined to baseflow and air and water temperatures began to decrease. Diel timing of emergence generally occurred at dusk and at night when temperatures were low, and generally during waxing lunar phases. Decreasing diel temperatures (Hays et al., 1992; Gyuris, 1993) or a temperature threshold (Bustard, 1967; Mrosovsky, 1968; Plummer et al., 2008) following the onset of darkness may initiate SST emergence from the nest, after eggs have been pipped, similar to other riverine turtles. However, these two temperature cues are probably interrelated as previously suggested (Moran et al., 1999; Doody et al., 2001). A bright lunar phase may facilitate navigation and SSTs may use differences in brightness between aquatic and terrestrial areas as a directional cue. Such differences are known to influence the direction in which emerging sea turtles move, but it is unknown if similar or other directional cues are used by hatchling river turtles (Witherington, 1995; Moll and Moll, 2004). Hatchling SSTs may also use olfactory cues of previously emerged hatchlings (i.e., scent trails) to navigate to water similar to other riverine turtles (Butler and Graham, 1995).

Individual or groups of hatchling SSTs emerged from individual nests over minutes, hours, or days, similar to *A. muticus* hatchlings (Plummer et al., 2008). Most hatchlings appeared to enter the water immediately after emergence, similar to other freshwater turtles (Anderson, 1958; Butler and Graham, 1995; Burke et al., 2000). Staggered emergence may be a predation avoidance tactic or a result of thermal

stratification within the nest chamber. Egg development is influenced by egg depth such that shallow nests and eggs typically receive more degree-days than deeper nests and eggs (Burger, 1976; Ewert, 1979; Packard and Packard, 1988; Thompson, 1988; Congdon and Gibbons, 1990). However, our study suggests that a predation avoidance tactic is more likely for SSTs in Montana because temperature in simulated nests was not significantly different between depths. Nocturnal emergence may serve to avoid diurnal predators (Janzen et al., 2000) and may also reduce the potential for overheating and desiccation (Janzen et al. 2000; Kolbe and Janzen 2002; Plummer 2007).

Habitat conditions at nests during emergence were different than during nesting. Nests were up to 2 times further from water, with lower shoreline slopes and depths. We located several hatchlings buried in fine substrates in warm, shallow, slow current velocity water adjacent to nesting sites following emergence. Such habitats may provide hatchlings easier access to water, time to acclimate to their new environment, protection from displacement, reduce predation risk, and increase growth rates (Plummer et al., 2008).

Predation of nests was higher on main channel shorelines than on islands and was probably related to isolation of islands. Island-specific nest predation rates were higher in 2012, when annual discharge was lower. Although we observed coyotes swimming between mainland shorelines and islands, this was during baseflow and coyotes may have difficulty reaching islands during runoff. We observed that most (about 70%) nest depredation occurred in localized areas. For example, in 2011, 100% of mainland nest depredations occurred at a single site, and in 2012, 90% of mainland nest depredations occurred at a single site. This suggests that once predators have located a nesting site, the

probability of further nest depredation at the site increases. Timing of predation could also be related to olfactory cues produced by emerging hatchlings because predation typically began about the time of emergence and we observed predation on emerged nests surrounding non-emerged nests.

Higher than average streamflow was probably the primary factor influencing later nesting, use of different nesting habitats, more nest aggregation, and reduced nesting effort and nest success in 2011. Discharge in 2011 had an annual exceedance probability of 4–10% (P. McCarthy, U.S. Geological Survey, personal communication) and peaked almost 2 times higher than in 2012 (a near-average year). Timing of nesting was three weeks later and emergence of hatchlings occurred nearly a month later in 2011 than in 2012, although incubation period was similar between years. However, we suspect that turtles were attempting to nest as soon as mid-June in 2011. We observed females along shorelines and on inundated islands at known nesting habitats before river stage receded. Fewer nests on islands and higher nest aggregation in 2011 were probably caused by higher and longer duration of discharge, which inundated islands and reduced overall area of nesting habitat. Nest locations were higher, further from shore, had higher bank slopes in 2011 than in 2012 and these habitat characteristics probably differed between years because of the higher river stage during nesting in 2011 than in 2012.

Our study site location, at the northwestern extent of the range of the species, coupled with the high and late runoff in 2011 probably resulted in delayed nesting and the termination of incubation by freezing temperatures in nest chambers. Although it has been suggested that hatchling SSTs may overwinter inside the nest (Minton, 1972), the low tolerance of the species to freezing temperatures (Costanzo et al., 1995) and the

frequent and extended freezing episodes we measured at all simulated nest depths probably prevents this. Moreover, we discovered eggs eroding out of a bank on a nesting island in November 2010, subsequent to below-freezing air temperatures. We excavated, collected, and incubated three SST eggs from a nearby nest, but none survived to hatch. Therefore, the snowmelt-driven hydrology coupled with the onset of freezing temperatures in autumn may create a “runoff-winter squeeze” that limits the northwestern range of this species.

Flood pulses play a fundamental role in shaping river-floodplain ecosystems (Leopold et al., 1964; Hupp and Osterkamp, 1985; Ward, 1989; Junk et al., 1989) and expose bare substrates essential for SST reproduction (Kuchling, 1999; Moll and Moll, 2004). Although the large and late flood pulse of 2011 may have reduced SST nest success in that year, it also deposited nesting substrate, created new alluvial bars, reshaped islands, and scoured substantial areas of riparian vegetation; many of these areas were subsequently used for SST nesting in 2012. Number of nests within a nesting location was more related to the scoured island area than total island area. Riverine ice dynamics also scour riparian vegetation (Scott et al., 1997) and create new nesting habitats as was observed subsequent to the winter of 2010. Variable streamflows, flood pulses, riparian scour, and sediment deposition provide disturbance mechanisms that produce varied seral stages and create and maintain nesting habitats for SSTs.

We suggest two areas where management can reduce anthropogenic influences on SST populations. First, maintaining near-natural streamflow with a single peak preserve occasional large floods, habitat heterogeneity, possible movement cues, reduce the possibility of nest inundation by late flows, and maintain early-seral island and shoreline

nesting habitats fundamental for SST reproduction. Anthropogenic disturbance such as the installation of new dams or channelization or both may also affect SSTs (Plummer et al., 1997; Barko and Briggler, 2006). Changes to hydrographs and damming of the main stem or tributaries could delay SST movement, affect nest-site choice, and affect survival by altering seasonal streamflow and water temperature, altering locations of scour, reducing habitat heterogeneity and nesting habitat availability, or a combination thereof.

Second, river recreation may have negative effects on SST basking and nesting. Decreased opportunities for behavioral thermoregulation by basking may influence pre-oviposition egg development. Recreation may also reduce SST nest success if females abandon nests following oviposition or SSTs are influenced to move to find secluded nesting habitats, which is energetically costly. Recreation is one of the most common land uses within the study site and human presence can be detrimental to turtles (Garber and Burger, 1995), and especially nesting SSTs (Bolton, 2007). Recreation within the study site is currently limited to non-motorized traffic during the nesting period, but all motorized traffic is allowed during autumn. Public outreach and potential restrictions on recreational activity near nesting sites could reduce negative effects on SSTs such as nest abandonment and reduced nest success, fitness, and annual recruitment.

Acknowledgments

Funding for this project was provided by PPL Montana, USFWS, MTFWP, and the Bureau of Reclamation. This study was conducted under the auspices of Montana State University Institutional Animal Care and Use protocols #2009-19 and #2012-24, two MTFWP scientific collection permits (#2009-056 and #2010-050), and a USFWS

special use permit (#10-012). We thank M. Plummer from Harding University, J. Chaffin and J. Peters from the U.S. Bureau of Land Management, L. Hanauska-Brown from Montana Fish, Wildlife & Parks, and D. Trimpe and J. Kucera from the U.S. Bureau of Reclamation for funding and logistical support. We thank J. J. Rotella and E. Kenison for comments on this manuscript. We also thank A. Dood, C. Jensen, C. Manning, M. Mayfield, D. Moore, R. Richards, and Z. Wenderott for invaluable logistical support and help with data collection or analysis. We also thank the Lewistown, Montana, USFWS and MTFWP offices and employees for shuttling vehicles and other logistical support; specific thanks to J. Dullum, R. Potts, and J. Fox. The Montana Cooperative Fishery Research Unit is jointly sponsored by the U.S. Geological Survey, Montana Fish, Wildlife & Parks, Montana State University, and the U.S. Fish and Wildlife Service. The use of trade names or products does not constitute endorsement by the U.S. Government.

Tables

Table 3.1. Discharge summary statistics for the Missouri River from USGS gaging station 06115200 on the Missouri River at the Fred Robinson Bridge near Landusky, Montana, for water years 2010 – 2012 and the average at this site (1935-2012).

Variable	Water year			
	2010	2011	2012	Average
Annual median flow (m ³ /sec)	201.3	261.9	195.4	193.1
Standard deviation	164.3	361.9	81.2	113.2
Maximum daily mean flow (m ³ /sec, date)	945.8 (6/20)	2,019.0 (6/11)	512.5 (6/11)	
Minimum daily mean flow (m ³ /sec, date)	138.5 (12/9)	139.3 (2/2)	96.3 (1/20)	
Annual runoff (million acre-ft)	6.8	10.7	6.0	6.5

Table 3.2. Start and end dates of nesting and emergence periods in 2011 and 2012, number of nests (*n*) and duration (d) of the nesting, incubation (Inc.), and emergence periods in 2011 and 2012.

Variable	2011			2012		
	Nesting	Inc.	Emergence	Nesting	Inc.	Emergence
<i>n</i>	25	10	25	97	24	97
Duration (d)	17	63	24	24	59	27
Start	July 7		September 4	June 14		August 11
End	July 23		September 27	July 7		September 6

Table 3.3. Minimum, maximum, and mean time for each nesting step (1–4; $n = 8$) and all steps (Total) of the nesting process and number of test digs during step 1. Basking events were observed directly prior to nesting events. Steps are (1) searching for a site, (2) digging with front legs, (3) digging with rear legs, and (4) oviposition and burying eggs.

	Min	Max	Mean
Bask	13	60	34
1	10	82	22
Test digs (#)	0	3	2
2	5	25	17
3	6	35	14
4	5	35	13
Total	39	127	66

Table 3.4. Numbers of observed nests (N), emergences (E), and nest predations (P) at 18 nesting areas used in 2011, or 2012, or both. Camera indicates if a remote camera was placed at the site during the 2012 nesting period. Habitat indicates if the nesting area was located on a main channel shoreline (M) or island (I).

Site	rkm	Habitat	Camera	2011			2012		
				N	E	P	N	E	P
Council	3191.2	I	N	1			13	6	7
RO	3190.5	M	Y	12	4	8	2	1	1
Lower RO	3189.7	M	N				8		8
Gravel	3181.5	I	Y				9	2	7
Dauphin	3169.6	I	Y				10	9	1
Shitrock	3165.3	I	N				6	6	
Little bird	3147.5	I	Y	3	3				
Big bird	3147.2	M	N	2	1				
Sturgeon	3141.4	I	N	1					
Lower Gist	3132.7	I	N				2	1	1
N1	3131.8	I	Y				4	4	
Cow	3127.8	I	Y	2			6	6	
Across N2	3125.5	I	N				1	1	
N2	3125.3	I	Y	3	1	2	15	9	6
N3	3118.9	I	Y				11	8	1
Hideaway	3112.1	I	Y	1			6	3	3
Skull	3104.4	I	N				3	2	1
Lower skull	3104.3	I	N				1	1	
Total		15	9	25	9	10	97	58	36

Table 3.5. Island locations, characteristics, and dimensions for those nested upon in 2012 including number of nests and nest density (# of nests/m²) per site. Island type indicates if the nest was on a mature (M), pioneer (P), or bare (B) island.

Site	RKM	Island type	Max. length (m)	Max. width (m)	Total area (m ²)	Nesting area (m ²)	Num. nests	Nest density
Council	3191.17	M	815	362	212340	988	13	0.013
Gravel	3181.51	P	370	62	19901	692	9	0.013
Dauphin	3169.60	P	320	55	14857	533	10	0.019
Shitrock	3165.26	P	290	54	11700	527	6	0.011
Lower gist	3132.75	P	860	153	98393	196	2	0.010
N1	3131.78	P	610	103	41007	456	4	0.009
Cow	3127.76	M	1871	167	200651	69	6	0.087
Across n2	3125.51	P	294	36	13102	106	1	0.009
N2	3125.35	P	49	19	7424	909	15	0.017
N3	3118.91	P	539	97	48568	1078	11	0.010
Hideaway	3112.15	M	767	225	99715	394	6	0.015
Skull	3104.42	P	389	90	23252	412	3	0.007
Lwr. skull	3104.26	B	109	19	1306	114	1	0.009

Table 3.6. Number of observations, minimum, maximum, median, and standard deviation (SD) for microhabitat variables at *Apalone spinifera* nests during the nesting and emergence periods in 2011 and 2012. Subscript letters indicate a microhabitat characteristic that was statistically different between the 2011 and 2012 nesting (^a) or emergence (^b) period using a Mann-Whitney U-test, $P < 0.05$.

Year	Period	<i>n</i> obs.	Minimum	Maximum	Median	SD
<i>Distance to shore (m)</i>						
2011	Nesting	18	1.9	27.0	10.3	78.0
	Emergence	17	11.9	45.9	17.0	7.9
2012	Nesting	24	2.3	48.5	11.8	13.2
	Emergence	95	3.9	56.7	15.8	13.9
<i>Maximum vegetation height (cm)</i>						
2011	Nesting	18	0.0	41.0	0.0	13.3
	Emergence	17	0.0	77.0	5.0	21.6
2012	Nesting	24	0.0	51.0	2.0	18.9
	Emergence	95	0.0	93.0	11.0	24.3
<i>Depth at shore (m)^{a,b}</i>						
2011	Nesting	15	0.05	0.33	0.10	0.08
	Emergence	17	0.05	0.58	0.26	0.13
2012	Nesting	24	0.02	0.21	0.06	0.05
	Emergence	95	0.01	0.32	0.03	0.04
<i>Slope (°)^{a,b}</i>						
2011	Nesting	18	0	26	10	9.0
	Emergence	17	0	25	10	5.2
2012	Nesting	24	0	5	1	1.7
	Emergence	95	0	27	0	4.6
<i>Percent vegetative cover (%)</i>						
2011	Nesting	18	0	70	0	16.5
	Emergence	17	0	60	2	19.3
2012	Nesting	24	0	25	0	7.3
	Emergence	95	0	30	2	7.9
<i>Nest elevation (m)^{a,b}</i>						
2011	Nesting	16	0.2	1.9	0.8	0.4
	Emergence	17	1.1	2.2	2.0	0.3
2012	Nesting	24	0.2	1.4	0.5	0.3

Emergence	95	0.4	2.4	0.9	0.4
-----------	----	-----	-----	-----	-----

Table 3.7. Number of observations, minimum, maximum, median, and standard deviation (SD) for microhabitat variables at *Apalone spinifera* nests during the nesting and emergence periods. An asterisk (*) indicates a microhabitat characteristic that was statistically different between the nesting and emergence periods using a Mann-Whitney U-test, $P < 0.05$

Period	<i>n</i> obs.	Minimum	Maximum	Median	SD
<i>Distance to shore (m)*</i>					
Nesting	42	1.9	48.5	10.6	11.4
Emergence	112	3.9	56.7	15.8	13.2
<i>Maximum vegetation height (cm)</i>					
Nesting	42	0	51	0	16.9
Emergence	112	0	93	9.5	23.9
<i>Depth at shore (m)*</i>					
Nesting	39	0.02	0.33	0.07	0.07
Emergence	112	0.01	0.58	0.04	0.11
<i>Slope (°)*</i>					
Nesting	42	0	26	2	7.8
Emergence	112	0	27	0	5.3
<i>Percent vegetative cover (%)</i>					
Nesting	42	0	70	0	12
Emergence	112	0	60	2	10.4
<i>Nest elevation (m)*</i>					
Nesting	40	0.2	1.9	0.7	0.4
Emergence	112	0.4	2.4	0.9	0.5

Table 3.8. Number of observations, minimum, maximum, median, and standard deviation (SD) for microhabitat variables at *Apalone spinifera* nests and basking site parameters. An asterisk (*) indicates a microhabitat characteristic was statistically different between nesting sites during the nesting period and basking sites using a Mann-Whitney U-test, $P < 0.05$

Period	<i>n</i> obs.	Minimum	Maximum	Median	SD
<i>Distance to shore (m)*</i>					
Nesting	42	1.9	48.5	10.6	11.4
Basking	56	0	1.3	0.3	0.3
<i>Maximum vegetation height (cm)*</i>					
Nesting	42	0	51	0	16.9
Basking	63	0	56	0	11.6
<i>Depth at shore (m)*</i>					
Nesting	39	0.02	0.33	0.07	0.07
Basking	63	0	2	0.16	0.34
<i>Slope (°)*</i>					
Nesting	42	0	26	2	7.8
Basking	63	0	58	15	13.6
<i>Percent vegetative cover (%)</i>					
Nesting	42	0	70	0	12
Basking	63	0	65	12	14
<i>Nest elevation (m)*</i>					
Nesting	40	0.2	1.9	0.7	0.4
Basking	63	0	0.6	0.1	0.1

Table 3.9. Summary statistics for potential freezing episodes (PFE) at known *Apalone spinifera* nesting sites in simulated nests in mixed (predominantly gravel and sand) and pure sand substrates on the Missouri River in Montana from 9 November 2011 to 1 June 2012. Letters indicate significant differences among median parameters of depths within substrate types using a KW followed by multiple comparisons with Wilcoxon matched pairs tests ($P < 0.05$); depths with the same letter are not significantly different. Asterisks (*) indicate significant differences between median parameters of substrate types of the same depth using a Mann-Whitney U-test ($P < 0.05$).

PFE parameter	Depth (cm)		
	5	12.5	20
<i>Mixed</i>			
Frequency			
<i>n</i>	177	64	43
Median	63	21	14
Range	48 to 66	21 to 22	23 to 16
Duration (h)			
Mean $\pm$ SD	28.2 $\pm$ 51.6	72.3 $\pm$ 129.4	98.1 $\pm$ 143.4
Median	16.8 ^a	15.5 ^{a,b*}	41.8 ^b
Range	0.17 to 351.0	0.7 to 503.8	3.7 to 490.5
Avg. cum.	1662.9	1542.2	1405.9
Min. temp. (°C)			
Mean $\pm$ SD	-5.46 $\pm$ 3.2	-3.90 $\pm$ 3.3	-3.41 $\pm$ 2.9
Median	-5.16 ^{a*}	-3.26 ^b	-2.68 ^b
Range	-20.26 to -0.56	-15.10 to -0.56	-12.20 to -0.56
<i>Sand</i>			
Frequency			
<i>n</i>	109	40	30
Median	39	15	10
Min	29 to 41	9 to 16	9 to 11
Duration (h)			
Mean $\pm$ SD	46.8 $\pm$ 90.1	122.6 $\pm$ 173.0	138.6 $\pm$ 175.1
Median	17.0 ^a	48.4 ^{b*}	68.3 ^b
Range	0.33 to 444.8	1.33 to 575.2	0.17 to 496.0
Avg. cum.	1701.1	1634.3	1386.0
Min. temp. (°C)			

Mean $\pm$ SD	-4.25 $\pm$ 2.9	-3.73 $\pm$ 2.8	-2.59 $\pm$ 2.0
Median	-3.81 ^{a*}	-2.76 ^{a,b}	-2.33 ^b
Range	-15.26 to -0.56	-11.40 to -0.59	-7.38 to -0.56

Figures

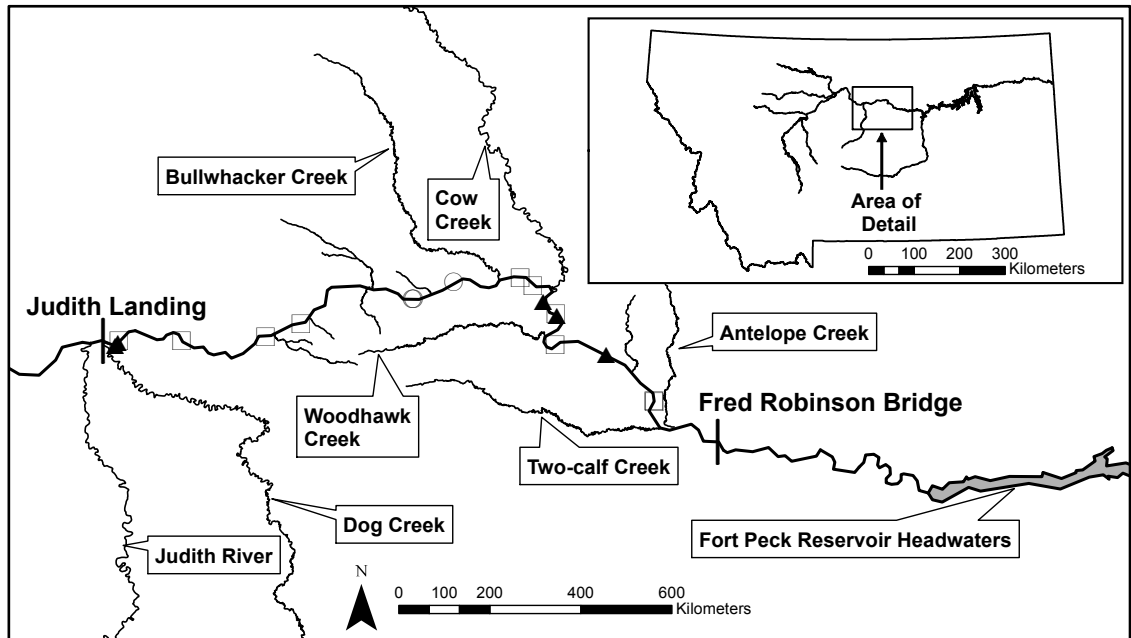


Figure 3.1. Study site on the Missouri River in Montana. Open circles represent *Apalone spinifera* nesting sites used in 2011, open squares represent sites used in 2012, and closed triangles represent sites used in both years. Vertical lines represent the locations of bridges at the Judith River confluence (Judith Landing) and Fred Robinson Bridge.

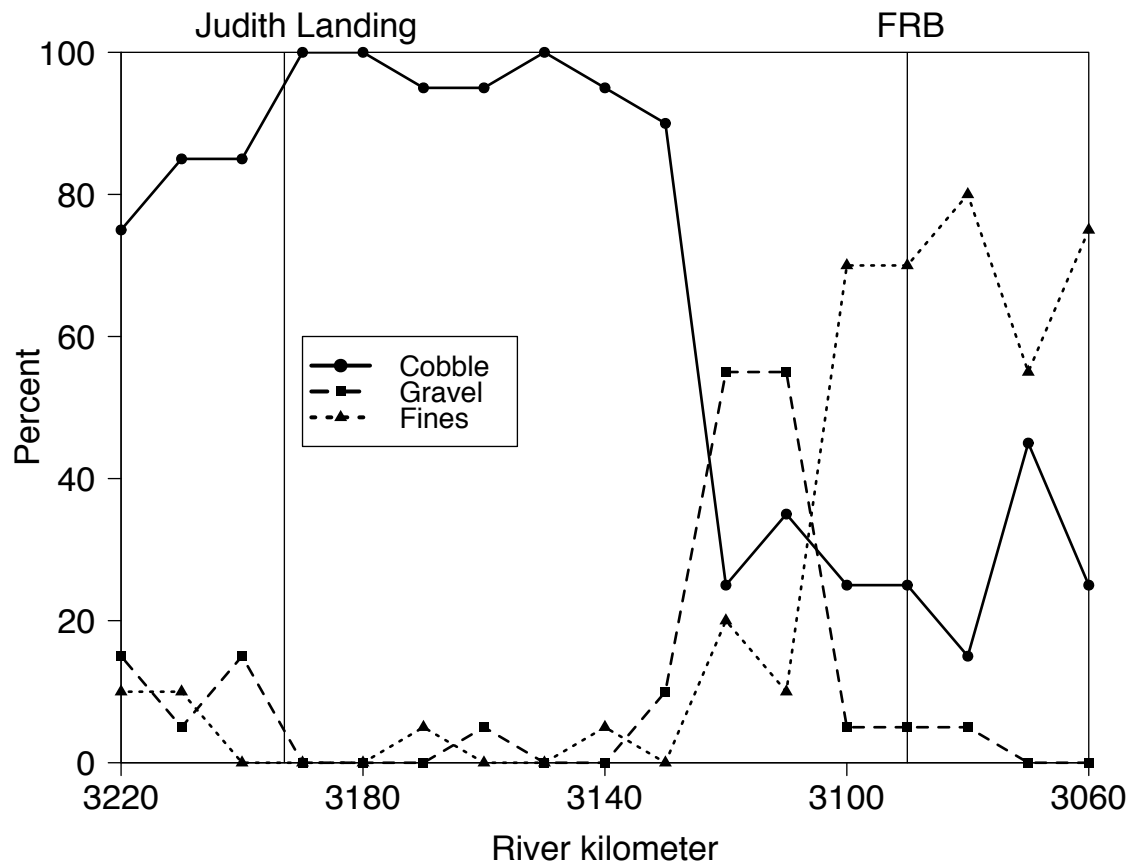


Figure 3.2. Distribution of channel bottom substrate types in the Missouri River in Montana upstream of Fort Peck reservoir estimated by Richards (2012). Vertical solid lines represent the location of the Judith River confluence (Judith Landing) and Fred Robinson Bridge (FRB). River kilometer is the distance from the confluence with the Mississippi River.

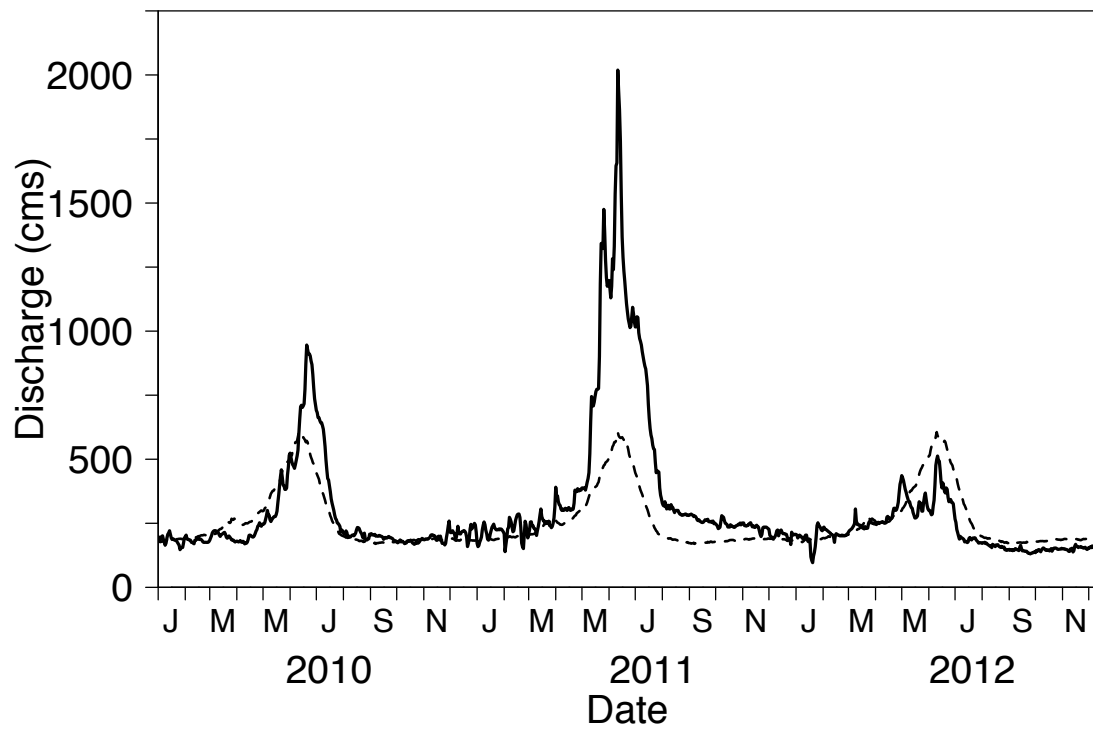


Figure 3.3. Average (1934–2012; dashed line) and January 2010 through November 2012 (solid line) mean daily discharge (cms = cubic meters per second) in the Missouri River at the Fred Robinson Bridge near Landusky, Montana.

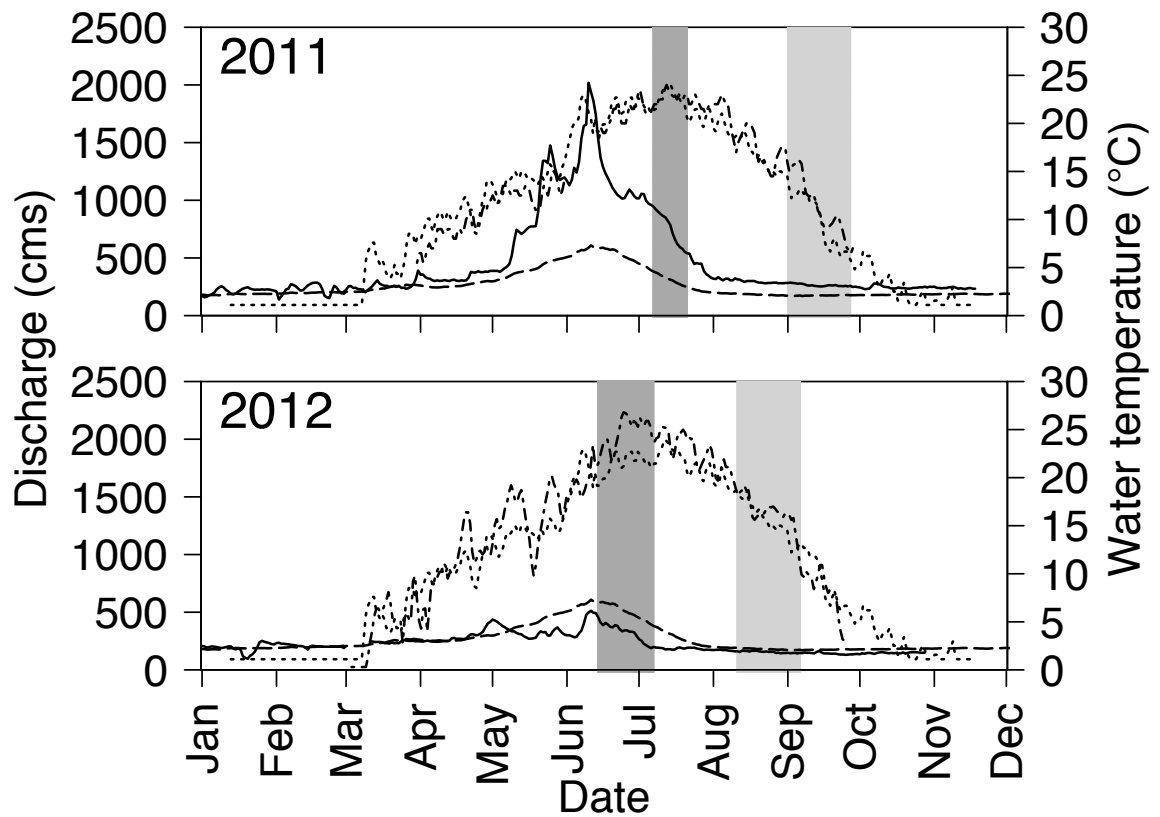


Figure 3.4. Nesting (dark grey rectangles) and emergence (light grey rectangles) periods of *Apalone spinifera* in 2011 (top) and 2012 (bottom) plotted against annual discharge (solid line), average discharge (1935-2012; dashed line), annual air temperature (dot-dash line), and average water temperature (2002-2012; dotted line). Ticks on the x-axis represent the first day of that month.

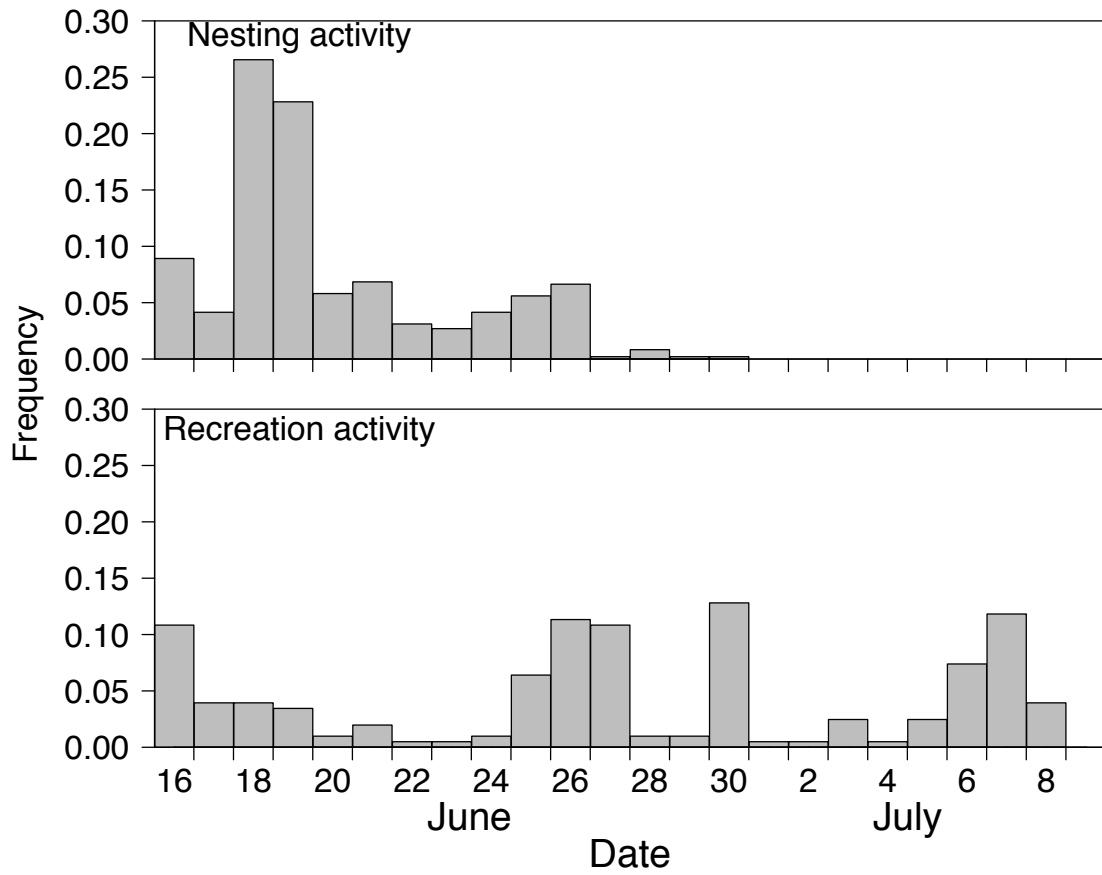


Figure 3.5. Frequency distribution of *Apalone spinifera* nesting ($n = 482$) and human recreation activity ($n = 208$) observed by remote cameras from 16 June to 9 July 2012 binned by day.

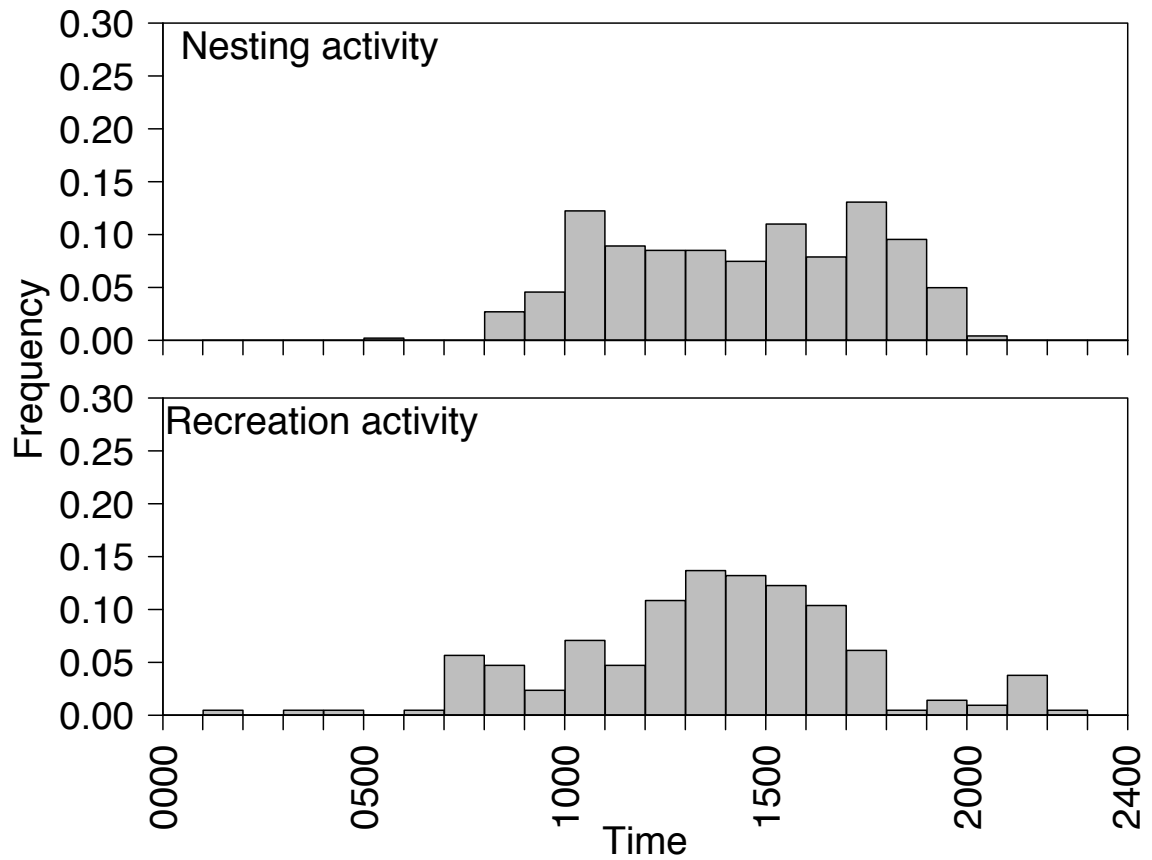


Figure 3.6. Frequency distribution of *Apalone spinifera* nesting ($n = 482$) and human recreation activity ($n = 208$) observed by remote cameras from 16 June to 9 July 2012 by time of day (h).

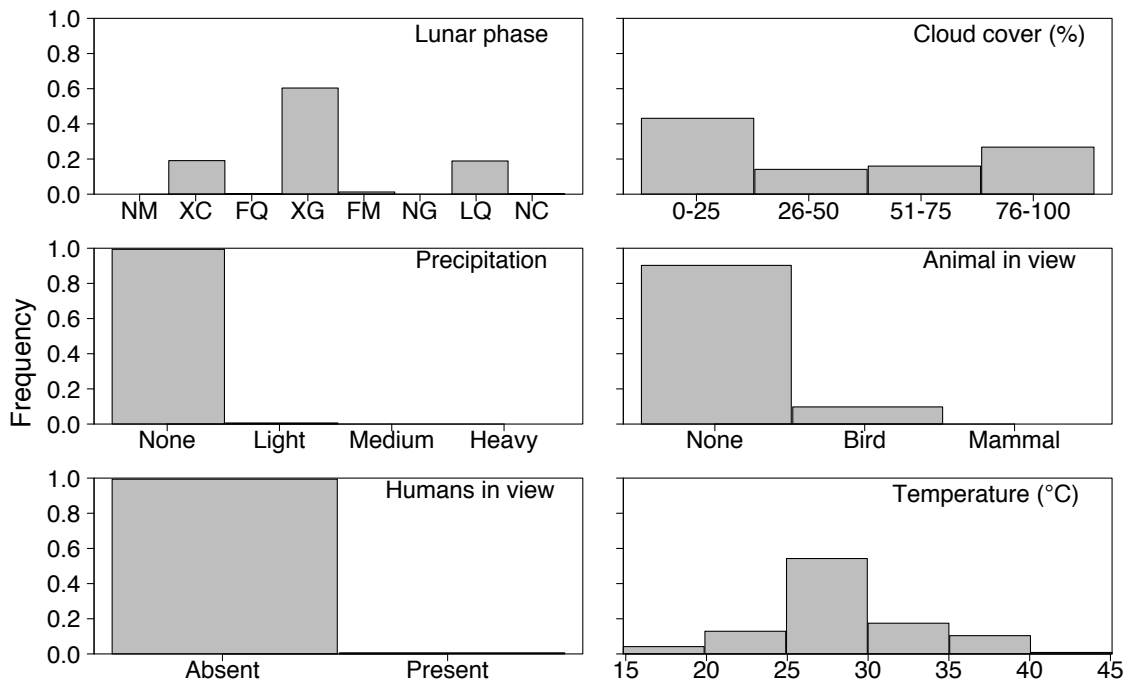


Figure 3.7. Frequency of *Apalone spinifera* exhibiting nesting behavior from remote cameras ($n = 482$) by lunar phase (NM = new moon, XC = waxing crescent, FQ = first quarter, XG = waxing gibbous, FM = full moon, NG = waning gibbous, LQ = last quarter, NC = waning crescent), cloud cover, precipitation, if an animal was in view, if humans were in view, and temperature.

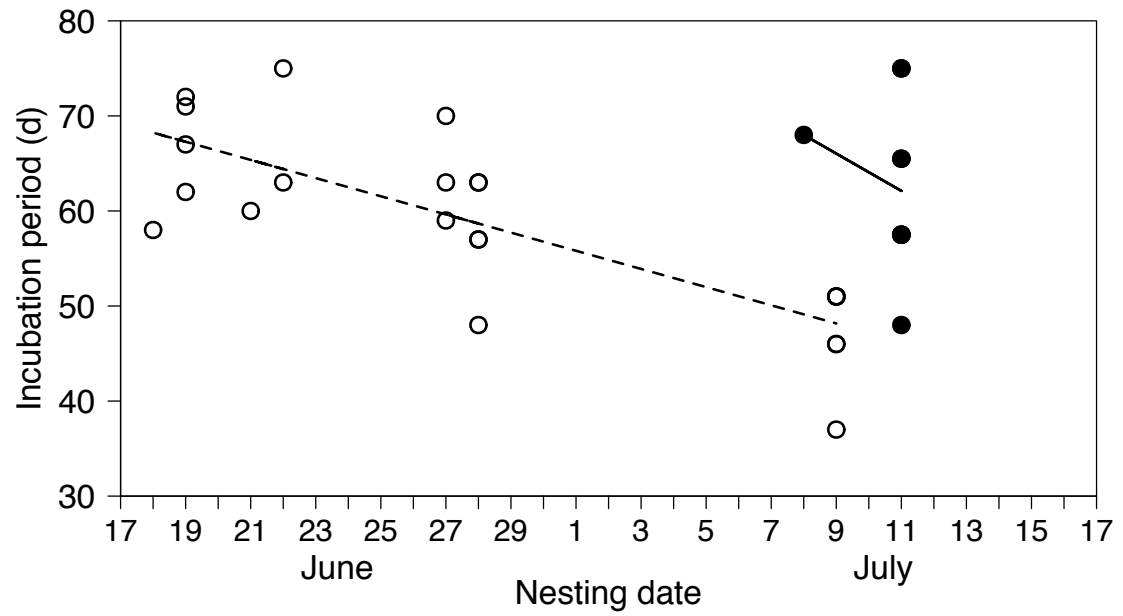


Figure 3.8. Relationship between nesting date and incubation period for *Apalone spinifera* nests laid in 2011 (solid dots and line; $n = 10$) and 2012 (open circles and dashed line; $n = 23$).

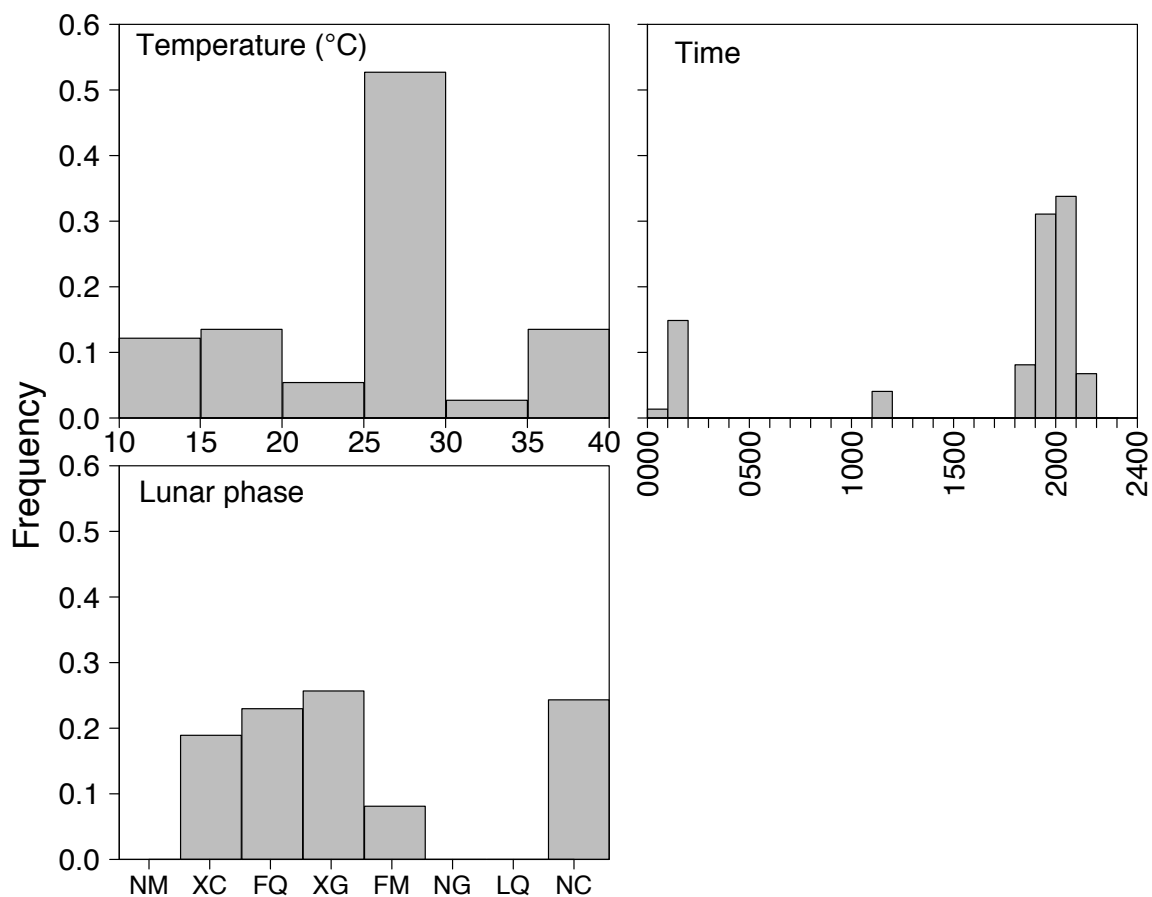


Figure 3.9. Frequency of *Apalone spinifera* hatchlings or hatchling tracks emerging from nests from remote cameras ($n = 74$) by temperature ($^{\circ}\text{C}$), time of day (h), and lunar phase (NM = new moon, XC = waxing crescent, FQ = first quarter, XG = waxing gibbous, FM = full moon, NG = waning gibbous, LQ = last quarter, NC = waning crescent).

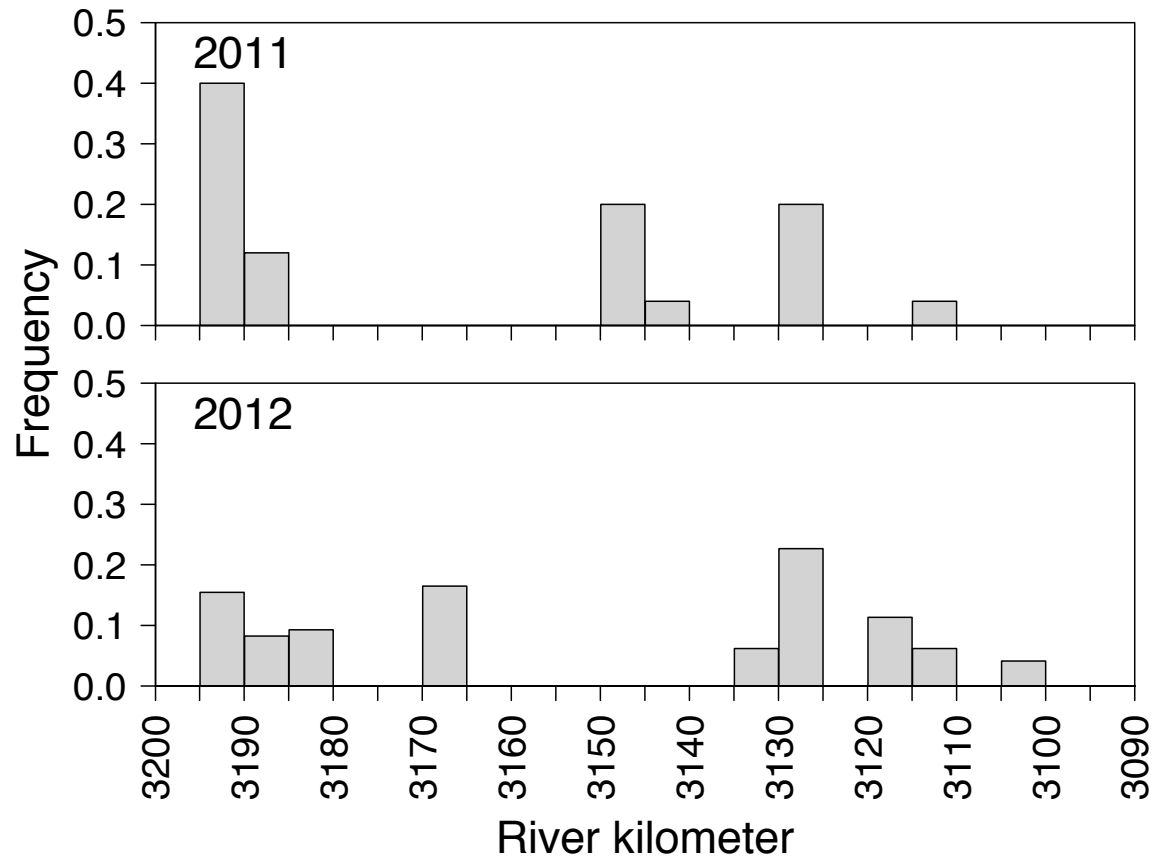


Figure 3.10. Longitudinal distribution of *Apalone spinifera* nests in 2011 (top; $n = 25$) and 2012 (bottom; $n = 97$).

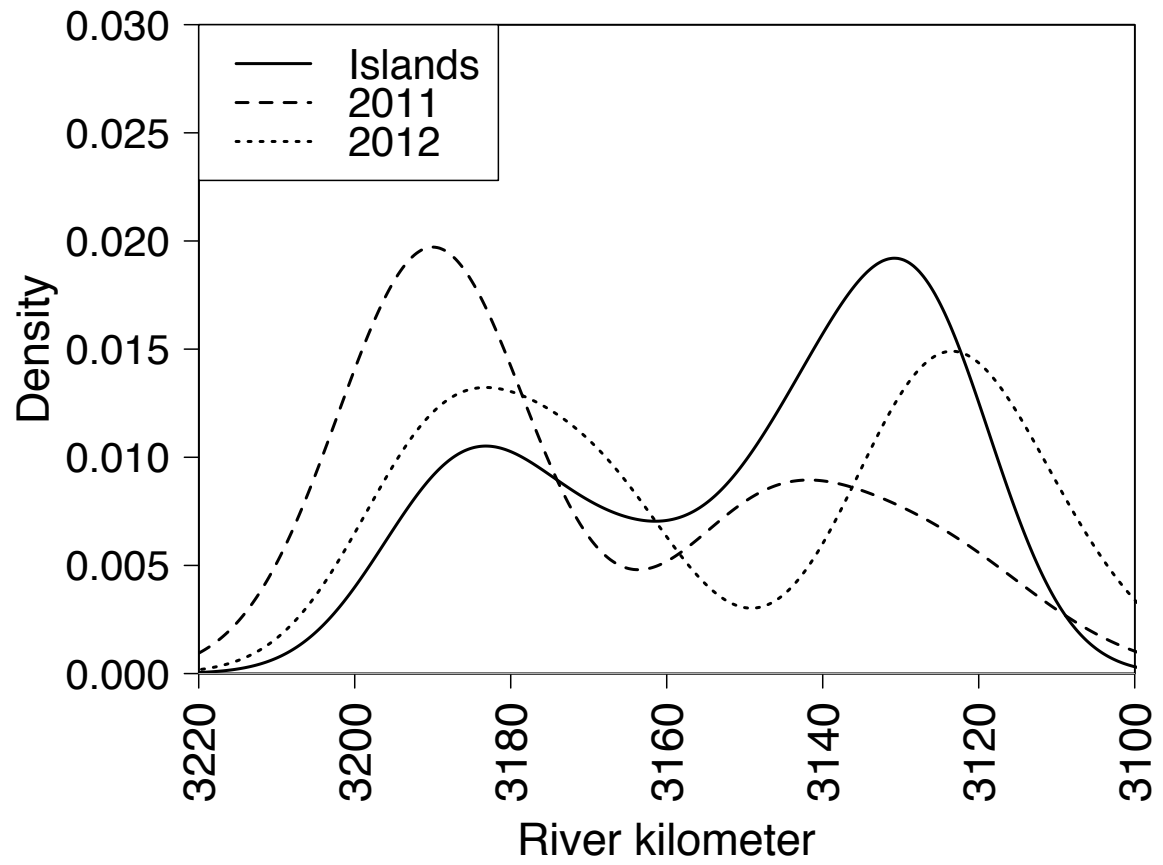


Figure 3.11. Longitudinal density distribution of *Apalone spinifera* nests in 2011 ($n = 25$; dashed line), 2012 ($n = 97$; dotted line), and of islands ($n = 111$; solid line).

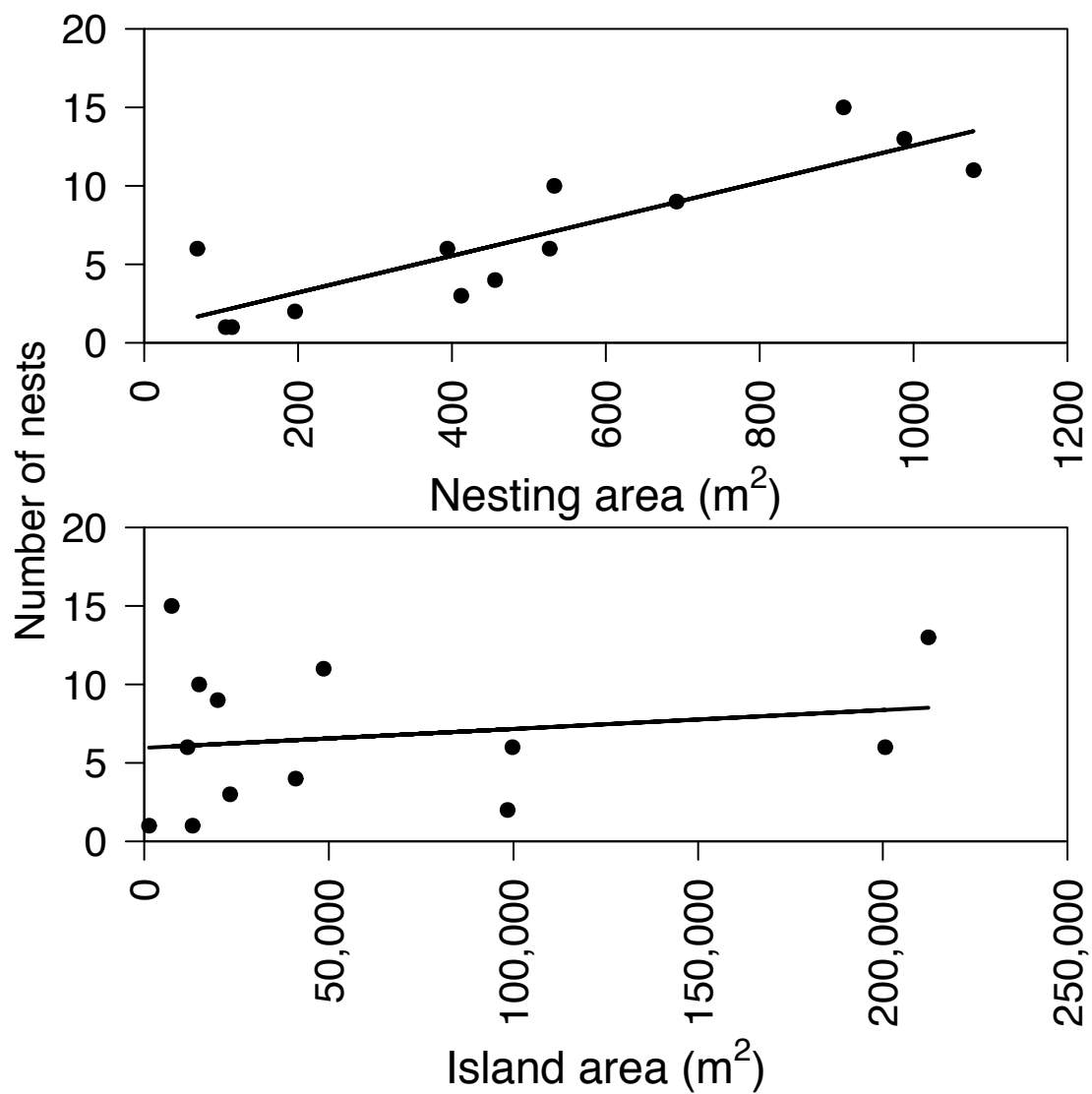


Figure 3.12. Relationship between potential area for nesting (nesting area) and total island area (island area) and number of *Apalone spinifera* nests laid in that location ($n = 13$).

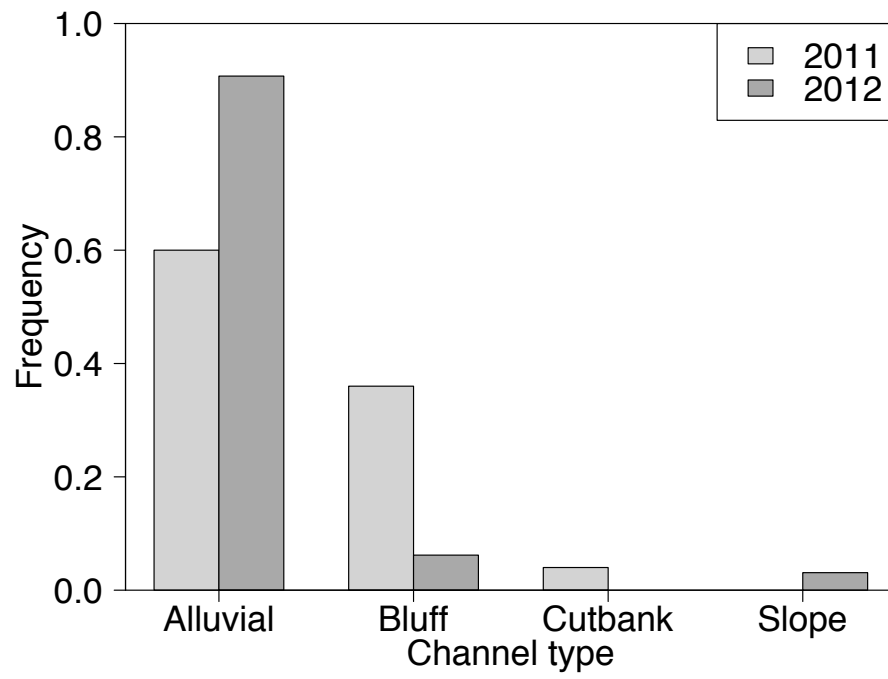


Figure 3.13. Channel types at *Apalone spinifera* nests in 2011 ($n = 25$; light grey) and 2012 ($n = 97$; dark grey).

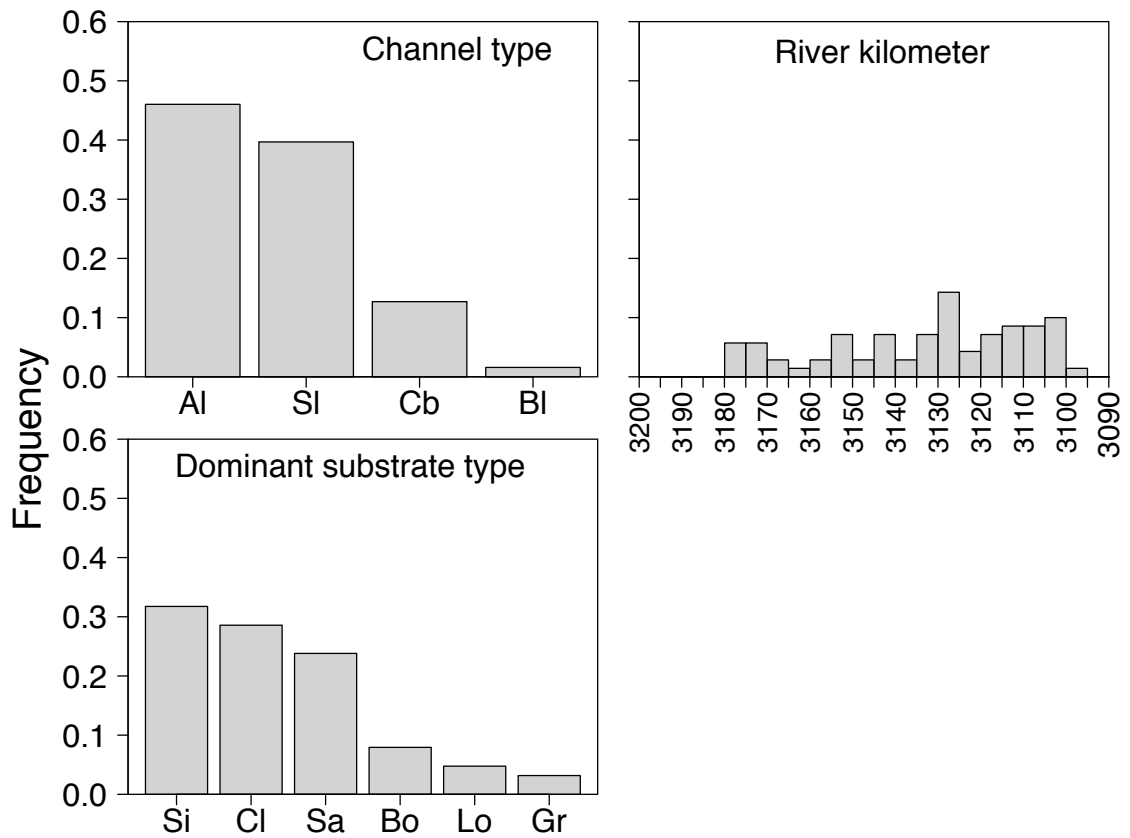


Figure 3.14. Channel types, longitudinal distribution, and dominant substrate types at *Apalone spinifera* basking sites ($n = 70$) from May through August 2010 and May and late June of 2011. For channel types: AI = alluvial, SI = slope, Cb = cut bank, and BI = bluff. For Substrate types Si = silt, Cl = clay, Sa = sand, Bo = boulder, Lo = log, and Gr = gravel. River kilometer is the distance from the confluence with the Mississippi River and basking sites are binned by 10 km reach.

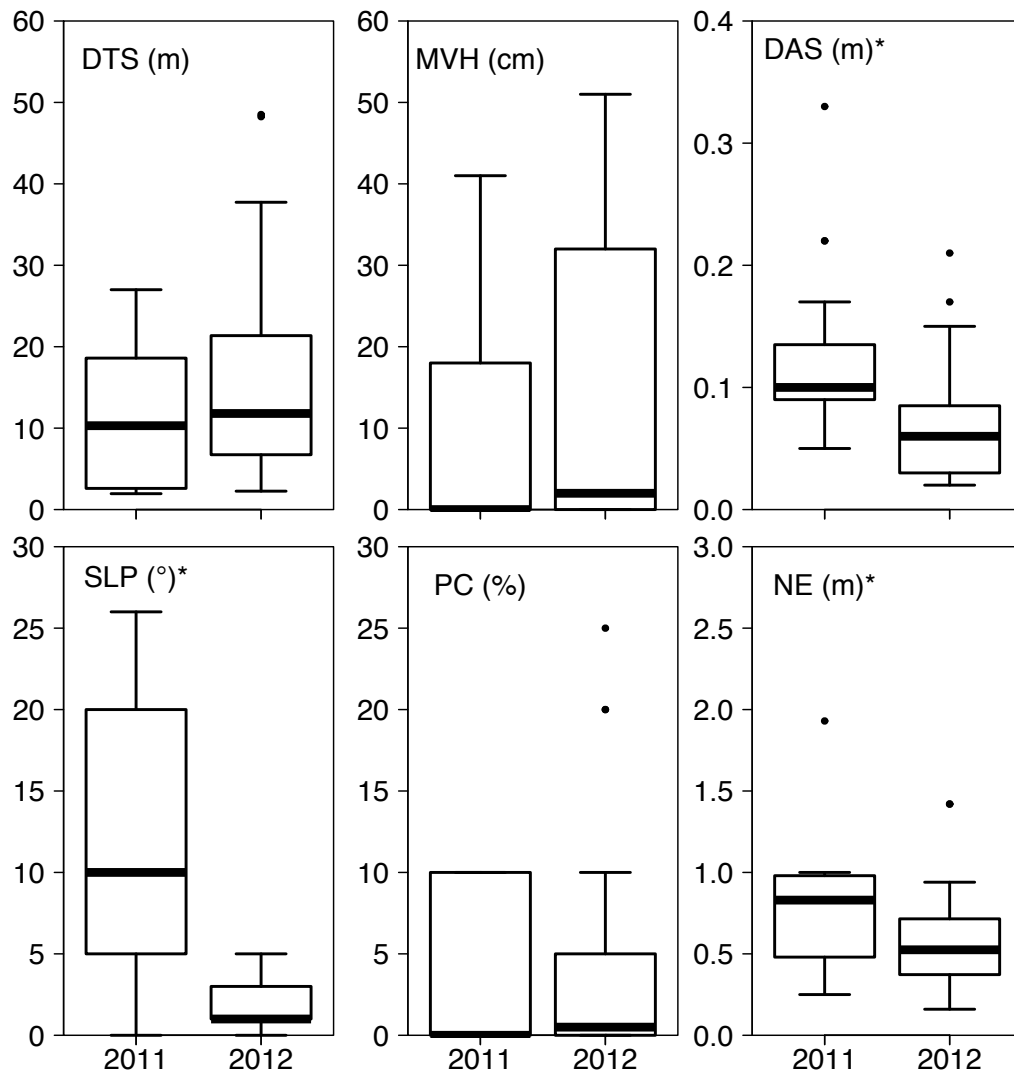


Figure 3.15. Microhabitat characteristics of *Apalone spinifera* nests in 2011 and 2012. DTS = distance to shore (m), MVH = maximum vegetation height (cm), DAS = depth at shore (m), SLP = slope (°), PC = percent vegetative cover (%), and NE = nest elevation (m). An asterisk (*) denotes a significant difference in a nesting microhabitat characteristic between years 2011 and 2012.

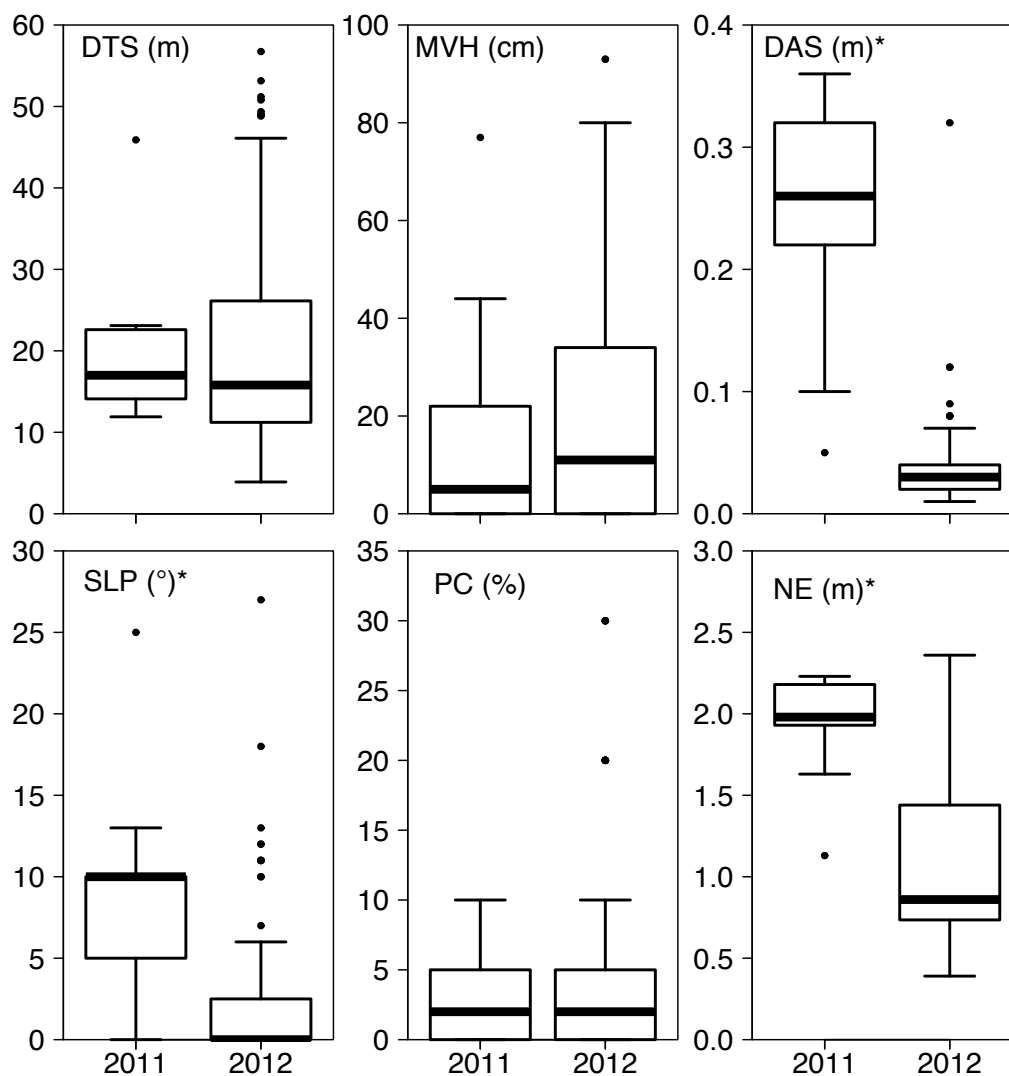


Figure 3.16. Microhabitat characteristics of *Apalone spinifera* nests during emergence in 2011 and 2012. DTS = distance to shore (m), MVH = maximum vegetation height (cm), DAS = depth at shore (m), SLP = slope (°), PC = percent vegetative cover (%), and NE = nest elevation (m). An asterisk (*) denotes a significant difference in an emergence microhabitat characteristic between years 2011 and 2012.

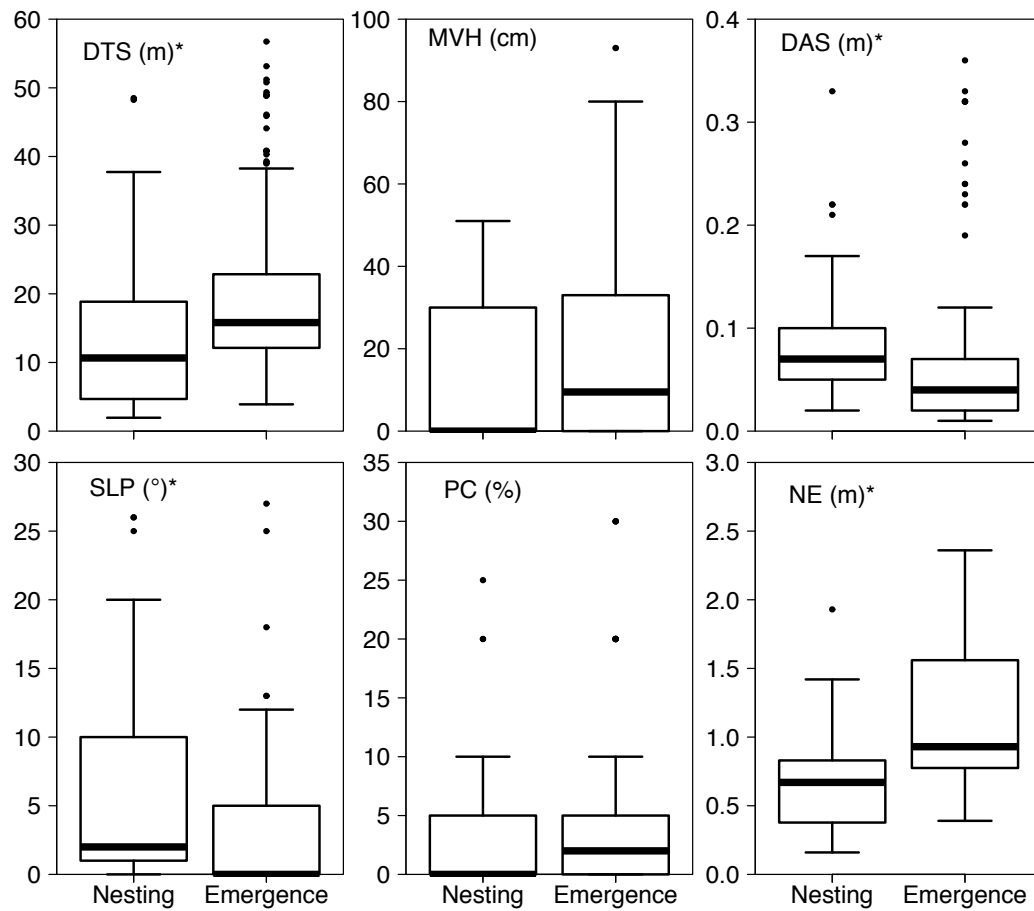


Figure 3.17. Microhabitat characteristics of *Apalone spinifera* nests during nesting and emergence. DTS = distance to shore (m), MVH = maximum vegetation height (cm), DAS = depth at shore (m), SLP = slope (°), PC = percent vegetative cover (%), and NE = nest elevation (m). An asterisk (*) denotes a significant difference in a microhabitat characteristic between nesting and emergence periods.

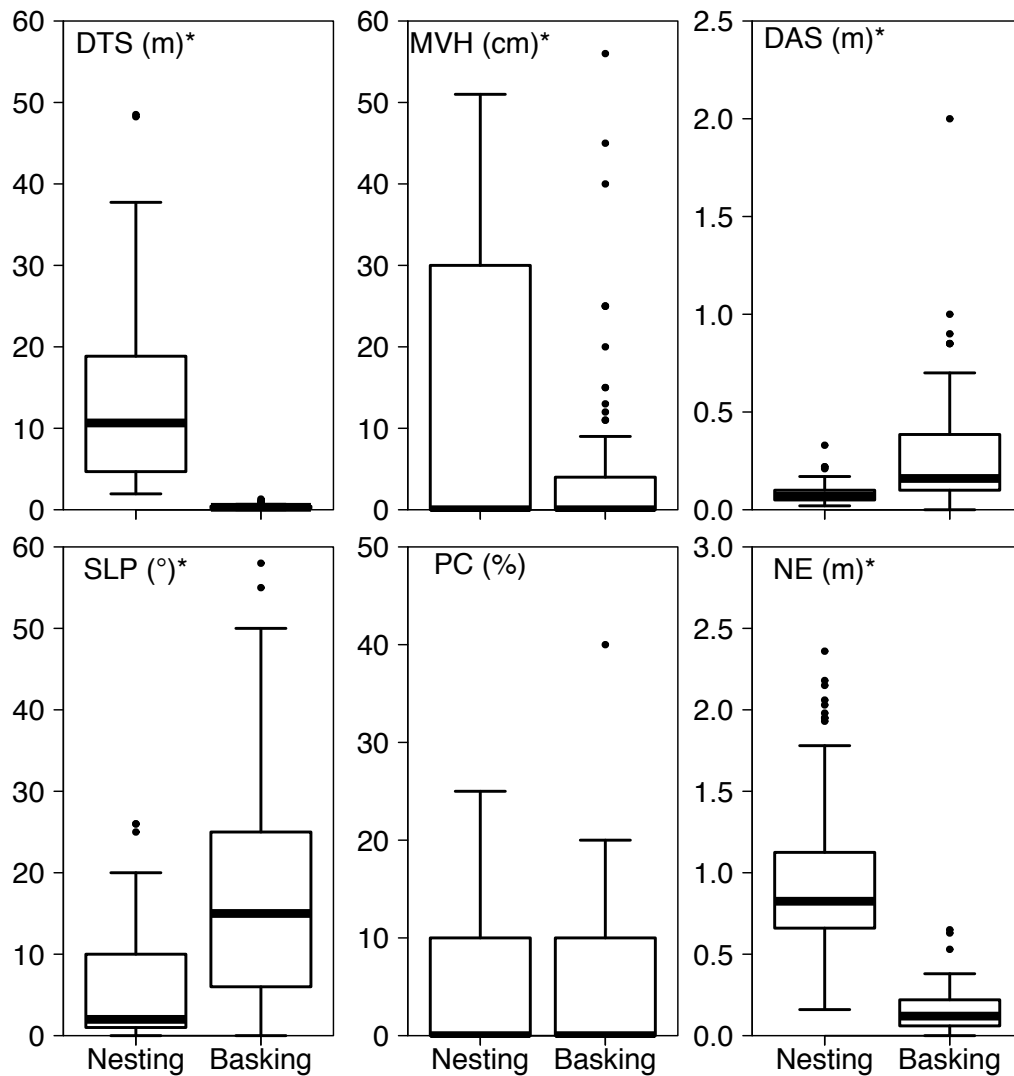


Figure 3.18. Microhabitat characteristics of *Apalone spinifera* nests and basking sites. DTS = distance to shore (m), MVH = maximum vegetation height (cm), DAS = depth at shore (m), SLP = slope (°), PC = percent vegetative cover (%), and NE = nest elevation (m). An asterisk (*) denotes a significant difference in a microhabitat characteristic between nesting and emergence periods.

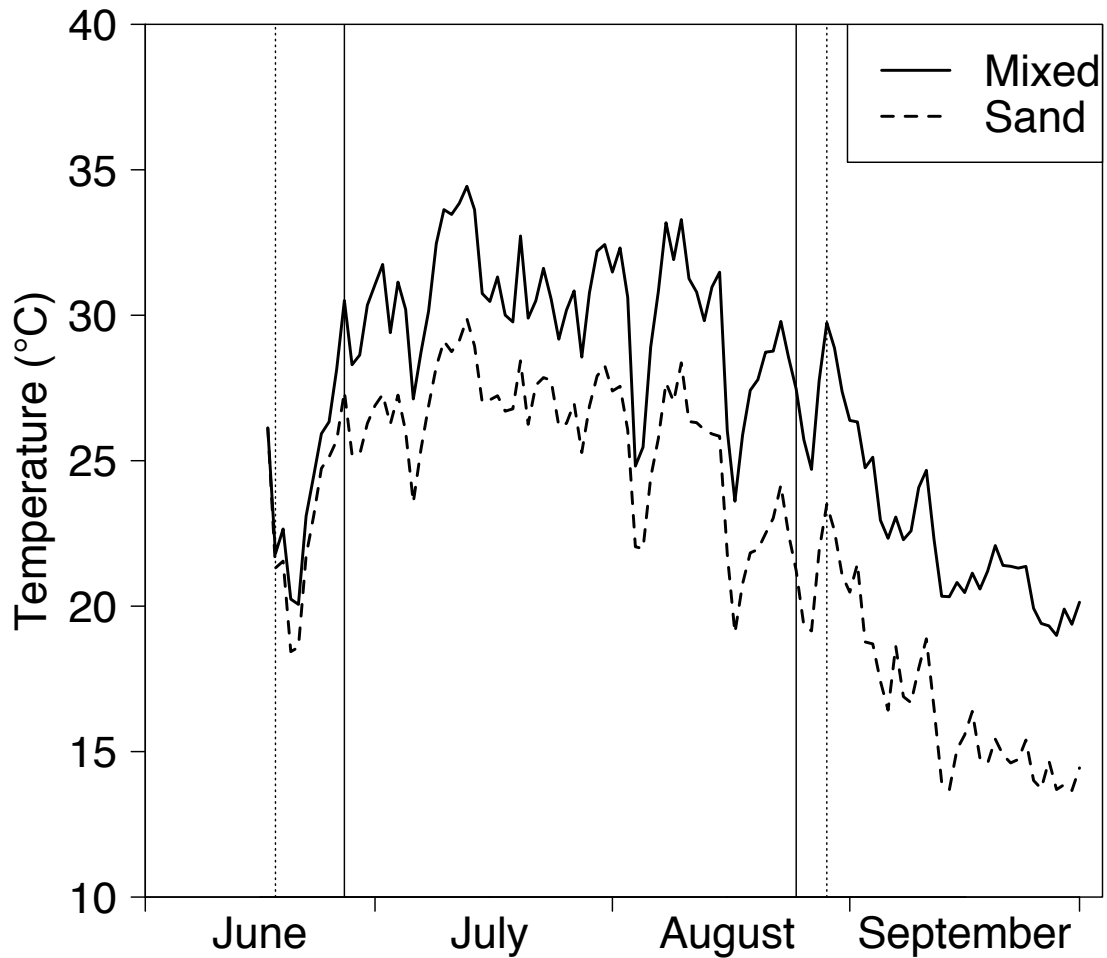


Figure 3.19. Mean daily substrate temperatures in simulated nests from 16 June through 30 September 2012 in mixed gravel with sand (mixed; solid line) and pure sand substrates (dashed line) at known nesting sites on the Missouri River in Montana. Vertical solid lines represent the average nesting (left) and emergence date (right) and vertical dotted lines represent the minimum nesting date (left) and maximum emergence date (right).

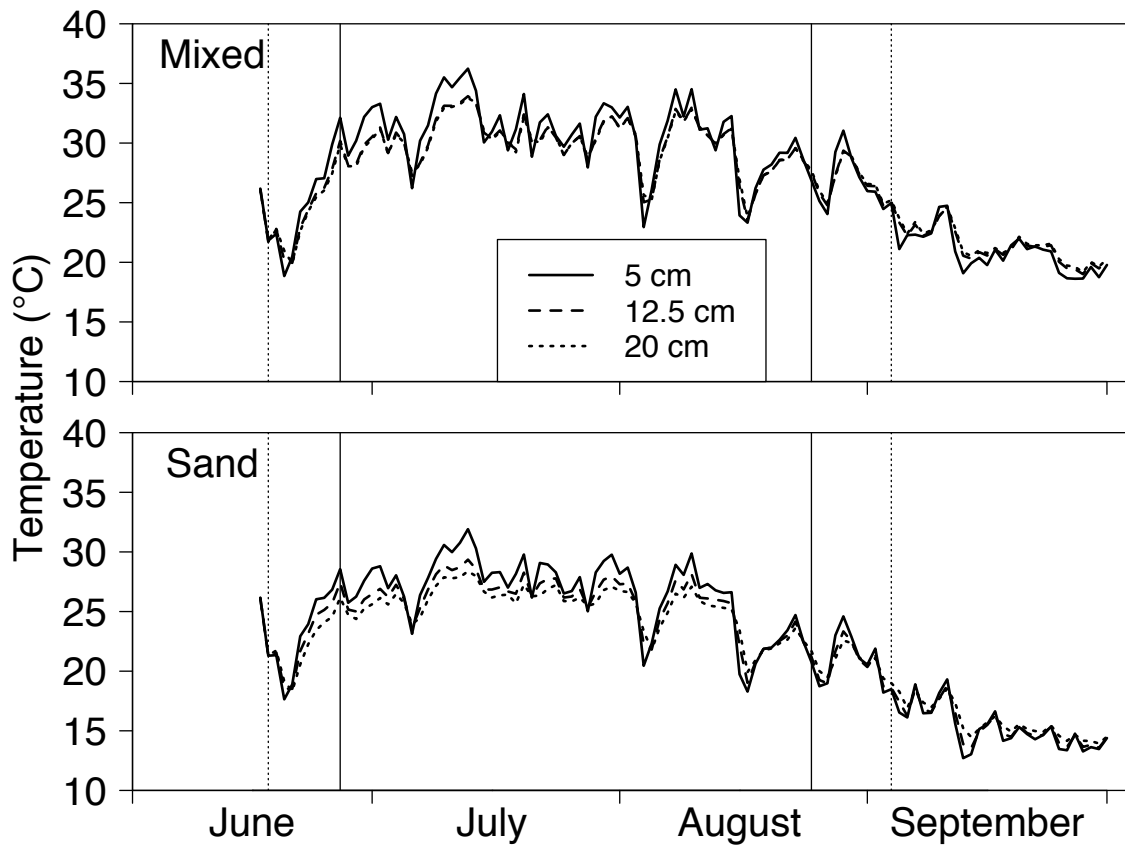


Figure 3.20.—Mean daily substrate temperatures in simulated nests from 16 June through 30 September 2012 in mixed gravel with sand (mixed; top) and pure sand (bottom) substrates by depth (solid = 5 cm, dashed = 12.5 cm, and dotted = 20 cm) at known nesting sites on the Missouri River in Montana. Vertical solid lines represent the average nesting (left) and emergence date (right) and vertical dotted lines represent the minimum nesting date (left) and maximum emergence date (right).

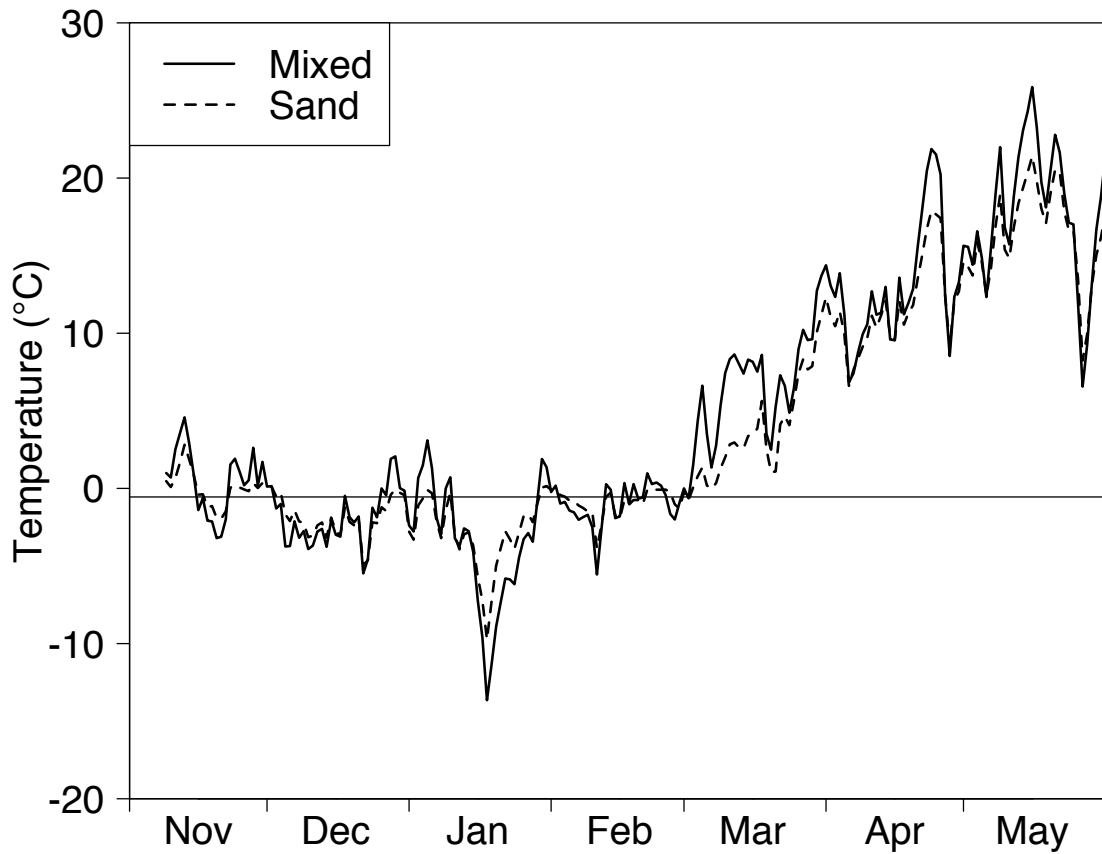


Figure 3.21. Mean daily overwintering substrate temperatures in simulated nests from 11 November through 30 May 2012 in mixed gravel with sand (mixed; solid line) and sand substrates (dashed line) at known nesting sites on the Missouri River in Montana. The horizontal solid line represents the upper limit of potential freezing episodes (-0.55°C), the estimated point at which turtle tissues reach equilibrium freezing point.

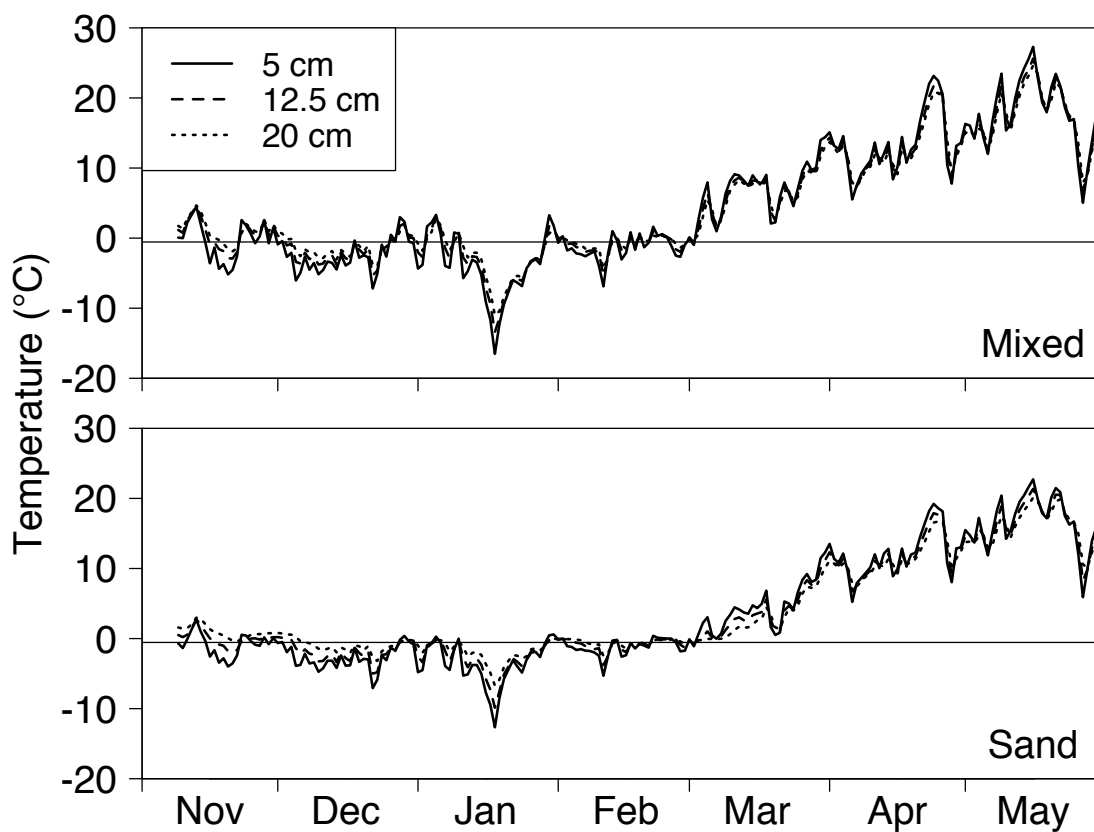


Figure 3.22. Mean daily overwintering substrate temperatures in simulated nests from 11 November through 30 May 2012 in mixed gravel with sand (mixed; top) and pure sand substrates (bottom) by depth (solid = 5 cm, dashed = 12.5 cm, and dotted = 20 cm) at known nesting sites on the Missouri River in Montana. The horizontal solid line represents the upper limit of potential freezing episodes (-0.55°C), the estimated point at which turtle tissues reach equilibrium freezing point.

Literature Cited

- Anderson, P.K. 1958. The photic responses and water approach behavior of hatchling turtles. *Copeia* 1958:221–215.
- Barko, V.A., and J.T. Briggler. 2006. Midland smooth softshell (*Apalone mutica*) and spiny softshell (*Apalone spinifera*) turtles in the middle Mississippi River: habitat associations, population structure, and implications for conservation. *Chelonian Conservation Biology* 5:225–231.
- Boby, M.L., and R.J. Brooks. 1994. Incubation conditions as potential factors limiting the northern distribution of snapping turtles, *Chelydra serpentina*. *Canadian Journal of Zoology* 72:28–37.
- Bolton, R.M. 2007. Effects of anthropogenic disturbance, nest-site selection, and dipteran infestation on spiny softshells (*Apalone spinifera*). M.S. Thesis, The University of Guelph, Ontario, Canada.
- Bowen, Z.H., K.D. Bovee, and T.J. Waddle. 2003. Effects of flow regulation on shallow-water habitat dynamics and floodplain connectivity. *Transactions of the American Fisheries Society* 132:809–823.
- Bull, J.J., and R.C. Vogt. 1979. Temperature-dependent sex determination in turtles. *Science* 206:1186–1188.
- Bunn, S.E., and A.H. Arthington. 2002. Basic principles and ecological consequences of altered flow regimes for aquatic biodiversity. *Environmental Management* 30:492–507.
- Burger, J. 1976. Determinants of hatching success in diamondback terrapin, *Malaclemys terrapin*. *American Midland Naturalist* 97:444–464.
- Burke, V.J., J.E. Lovitch, and J.W. Gibbons. 2000. Conservation of freshwater turtles. Pp. 156–179 in M. W. Klemens (Eds.), *Turtle Conservation*. Smithsonian Institution Press, Washington, D.C., USA.
- Bustard, H.R. 1967. Mechanism of nocturnal emergence from the nest in Green Turtle hatchlings. *Nature (London)* 214:317.
- Butler, B.O., and T.E. Graham. 1995. Early post-emergent behavior and habitat selection in hatchling Blanding's turtles, *Emydoidea blandingii*, in Massachusetts. *Chelonian Conservation Biology* 1:187–196.

- Churchill, T.A., and K.B. Storey. 1992a. Natural freezing survival by painted turtles *Chrysemys marginata* and *C. picta belli*. *Survival* 80:4.
- Churchill, T.A., and K.B. Storey. 1992b. Responses to freezing exposure of hatchling turtles *Trachemys scripta elegans*: factors influencing the development of freeze tolerance by reptiles. *Journal of Experimental Biology* 167:221–233.
- Congdon, J.D., and J.W. Gibbons. 1990. Turtle eggs: their ecology and evolution. Pp. 109–123 in J.W. Gibbons (Ed.), *Life history and ecology of the slider turtle*. Smithsonian Institution Press, Washington, D.C., USA.
- Costanzo, J.P., J.B. Iverson, M.F. Wright, and R.E. Lee Jr. 1995. Cold hardiness and overwintering strategies of hatchlings in an assemblage of northern turtles. *Ecology* 76:1772–1785.
- Dood, A.R., B. Schmitz, V. Riggs, N. McClenning, M. Jaeger, D. Fuller, R. Rauscher, S. Leathe, D. Moore, J. Dullum, J. Ensign, S. Story, and M. Backes. 2009. Relative abundance of spiny softshell turtles (*Apalone spinifera*) on the Missouri and Yellowstone rivers in Montana, Final Report. Montana Fish, Wildlife & Parks, Montana, USA.
- Doody, J.S. 1995. A comparative study of two syntopic species of softshell turtles (*Apalone mutica* and *Apalone spinifera*) in southcentral Louisiana. M.S. Thesis, Southeastern Louisiana University, Hammond, USA.
- Doody, J.S. 1999. A test of the comparative influences of constant and fluctuating incubation temperatures on phenotypes of hatchling turtles. *Linnaeus Fund Research Report. Chelonian Conservation Biology* 3:529–531.
- Doody, J.S., A. Georges, J.E. Young, M.D. Pauza, A.L. Pepper, R.L. Alderman, and M.A. Welsh. 2001. Embryonic aestivation and emergence behavior in the Pig-nosed turtle, *Carettochelys insculpta*. *Canadian Journal of Zoology* 79:1062–1072.
- Ernst, C.H., and J.E. Lovich. 2009. *Turtles of the United States and Canada*. The Johns Hopkins University Press, Maryland, USA.
- Ewert, M.A. 1979. The embryo and its egg: development and natural history. Pp. 33–416 in M. Harless and H. Morlock (Eds.), *Turtles: Perspectives and Research*. John Wiley and Son, New York, USA.
- Funk, J.L., and J.W. Robinson. 1974. Changes in the channel of the lower Missouri River and effects on fish and wildlife. Missouri Department of Conservation, Aquatic Series 11, Missouri, USA.

- Galat, D.L., C.R. Berry, W.M. Gardner, J.C. Hendrickson, G.E. Mestl, G.J. Power, C. Stone, and M.R. Winston. 2005. Spatiotemporal patterns and changes in Missouri River fishes. *American Fisheries Society Symposium* 45:249–291.
- Galois, P., M. Léveillé, L. Bouthillier, C. Daigle, and S. Parren. 2002. Movement patterns, activity, and home range of the eastern spiny softshell turtle (*Apalone spinifera*) in northern Lake Champlain, Québec, Vermont. *Journal of Herpetology* 36:402–411.
- Garber, S.D., and J. Burger. 1995. A 20-yr study documenting the relationship between turtle decline and human recreation. *Ecological Applications* 5:1151–1162.
- Gardner, W.M., and C.B. Jensen. 2011. Upper Missouri River basin pallid sturgeon study 2005–2010 final report. United States Bureau of Reclamation, Montana Department of Fish, Wildlife & Parks, Helena, Montana.
- Georges, A. and M. Rose. 1992. Conservation biology of the Pignose Turtle, *Carretochelys insculpta*. *Chelonian Conservation and Biology* 1:3–12.
- Graham, T.E., and A.A. Graham. 1991. *Trionyx spiniferus spiniferus* (Eastern Spiny Softshell). Burying behavior. *Herpetological Review* 22:56–57.
- Graham, T.E., and A.A. Graham. 1997. Ecology of the eastern spiny softshell, *Apalone spinifera spinifera*, in the Lamoille River, Vermont. *Chelonian Conservation and Biology* 2:363–369.
- Greenberg, S. and T. Godin. 2012. Timelapse Image Analysis Manual. Technical Report 2012-1028-11. Department of Computer Science, University of Calgary, Canada. <http://grouplab.cpsc.ucalgary.ca/cookbook/index.php/Demos/TimelapseCoder>
- Gyuris, E. 1993. Factors that control the emergence of Green Turtle hatchlings from the nest. *Wildlife Research* 20:345–353.
- Hesse, L.W., J.C. Schmulbach, J.M. Carr, K.D. Keenlyne, D.G. Unkenholz, J.W. Robinson, and G.E. Mestl. 1989. Missouri River fishery resources in relation to past, present, and future stresses. Pp. 352–371 In D. P. Dodge (Ed.), *Proceedings of the International Large River Symposium*. Canadian Special Publication of Fisheries Aquatic Science 106.
- Holman, J.A. and K.D. Andrews. 1994. North American Quaternary cold-tolerant turtles: distributional adaptations and constraints. *Boreas* 23:44–52.
- Hupp, C.R., and W.R. Osterkamp. 1985. Bottomland vegetation distribution along Passage Creek, Virginia in relation to fluvial landforms. *Ecology* 66:670–681.

- Hutchison, V.H., A. Vinegar, and R.J. Kosh. 1966. Critical thermal maxima in turtles. *Herpetologica* 1:32-41.
- Janzen, F.J. 1993. An experimental analysis of natural selection on body size of hatchling turtles. *Ecology* 74:332-341.
- Janzen, F.J. 1994. Vegetational cover predicts the sex ratio of hatchling turtles in natural nests. *Ecology* 75:1593-1599.
- Janzen, F.J., J.K. Tucker, and G.L. Paukstis. 2002. Experimental analysis of an early life-history stage: avian predation selects for larger body size of hatchling turtles. *Journal of Evolutionary Biology* 13:947-954.
- Junk, W.J., P.B. Bayley, and R.E. Sparks. 1989. The flood pulse concept in river-floodplain systems. Canadian Special Publication of fisheries and Aquatic Sciences 106-110-127.
- Kolbe, J.J., and F.J. Janzen. 2002. Impact of nest-site selection on nest success and nest temperature in natural and disturbed habitats. *Ecology* 83:269-281.
- Kuchling, G. 1999. The reproductive biology of chelonian-zoophysiology. Springer-Verlag, New York, USA.
- Larsen, K.W., and P.T. Gregory. 1989. Population size and survivorship of the common garter snake, *Thamnophis sirtalis*, near the northern limit of its distribution. *Holarctic Ecology* 12:81-86.
- Leopold, L.B., M.G. Wolman, and J.P. Miller. 1964. Fluvial processes in geomorphology. Dover Publications, Inc., New York, USA.
- Lindeman, P.V. 2001. A contrast in the basking habits of the sympatric trionychid turtles *Apalone mutica* and *A. spinifera*. *Herpetological Natural History* 8:87-89.
- Lytle, D.A., and N.L. Poff. 2004. Adaptation to natural flow regimes. *Trends in Ecology and Evolution* 19:94-100.
- Miller, K., G.C. Packard, and M.J. Packard. 1987. Hydric conditions during incubation influence locomotor performance of hatchling snapping turtles. *Journal of Experimental Biology* 127:401-412.
- Minton, S.A., Jr. 1972. Amphibians and Reptiles of Indiana. Indiana Academy of Scientific Monographs 3:1-346.
- Moll, D., and E.O. Moll. 2004. The ecology, exploitation, and conservation of river turtles. Oxford University Press, New York, USA.

- Moran, K.L., K.A. Bjorndal, and A.B. Bolton. 1999. Effects of the thermal environment on the temporal pattern of emergence of hatchling Loggerhead Turtles *Caretta caretta*. Marine Ecology Progress Series 189:251–261.
- Mrosovsky, N. 1968. Nocturnal emergence of hatchling sea turtles: control by thermal inhibition of activity. Nature (London) 220:531–547.
- Packard, G.C., and M.J. Packard. 1988. The physiological ecology of reptilian eggs and embryos. Pp. 523–603, in C. Gans and R.B. Huey, Biology of the Reptilia. Vol. 16. Alan R. Liss, Inc., New York, USA.
- Packard, G.C., M.J. Packard, K. Miller, and T.J. Boardman. 1987. Influence of moisture, temperature, and substrate on snapping turtle eggs and embryos. Ecology 68:983–993.
- Parmley, D. 1992. Turtles from the late Hemphillian (latest Miocene) of Knox County, Nebraska. Texas Journal of Science 44:339–348.
- Pegg, M. A., C. L. Pierce, and A. Roy. 2003. Hydrological alteration along the Missouri River basin: a time series approach. Aquatic Sciences 65:63–72.
- Plummer, M.V. 1976. Some aspects of nesting success in the turtle, *Trionyx muticus*. Herpetologica 32:353–359.
- Plummer, M.V. 2007. Nest emergence of smooth softshell turtle (*Apalone mutica*) hatchlings. Herpetological Conservation and Biology 2:61–64.
- Plummer, M.V., and J.S. Doody. 2010. Terrestrial burrowing in nesting softshell turtles (*Apalone mutica* and *A. spinifera*). International Reptile Conservation Foundation Journal Reptiles and Amphibians 17:79–81.
- Plummer, M.V., T.N. Lee, and N.E. Mills. 2008. Effect of a sand substrate on the growth and condition of *Apalone mutica* hatchlings. Journal of Herpetology 42:550–554.
- Plummer, M.V., N.E. Mills, and S.L. Allen. 1997. Activity, habitat, and movement patterns of softshell turtles (*Trionyx spiniferus*) in a small stream. Chelonian Conservation Biology 2:514–520.
- Pritchard, P.C.H., and P. Trebbau. 1984. The Turtles of Venezuela. Society for the Study of Amphibians and Reptiles, New York, USA.
- R Core Team. 2013. R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. <http://www.R-project.org/>.

- Ramey, M.P., S.M. Beck, and D.W. Reiser. 1993. Determination of flushing flow needs – Madison and upper Missouri rivers. Supplemental Report. Prepared by R2 Resource Consultants for Montana Power Company. Butte, Montana.
- Resetarits, W.J., Jr. 1996. Oviposition site choice and life history evolution. *American Zoologist* 36:205–215.
- Richards, R.R. 2012. Spawning related migration *Scaphirhynchus* species in the Missouri River above Fort Peck reservoir, Montana. M.Sc. Thesis, Montana State University, Bozeman, USA.
- Sanford, J.P. 2007. Dam regulation effects on sand bar migration on the Missouri River: Southeastern South Dakota. M.A. Thesis, The University of Montana, Missoula, USA.
- Scott, M.L., G.T. Auble, and J.M. Friedman. 1997. Flood dependency of cottonwood establishment along the Missouri River, Montana, USA. *Ecological Applications* 7:677–690.
- Smith, E.N., S.L. Robertson, and S.R. Adams. 1981. Thermoregulation of the spiny soft-shelled turtle *Trionyx spinifer*. *Physiological Zoology*, 74-80.
- Thompson, M.B. 1988. Nest temperatures in the pleurodiran turtle, *Emydura macquarii*. *Copeia* 1988:996–1000.
- Tinkle, D.W., J.D. Congdon, and P.C. Rosen. Nesting frequency and success: implications for the demography of painted turtles. *Ecology* 62:1426–1432.
- USHR (United States House of Representatives). 1976. Designation of Missouri River segment as a Wild and Scenic River. USHR, Subcommittee on National Parks and Recreation Report, Washington, D.C., USA.
- Valenzuela, N. 2001. Maternal effects on life-history traits in the Amazonian giant river turtle *Podocnemis expansa*. *Journal of Herpetology* 35:368–378.
- Vogt, R.C. 1980. Natural history of the map turtles *Graptemys pseudogeographica* and *G. ouachitensis* in Wisconsin. *Tulane Studies in Zoology and Botany* 22:17–48.
- Vogt, R.C. 1997. Freshwater turtle nesting and reproduction in the neotropics. Abstract, p. 301. ASIH/HL/SSAR/AFS-ELHS/AES/GIS Joint Meetings, Washington, USA.
- Vuke, S.M., K.W. Porter, J.D. Lonn, and D.A. Lopez. 2007. Geologic map of Montana. Montana Bureau of Mines and Geology. Geologic Map 62B, 1:500,000.

- Ward, J.V. 1989. The four-dimensional nature of lotic ecosystems. *Journal of the North American Benthological Society* 8:2–8.
- Ward, J.V., and J.A. Stanford. 1983. The serial discontinuity concept of lotic ecosystems. Pp. 29-42 in T.D. Fontaine and S.M. Bartell, *Dynamics of lotic ecosystems*. Ann Arbor Science Publishers, Inc., Michigan, USA.
- Webb, R.G. 1962. North American recent soft-shelled turtles (family Trionychidae). *University of Kansas Publications Museum of Natural History* 13:429–611.
- Webb, R.G. 1973. *Trionyx spiniferus*. *Catalog of American Amphibians and Reptiles* 140:1–4.
- Weisrock, D.W., and F.J. Janzen. 1999. Thermal and fitness-related consequences of nest location in painted turtles (*Chrysemys picta*). *Functional Ecology* 13:94–101.
- Werner, J.K., B.A. Maxell, P. Hendricks, and D.L. Flath. 2004. *Amphibians and reptiles of Montana*. Mountain Press, Montana, USA.
- Wilson, D.S. 1998. Nest-site selection: microhabitat variation and its effects on the survival of turtle embryos. *Ecology* 79:1884–1892.
- Witherington, B.E. 1995. Hatchling orientation. Pp. 577–578 in K.A. Bjorndal, *Biology and Conservation of Sea Turtles*. Smithsonian Institution Press, Washington, D.C., USA.
- Wood, D.W., and K.A. Bjorndal. 2000. Relation of temperature, moisture, salinity and slope to nest site selection in loggerhead sea turtles. *Copeia* 2000:119–128.
- Zuur, A.F., E.N. Ieno, N.J. Walker, A.A. Saveliev, and G.M. Smith. 2009. *Mixed Effects Models and Extensions in Ecology with R*. Springer Science+Business Media, LLC, New York, USA.

CHAPTER FOUR

CONCLUSIONS AND IMPLICATIONS FOR
MANAGEMENT AND CONSERVATIONConclusions

Our objectives were to describe movement, habitats, and nesting ecology of spiny softshell turtles (herein, SSTs or turtles) in relation to natural and anthropogenic factors. In Chapter Two we described and compared movements and habitat selection of turtles between two years and among four seasons with varied streamflow and thermal profiles. Biological function and environmental conditions (e.g., streamflow and temperature) influenced spatiotemporal movement and habitats of SSTs in a large river-floodplain ecosystem. The fundamental periods in the annual cycle of SSTs in this ecosystem were runoff, nesting, post-nesting, and hibernation periods and SST behavior differed among these periods. Moreover, fluctuations in streamflow and temperature probably initiated important life events (e.g., nesting) and movement to seasonal habitats.

Turtles inhabited, aggregated, and showed fidelity to lateral habitats during spring, braided and mainstem reaches in the summer, and outside bends of mainstem reaches in the winter. Lateral habitats, braided mainstem, and mainstem reaches occupied in the spring and summer were typically near-shore with shallow depth, slow to no water velocity, had fine substrates, and higher water temperature than the mainstem. Turtles probably occupy these habitats in the spring and summer to avoid peak flows and the chance of being displaced, to seek areas with warmer temperatures to increase

metabolism, or to locate habitats with increased productivity and food availability (Moll and Legler, 1971; Brinson et al., 1981; MacCulloch and Secoy, 1983; Galat et al., 1998). Hibernacula were usually in outside bends of main channel reaches without islands, between shore and river thalweg, with moderate depth and water velocity. Greater depths at hibernacula probably allow SST to avoid freezing and deep-ice scour (Scrimgeour et al., 1994; Ultsch, 2006) and moderate velocity may provide ample dissolved oxygen without displacing torpid SSTs (Reese et al., 2003; Ultsch, 2006). Moreover, ice dynamics may have influenced the winter distribution of SSTs because ice formation, breakup, and scour differed at camera-monitored hibernacula and control sites.

In Chapter Three, we described the nesting ecology of SSTs between two years with disparate discharge profiles, one of which incurred a major flood event. We observed that annual nest success was influenced by the timing and magnitude of flood pulses and the truncated active season in this river-floodplain ecosystem at the extreme northern portion of the range of the species. Recreation may have influenced nesting behavior, nest sites had specific habitat characteristics that were probably influenced by streamflow and are related to nest success and fitness (Bull and Vogt, 1979; Janzen, 1993; Wilson, 1998), substrate choice may have also influenced nest success, and emergence was dependent on timing of nesting and temperature profiles.

Flood pulses play a fundamental role in shaping river-floodplain ecosystems (Leopold et al., 1964; Hupp and Osterkamp, 1985; Ward, 1989; Junk et al., 1989) and expose bare substrates essential for SST reproduction (Kuchling, 1999; Moll and Moll, 2004). Although the large and late flood pulse of 2011 may have reduced SST nest success in that year, it also deposited nesting substrate, created new alluvial bars,

reshaped islands, and scoured substantial areas of riparian vegetation; many of these areas were subsequently used for SST nesting in 2012. Riverine ice dynamics also scours riparian vegetation (Scott et al., 1997) and creates new nesting habitats as was observed subsequent to the winter of 2010. Variable streamflows, flood pulses, riparian scour, and sediment deposition provide disturbance mechanisms that create and maintain nesting habitats for SSTs.

Our study site location, at the northwestern extent of the range of the species, coupled with the high and late runoff in 2011 probably resulted in delayed nesting and the termination of incubation by freezing temperatures in nest chambers. Although it has been suggested that hatchling SSTs may overwinter inside the nest (Minton, 1972), the low tolerance of the species to freezing temperatures (Costanzo et al., 1995) and the frequent and extended freezing episodes we measured at all simulated nest depths probably prevents this. Moreover, we discovered eggs eroding out of a bank on a nesting island in November 2010, subsequent to below-freezing air temperatures. We excavated, collected, and incubated three SST eggs from a nearby nest, but none survived to hatch. Therefore, the snowmelt-driven hydrology coupled with the onset of freezing temperatures in autumn may create a “runoff-winter squeeze” that limits the northwestern range of this species.

Spiny softshell turtles in a large river-floodplain ecosystem at the northern extent of their range experienced high and variable streamflow, indeterminate timing of habitat availability, often cold and prolonged winters, and sometimes powerful ice dynamics. Limited and spatiotemporally separated fundamental habitats may have necessitated movement, aggregation, and fidelity of SSTs to locate habitats that provided specific

resources in order to complete life history processes similar to other riverine turtles (Gibbons et al., 1990; Graham and Graham, 1997; Bodie, 2001; Galois et al., 2002; Moll and Moll 2004).

Implications for Management and Conservation

Populations of SSTs in the Missouri River in Montana could be especially sensitive to various forms of disturbance because they are disjunct from downstream populations by Fort Peck Dam, are at the extreme northern extent of their range, have a truncated active period, and make spatiotemporal and nesting-related movements to disparate habitats. Changes to the already quasi-natural flow regime, habitat alteration, or increasing human activities could affect SST populations by creating asynchrony between environmental cues and movement, reducing or eliminating critical habitat, reducing population size, or a combination thereof.

Spiny softshell turtles have inhabited large rivers for thousands of years (Parmley, 1992; Holman and Andrews, 1994) and their life-history strategy is probably dependent on local environmental conditions and natural flow regimes (Bunn and Arthington, 2002; Wildhaber et al., 2011). Changes to peak streamflow timing, duration, and magnitude could influence SST movement, habitat selection, nest-site choice, and survival by altering seasonal temperatures, reducing habitat heterogeneity, or changing the locations of ice jams and scour. Dams or channelization or both could also decrease habitat heterogeneity and alter or eliminate shallow-water habitat used by SSTs in the summer for feeding and reproduction, braided reaches for nesting, and deep-water hibernacula used for overwintering (Plummer et al., 1997; Barko and Briggler, 2006). The installation

of new dams could also influence SST populations by further dividing the Missouri River population and increasing the chances of a genetic bottleneck. Moreover, if extirpation occurs, downstream dams and reservoirs could obstruct recolonization by nearby populations.

Recreation is one of the most common land uses within the study site and the presence of humans in relatively pristine habitat can be as detrimental to turtles as habitat degradation (Garber and Burger, 1995). The persistence of a population could be imperiled in only a few years because of the annual loss of reproductively active females in addition to natural mortality (Congdon et al., 1993, 1994; Garber and Burger, 1995). Disjunct populations such as this one are especially vulnerable to extirpation because of limited possibilities for recolonization. Recreation within the study site is largely limited to non-motorized traffic during the nesting period, but all motorized traffic is allowed during spring and summer. Basking and nesting are important life history characteristics for SST thermoregulation, incubation, and reproduction and could be influenced by river recreation because of the wary nature of this species while on land (Bolton, 2007). Increased traffic near heavily used basking and nesting habitats could cause SSTs to abandon basking and nesting. This could decrease opportunities for behavioral thermoregulation, which may be important for egg development, or influence SSTs to move further distances to find secluded habitats, which is energetically costly. These disturbances eventually led to limitations on recreation near critical nesting sites in Lake Erie because female SSTs would not return to cover abandoned nests and these nests failed to hatch (Bolton, 2007). Traumatic injuries caused by recreational activities, such as boating or fishing, have also been documented (Gibbons et al., 2001; Moll and Moll,

2004; Galois and Ouellet, 2007) and SSTs are exceptionally susceptible to propeller injury because of their affinity for shallow water (e.g., water depth < 1.5 m; Galois and Ouellet, 2007). No boat-induced injuries were documented, but anglers frequently hooked SSTs in the study area and SSTs would usually be cut free with hook-in-mouth or, less commonly, killed .

We suggest two forms of management to reduce negative influences on SST populations and two areas for future research to increase our understanding of their ecology in the Missouri River in Montana. First, maintaining near-natural streamflow with a single peak would preserve possible movement cues, enhance habitat heterogeneity, reduce the possibility of nest inundation by late flows, and maintain diverse habitats fundamental for SST feeding, mating, nesting, and overwintering. Second, public outreach and signage and potential restrictions on recreational activity near, and foot traffic on, nesting sites could reduce possible negative influences such as nest abandonment, decreased nest success and recruitment, or propeller injury. Additionally, signs at popular angling locations could be used to suggest that anglers free SSTs that are inadvertently hooked.

The estimation of population abundance and population viability analyses may be an important next step in understanding SST ecology on the Missouri River in Montana because population abundance and structure are largely unknown there. Moreover, genetic analyses should be completed to determine if Missouri River populations are experiencing a genetic bottleneck that could influence the survival of these disjunct SST populations. Sparse data exists for river-floodplain ecosystem managers to base management decisions on nongame wildlife, such as turtles (Galat et al., 1998). The

continued survival of SSTs in the Missouri River in Montana is largely dependent on furthering our understanding of the ecology of the species there. This will aid in protecting populations and critical habitats and managing anthropogenic influences.

Literature Cited

- Barko, V. A., and J. T. Briggler. 2006. Midland smooth softshell (*Apalone mutica*) and spiny softshell (*Apalone spinifera*) turtles in the middle Mississippi River: habitat associations, population structure, and implications for conservation. *Chelonian Conservation and Biology* 5:225–231.
- Bodie, J. R. 2001. Stream and riparian management for freshwater turtles. *Journal of Environmental Management* 62:443–455.
- Bolton, R. M. 2007. Effects of anthropogenic disturbance, nest-site selection, and dipteran infestation on spiny softshells (*Apalone spinifera*). M.S. Thesis, The University of Guelph, Ontario, Canada.
- Bull, J. J., and R. C. Vogt. 1979. Temperature-dependent sex determination in turtles. *Science* 206:1186–1188.
- Bunn, S. E., and A. H. Arthington. 2002. Basic principles and ecological consequences of altered flow regimes for aquatic biodiversity. *Environmental Management* 30:492–507.
- Congdon, J. D., A. E. Dunham, and R. C. Van Loben Sels. 1993. Delayed sexual maturity and demographics of Blanding's turtles (*Emydoidea blandingii*): implications for conservation and management of long-lived organisms. *Conservation Biology* 7:826–833.
- Congdon, J. D., A. E. Dunham, and R. C. Van Loben Sels. 1994. Demographics of common snapping turtles (*Chelydra serpentina*): implications for conservation and management of long-lived organisms. *Integrative and Comparative Biology* 34:397.
- Costanzo, J. P., J. B. Iverson, M. F. Wright, and R. E. Lee Jr. 1995. Cold hardiness and overwintering strategies of hatchlings in an assemblage of northern turtles. *Ecology* 76:1772–1785.
- Galat, D. L., L. H. Fredrickson, D. D. Humburg, K. J. Bataille, J. R. Bodie, J. Dohrenwend, J. R. Jones, M. E. Knowlton, J. Mazourek, A. C. McColpin, R. B. Renken, and R. D. Semlitsch. 1998. Flooding to restore connectivity of regulated, large-river wetlands. *BioScience* 48:721–733.
- Galois, P., and M. Ouellet. 2007. Traumatic injuries in eastern spiny softshell turtles (*Apalone spinifera*) due to recreational activities in the northern Lake Champlain basin. *Chelonian Conservation and Biology* 6:288–293.

- Galois, P., M. L  veill  , L. Bouthillier, C. Daigle, and S. Parren. 2002. Movement patterns, activity, and home range of the eastern spiny softshell turtle (*Apalone spinifera*) in northern Lake Champlain, Qu  bec, Vermont. *Journal of Herpetology* 36:402–411.
- Garber, S. D., and J. Burger. 1995. A 20-yr study documenting the relationship between turtle decline and human recreation. *Ecological Applications* 5:1151–1162.
- Gibbons, J. W., J. L. Greene, and J. D. Congdon. 1990. Temporal and spatial movement patterns of sliders and other turtles, pp. 201–215. *In* Life History and Ecology of the Slider Turtle. J. W. Gibbons (Ed.). Smithsonian Institution Press, Washington D.C.
- Gibbons, J. W., J. E. Lovich, A. D. Tucker, N. N. FitzSimmons, and J. L. Greene. 2001. Demographic and ecological factors affecting conservation and management of the diamondback terrapin (*Malaclemys terrapin*) in South Carolina. *Chelonian Conservation and Biology* 4:66–74.
- Graham, T. E., and A. A. Graham. 1997. Ecology of the eastern spiny softshell, *Apalone spinifera spinifera*, in the Lamoille River, Vermont. *Chelonian Conservation and Biology* 2:363–369.
- Holman, J. A. and K. D. Andrews. 1994. North American quaternary cold-tolerant turtles: distributional adaptations and constraints. *Boreas* 23:44–52.
- Hupp, C. R., and W. R. Osterkamp. 1985. Bottomland vegetation distribution along Passage Creek, Virginia in relation to fluvial landforms. *Ecology* 66:670–681.
- Janzen, F.J. 1993. An experimental analysis of natural selection on body size of hatchling turtles. *Ecology* 74:332–341.
- Junk, W. J., P. B. Bayley, and R. E. Sparks. 1989. The flood pulse concept in river-floodplain systems. *Canadian Special Publication of fisheries and Aquatic Sciences* 106–110–127.
- Kuchling, G. 1999. The reproductive biology of chelonian-zoophysiology. Springer-Verlag, New York.
- Leopold, L. B., M. G. Wolman, and J. P. Miller. 1964. Fluvial processes in geomorphology. Dover Publications, Inc., Mineola, New York.
- Minton, S. A., Jr. 1972. Amphibians and Reptiles of Indiana. *Indiana Academy of Scientific Monographs* 3:1–346.
- Moll, D., and E. O. Moll. 2004. The ecology, exploitation, and conservation of river turtles. Oxford University Press, New York.

- Parmley, D. 1992. Turtles from the late Hemphillian (latest Miocene) of Knox County, Nebraska. *Texas Journal of Science* 44:339–348.
- Plummer, M. V., N. E. Mills, and S. L. Allen. 1997. Activity, habitat, and movement patterns of softshell turtles (*Trionyx spiniferus*) in a small stream. *Chelonian Conservation Biology* 2:514–520.
- Scott, M. L., G. T. Auble, and J. M. Friedman. 1997. Flood dependency of cottonwood establishment along the Missouri River, Montana. *Ecological Applications* 7:677–690.
- Ward, J. V. 1989. The four-dimensional nature of lotic ecosystems. *Journal of the North American Benthological Society* 8:2–8.
- Wildhaber, M. L., A. J. DeLonay, D. M. Papoulias, D. L. Galat, R. B. Jacobsen, D. G. Simpkins, P. J. Braaten, C. E. Korschgen, and M. J. Mac. 2011. Identifying structural elements needed for development of a predictive life-history model for pallid and shovelnose sturgeons. *Journal Applied Ichthyology* 27:462–469.
- Wilson, D. S. 1998. Nest-site selection: microhabitat variation and its effects on the survival of turtle embryos. *Ecology* 79:1884–1892.

REFERENCES

- Anderson, R. V., M. L. Gutierrez, and M. A. Romano. 2002. Turtle habitat use in a reach of the upper Mississippi River. *Journal of Freshwater Ecology* 17:171–177.
- Auble, G. T., J. M. Friedman, and M. L. Scott. 1994. Relating riparian vegetation to present and future streamflows. *Ecological Applications* 4:544–554.
- Bain, M. B., J. T. Finn, and H. E. Brooke. 1988. Streamflow regulation and fish community structure. *Ecology* 69:382–392.
- Barko, V. A., and J. T. Briggler. 2006. Midland smooth softshell (*Apalone mutica*) and spiny softshell (*Apalone spinifera*) turtles in the middle Mississippi River: habitat associations, population structure, and implications for conservation. *Chelonian Conservation and Biology*, 5:225–231.
- Bellgraph, B. J., C. S. Guy, W. M. Gardner, and S. A. Leathe. 2008. Competition potential between saugers and walleyes in nonnative sympatry. *Transactions of the American Fisheries Society* 137:790–800.
- Beltaos, S. 2003. Threshold between mechanical and thermal breakup of river ice cover. *Cold Regions Science and Technology* 37:1–113.
- Boby, M. L., and R. J. Brooks. 1994. Incubation conditions as potential factors limiting the northern distribution of snapping turtles, *Chelydra serpentina*. *Canadian Journal of Zoology* 72:28–37.
- Bodie, J. R. 2001. Stream and riparian management for freshwater turtles. *Journal of Environmental Management* 62:443–455.
- Bodie, J. R., and R. D. Semlitsch. 2000. Spatial and temporal use of floodplain habitats by lentic and lotic species of aquatic turtles. *Oecologia* 122:138–146.
- Bolton, R. M. 2007. Effects of anthropogenic disturbance, nest-site selection, and dipteran infestation on spiny softshells (*Apalone spinifera*). M.S. Thesis, The University of Guelph, Ontario, Canada.
- Bowen, Z. H., K. D. Bovee, and T. J. Waddle. 2003. Effects of flow regulation on shallow-water habitat dynamics and floodplain connectivity. *Transactions of the American Fisheries Society* 132:809–823.
- Bramblett, R. G., and R. G. White. 2001. Habitat use and movements of pallid and shovelnose sturgeon in the Yellowstone and Missouri Rivers in Montana and North Dakota. *Transactions of the American Fisheries Society* 130:1006–1025.

- Brinson, M. M., A. E. Lugo, and S. Brown. 1981. Primary productivity, decomposition and consumer activity in freshwater wetlands. *Annual Review of Ecology and Systematics* 12:123–161.
- Bull, J. J., and R. C. Vogt. 1979. Temperature-dependent sex determination in turtles. *Science* 206:1186–1188.
- Bunn, S. E., and A. H. Arthington. 2002. Basic principles and ecological consequences of altered flow regimes for aquatic biodiversity. *Environmental Management* 30:492–507.
- Burger, J. 1976. Determinants of hatching success in diamondback terrapin, *Malaclemys terrapin*. *American Midland Naturalist* 97:444–464.
- Burke, V. J., J. E. Lovitch, and J. W. Gibbons. 2000. Conservation of freshwater turtles. Pp. 156–179. *In* Turtle Conservation. M. W. Klemens (ed). Smithsonian Institution Press, Washington, D.C.
- Butler, B. O., and T. E. Graham. 1995. Early post-emergent behavior and habitat selection in hatchling Blanding's turtles, *Emydoidea blandingii*, in Massachusetts. *Chelonian Conservation Biology* 1:187–196.
- Churchill, T. A., and K. B. Storey. 1992a. Natural freezing survival by painted turtles *Chrysemys marginata* and *C. picta belli*. *Survival* 80:4.
- Churchill, T. A., and K. B. Storey. 1992b. Responses to freezing exposure of hatchling turtles *Trachemys scripta elegans*: factors influencing the development of freeze tolerance by reptiles. *Journal of Experimental Biology* 167:221–R233.
- Congdon, J. D., and J. W. Gibbons. 1990. Turtle eggs: their ecology and evolution. pp. 109–123. *In* Life history and ecology of the slider turtle. J. W. Gibbons (ed). Smithsonian Institution Press, Washington, D.C.
- Congdon, J. D., A. E. Dunham, and R. C. Van Loben Sels. 1993. Delayed sexual maturity and demographics of Blanding's turtles (*Emydoidea blandingii*): implications for conservation and management of long-lived organisms. *Conservation Biology* 7:826–833.
- Congdon, J. D., A. E. Dunham, and R. C. Van Loben Sels. 1994. Demographics of common snapping turtles (*Chelydra serpentina*): implications for conservation and management of long-lived organisms. *Integrative and Comparative Biology* 34:397.

- Costanzo, J. P., J. B. Iverson, M. F. Wright, and R. E. Lee Jr. 1995. Cold hardiness and overwintering strategies of hatchlings in an assemblage of northern turtles. *Ecology* 76:1772–1785.
- Dood, A. R., B. Schmitz, V. Riggs, N. McClenning, M. Jaeger, D. Fuller, R. Rauscher, S. Leathe, D. Moore, J. Dullum, J. Ensign, S. Story, and M. Backes. 2009. Relative abundance of spiny softshell turtles (*Apalone spinifera*) on the Missouri and Yellowstone rivers in Montana, Final Report. Montana Fish, Wildlife & Parks, Helena, Montana.
- Doody, J.S. 1995. A comparative study of two syntopic species of softshell turtles (*Apalone mutica* and *Apalone spinifera*) in southcentral Louisiana. M.S. Thesis, Southeastern Louisiana University, Hammond, USA.
- Doody, J. S. 1999. A test of the comparative influences of constant and fluctuating incubation temperatures on phenotypes of hatchling turtles. Linnaeus Fund Research Report. *Chelonian Conservation Biology* 3:529–531.
- Doody, J. S., A. Georges, J. E. Young, M. D. Pauza, A. L. Pepper, R. L. Alderman, and M.A. Welsh. 2001. Embryonic aestivation and emergence behavior in the Pig-nosed turtle, *Carettochelys insculpta*. *Canadian Journal of Zoology* 79:1062–1072.
- Ernst, C. H., and J. E. Lovich. 2009. Turtles of the United States and Canada. The Johns Hopkins University Press, Baltimore, Maryland.
- Ewert, M. A. 1979. The embryo and its egg: development and natural history. Pp. 33–416 *In* Turtles: Perspectives and Research. M. Harless and H. Morlock (eds.). John Wiley and Son, New York.
- Funk, J. L., and J. W. Robinson. 1974. Changes in the channel of the lower Missouri River and effects on fish and wildlife. Missouri Department of Conservation, Aquatic Series 11, Jefferson City, Missouri.
- Galat, D. L., C. R. Berry, W. M. Gardner, J. C. Hendrickson, G. E. Mestl, G. J. Power, C. Stone, and M. R. Winston. 2005. Spatiotemporal patterns and changes in Missouri River fishes. *American Fisheries Society Symposium* 45:249–291.
- Galat, D. L., L. H. Fredrickson, D. D. Humburg, K. J. Bataille, J. R. Bodie, J. Dohrenwend, J. R. Jones, M. E. Knowlton, J. Mazourek, A. C. McColpin, R. B. Renken, and R. D. Semlitsch. 1998. Flooding to restore connectivity of regulated, large-river wetlands. *BioScience* 48:721–733.

- Galois, P., and M. Ouellet. 2007. Traumatic injuries in eastern spiny softshell turtles (*Apalone spinifera*) due to recreational activities in the northern Lake Champlain basin. *Chelonian Conservation and Biology* 6:288–293.
- Galois, P., M. Léveillé, L. Bouthillier, C. Daigle, and S. Parren. 2002. Movement patterns, activity, and home range of the eastern spiny softshell turtle (*Apalone spinifera*) in northern Lake Champlain, Québec, Vermont. *Journal of Herpetology* 36:402–411.
- Garber, S. D., and J. Burger. 1995. A 20-yr study documenting the relationship between turtle decline and human recreation. *Ecological Applications* 5:1151–1162.
- Gardner, W. M., and C. B. Jensen. 2011. Upper Missouri River basin pallid sturgeon study 2005–2010 final report. United States Bureau of Reclamation, Montana Department of Fish, Wildlife & Parks, Helena, Montana.
- Georges, A. and M. Rose. 1992. Conservation biology of the Pignose Turtle, *Carretochelys insculpta*. *Chelonian Conservation and Biology* 1:3–12.
- Gibbons, J. W. 1986. Movement patterns among turtle populations: applicability to management of the desert tortoise. *Herpetologica* 42:104–113.
- Gibbons, J. W., and R. D. Semlitsch. 1982. Survivorship and longevity of a long-lived vertebrate species; how long do turtles live? *Journal of Animal Ecology* 51:523–527.
- Gibbons, J. W., J. L. Greene, and J. D. Congdon. 1990. Temporal and spatial movement patterns of sliders and other turtles. pp. 201–215. *In* Life History and Ecology of the Slider Turtle. J. W. Gibbons (ed.). Smithsonian Institution Press, Washington D.C.
- Gibbons, J. W., J. E. Lovich, A. D. Tucker, N. N. FitzSimmons, and J. L. Greene. 2001. Demographic and ecological factors affecting conservation and management of the diamondback terrapin (*Malaclemys terrapin*) in South Carolina. *Chelonian Conservation and Biology* 4:66–74.
- Graham, T. E., and A. A. Graham. 1991. *Trionyx Spiniferus Spiniferus* (Eastern Spiny Softshell). Burying behavior. *Herpetological Review* 22:56–57.
- Graham, T. E., and A. A. Graham. 1997. Ecology of the eastern spiny softshell, *Apalone spinifera spinifera*, in the Lamoille River, Vermont. *Chelonian Conservation and Biology* 2:363–369.

- Greenberg, S., and T. Godin. 2012. Timelapse Image Analysis Manual. Technical Report 2012-1028-11. Department of Computer Science, University of Calgary, Canada. <http://grouplab.cpsc.ucalgary.ca/cookbook/index.php/Demos/TimelapseCoder>
- Gregory, P. T. 1982. Reptilian hibernation, pp. 53–154. *In* Biology of the Reptilia. Gans, C., and Pough, F. H. (eds.). Vol. 13, Physiology D. Academic Press, New York.
- Gyuris, E. 1993. Factors that control the emergence of Green Turtle hatchlings from the nest. *Wildlife Research* 20:345–353.
- Hesse, L. W., J. C. Schmulbach, J. M. Carr, K. D. Keenlyne, D. G. Unkenholz, J. W. Robinson, and G. E. Mestl. 1989. Missouri River fishery resources in relation to past, present, and future stresses. Pp. 352–371 *In* D. P. Dodge (Ed.), *Proceedings of the International Large River Symposium*. Canadian Special Publication of Fisheries Aquatic Science 106.
- Holman, J. A. and K. D. Andrews. 1994. North American quaternary cold-tolerant turtles: distributional adaptations and constraints. *Boreas* 23:44-52.
- Humphries, P., and D. S. Baldwin. 2003. Drought and aquatic ecosystems: an introduction. *Freshwater Biology* 48:1141–1146.
- Hupp, C. R., and W. R. Osterkamp. 1985. Bottomland vegetation distribution along Passage Creek, Virginia in relation to fluvial landforms. *Ecology* 66:670–681.
- Hutchison, V. H., A. Vinegar, and R. J. Kosh. 1966. Critical thermal maxima in turtles. *Herpetologica* 1:32-41.
- Hynes, H. B. N. 1970. *The ecology of running waters*. University of Toronto Press, Toronto, Ontario, Canada.
- Iverson, J. B. 1991. Patterns of survivorship in turtles (Order Testudines). *Canadian Journal of Zoology* 69:385–391.
- Jackson, D. C., and G. R. Ultsch. 2010. Physiology of hibernation under the ice by turtles and frogs. *Journal of Experimental Zoology* 313A:311–327.
- Jaeger, M. E., A. V. Zale, T. E. McMahon, and B. J. Schmitz. 2005. Seasonal movements, habitat use, aggregation, exploitation, and entrainment of saugers in the lower Yellowstone River: an empirical assessment of factors affecting population recovery. *North American Journal of Fisheries Management* 25:1550–1568.
- Janzen, F. J. 1993. An experimental analysis of natural selection on body size of hatchling turtles. *Ecology* 74:332–341.

- Janzen, F. J. 1994. Vegetational cover predicts the sex ratio of hatchling turtles in natural nests. *Ecology* 75:1593–1599.
- Janzen, F. J., J. K. Tucker, and G. L. Paukstis. 2002. Experimental analysis of an early life-history stage: avian predation selects for larger body size of hatchling turtles. *Journal of Evolutionary Biology* 13:947–954.
- Junk, W. J., P. B. Bayley, and R. E. Sparks. 1989. The flood pulse concept in river-floodplain systems. *Canadian Special Publication of fisheries and Aquatic Sciences* 106–110–127.
- Karchesky, C. M., and D. H. Bennett. 2004. Winter habitat use by adult largemouth bass in the Pend Oreille River, Idaho. *North American Journal of Fisheries Management* 24:577–585.
- Kolbe, J. J., and F. J. Janzen. 2002. Impact of nest-site selection on nest success and nest temperature in natural and disturbed habitats. *Ecology* 83:269–281.
- Kuchling, G. 1999. *The reproductive biology of chelonian-zoophysiology*. Springer-Verlag, New York.
- Larsen, K. W., and P. T. Gregory. 1989. Population size and survivorship of the common garter snake, *Thamnophis sirtalis*, near the northern limit of its distribution. *Holarctic Ecology* 12:81–86.
- Leopold, L. B., M. G. Wolman, and J. P. Miller. 1964. *Fluvial processes in geomorphology*. Dover Publications, Inc., Mineola, New York.
- Lindeman, P. V. 2001. A contrast in the basking habits of the sympatric trionychid turtles *Apalone mutica* and *A. spinifera*. *Herpetological Natural History* 8:87–89.
- Litzgus, J. D., and T. A. Mousseau. 2004. Home range and seasonal activity of southern spotted turtles (*Clemmys guttata*): implications for management. *Copeia* 2004:804–817.
- Lytle, D. A., and N. L. Poff. 2004. Adaptation to natural flow regimes. *Trends in Ecology and Evolution*, 19:94–100.
- Maxell, B. A. 2013. Montana animal species of concern report. Montana natural heritage Program and Montana Fish, Wildlife, and Parks. Retrieved on 4/01/2013 from <http://mtnhp.org/SpeciesOfConcern/?AorP=a>
- MacCulloch, R. D., and D. M. Secoy. 1983. Movement in a river population *Chrysemys picta belli* in southern Saskatchewan. *Journal of Herpetology* 17:283–285.

- Miller, K., G. C. Packard, and M. J. Packard. 1987. Hydric conditions during incubation influence locomotor performance of hatchling snapping turtles. *Journal of Experimental Biology* 127:401–412.
- Minton, S. A., Jr. 1972. Amphibians and Reptiles of Indiana. *Indiana Academy of Scientific Monographs* 3:1–346.
- Mitro, M. G., and A. V. Zale. 2002. Seasonal survival, movement, and habitat use of age-0 rainbow trout in the Henrys Fork of the Snake River, Idaho. *Transactions of the American Fisheries Society* 131:271–286.
- Moll, E. O., and J. M. Legler. 1971. The life history of a neotropical slider turtle, *Pseudemys scripta* (Schoepff), in Panama. *Los Angeles County Museum Science Bulletin* 11:1–102.
- Moll, D., and E. O. Moll. 2004. The ecology, exploitation, and conservation of river turtles. Oxford University Press, New York.
- Moran, K. L., K. A. Bjorndal, and A. B. Bolton. 1999. Effects of the thermal environment on the temporal pattern of emergence of hatchling Loggerhead Turtles *Caretta caretta*. *Marine Ecology Progress Series* 189:251–261.
- Morreale, S. J., J. W. Gibbons, and J. D. Congdon. 1984. Significance of activity and movement in the yellow-bellied slider turtle (*Pseudemys scripta*). *Canadian Journal of Zoology* 62:1038–1042.
- Mrosovsky, N. 1968. Nocturnal emergence of hatchling sea turtles: control by thermal inhibition of activity. *Nature (London)* 220:531–547.
- Muhlfeld, C. C., and B. M. Marotz. 2005. Seasonal movement and habitat use by subadult bull trout in the upper Flathead River system, Montana. *North American Journal of Fisheries Management* 25:797–810.
- Packard, G. C., and M. J. Packard. 1988. The physiological ecology of reptilian eggs and embryos. pp. 523–603. *In* *Biology of the Reptilia*. Vol. 16. C. Gans and R. B. Huey (eds). Alan R. Liss, Inc., New York.
- Packard, G. C., M. J. Packard, K. Miller, and T. J. Boardman. 1987. Influence of moisture, temperature, and substrate on snapping turtle eggs and embryos. *Ecology* 68:983–993.
- Parmley, D. 1992. Turtles from the late Hemphillian (latest Miocene) of Knox County, Nebraska. *Texas Journal of Science* 44:339–348.

- Pegg, M. A., C. L. Pierce, and A. Roy. 2003. Hydrological alteration along the Missouri River basin: a time series approach. *Aquatic Sciences* 65:63–72.
- Plummer, M. V. 1976. Some aspects of nesting success in the turtle, *Trionyx muticus*. *Herpetologica* 32:353–359.
- Plummer, M. V. 2007. Nest emergence of smooth softshell turtle (*Apalone mutica*) hatchlings. *Herpetological Conservation and Biology* 2:61–64.
- Plummer, M. V., and J. C. Burnley. 1997. Behavior, hibernacula, and thermal relations of softshell turtles (*Trionyx spiniferus*) overwintering in a small stream. *Chelonian Conservation and Biology* 2:489–493.
- Plummer, M. V., and J. S. Doody. 2010. Terrestrial burrowing in nesting softshell turtles (*Apalone mutica* and *A. spinifera*). *International Reptile Conservation Foundation Journal Reptiles and Amphibians* 17:79–81.
- Plummer, M. V., and H. W. Shirer. 1975. Movement patterns in a river population of the softshell turtle, *Trionyx muticus*. *University of Kansas Natural History Museum Occasional Papers* 43:1–26.
- Plummer, M. V., T. N. Lee, and N. E. Mills. 2008. Effect of a sand substrate on the growth and condition of *Apalone mutica* hatchlings. *Journal of Herpetology* 42:550–554.
- Plummer, M. V., N. E. Mills, and S. L. Allen. 1997. Activity, habitat, and movement patterns of softshell turtles (*Trionyx spiniferus*) in a small stream. *Chelonian Conservation Biology* 2:514–520.
- Poff, N. L., and J. D. Allen. 1995. Functional organization of stream fish assemblages in relation to hydrological variability. *Ecology* 76:606–627.
- Poff, N. L. and K. H. Zimmerman. 2010. Ecological responses to altered flow regimes: a literature review to inform the science and management of environmental flows. *Freshwater Biology* 55:194–205.
- Poff, N. L., J. D. Allen, M. B. Bain, J. R. Karr, K. L. Prestegard, B. D. Richter, R. E. Sparks, and J. C. Stromberg. 1997. The natural flow regime. *BioScience* 47:769–784.
- Pritchard, P. C. H., and P. Trebbau. 1984. *The Turtles of Venezuela*. Society for the Study of Amphibians and Reptiles, New York.

- R Core Team. 2013. R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. URL <http://www.R-project.org/>.
- Ramey, M. P., S. M. Beck, and D. W. Reiser. 1993. Determination of flushing flow needs – Madison and upper Missouri rivers. Supplemental Report. Prepared by R2 Resource Consultants for Montana Power Company. Butte, Montana.
- Ramsey, F. L., and D. W. Schafer. 2002. The Statistical Sleuth, A course in Methods of Data Analysis. Second Edition. Duxbury Press, Belmont, California.
- Reese, D. A. 1996. Comparative demography and habitat use of western pond turtles in northern California: the effects of damming and related alterations. PhD dissertation, University of California, Berkley.
- Reese, S. A., D. C. Jackson, and G. R. Ultsch. 2003. Hibernation in freshwater turtles: softshell turtles (*Apalone spinifera*) are the most intolerant of anoxia among North American species. Journal of Comparative Physiology B: Biochemical, Systemic, and Environmental Physiology 173:263–268.
- Resetarits, W. J., Jr. 1996. Oviposition site choice and life history evolution. American Zoologist 36:205–215.
- Richards, R. R. 2012. Spawning related migration of *Scaphirhynchus* species in the Missouri River above Fort Peck reservoir, Montana. M.S. Thesis, Montana State University, Bozeman.
- Rogers, K. B., and G. C. White. 2007. Analysis of movement and habitat use from telemetry data. pp. 625–676. In Analysis and interpretation of freshwater fisheries data. C.S. Guy, and M.L. Brown (eds). American Fisheries Society, Bethesda, Maryland.
- Sanford, J. P. 2007. Dam regulation effects on sand bar migration on the Missouri River: Southeastern South Dakota. M.A. Thesis, The University of Montana, Missoula.
- Scott, M. L., G. T. Auble, and J. M. Friedman. 1997. Flood dependency of cottonwood establishment along the Missouri River, Montana. Ecological Applications 7:677–690.
- Scrimgeour, G. J., T. D. Prowse, J. M. Culp, and P. A. Chambers. 1994. Ecological effects of river ice break-up: a review and perspective. Freshwater Biology 32:261–275.
- Sexton, O. J. 1959. Spatial and temporal movements of a population of the painted turtle, *Chrysemys picta marginata* (Agassiz). Ecological Monographs 29:113–140.

- Shively, S. H., and J. F. Jackson. 1985. Factors limiting the upstream distribution of the Sabine map turtle. *American Midland Naturalist* 114:292–303.
- Sidle, J. G., and E. M. Kirsch. 1993. Least tern and piping plover nesting at sand pits in Nebraska. *Colonial Waterbirds* 16:139–148.
- Smith, E. N., S. L. Robertson, and S. R. Adams. 1981. Thermoregulation of the spiny soft-shelled turtle *Trionyx spinifer*. *Physiological Zoology*, 74-80.
- Smith, J. W., and R. B. Renken. 1991. Least tern nesting habitat in the Mississippi River valley adjacent to Missouri. *Journal of Field Ornithology* 62:497–504.
- Swales, S., R. B. Lauzier, and C. D. Levings. 1986. Winter habitat preferences of juvenile salmonids in two interior rivers in British Columbia. *Canadian Journal of Zoology* 64:1506–1514.
- Thompson, M. B. 1988. Nest temperatures in the pleurodiran turtle, *Emydura macquarii*. *Copeia* 1988:996–1000.
- Tinkle, D. W., J. D. Congdon, and P. C. Rosen. Nesting frequency and success: implications for the demography of painted turtles. *Ecology* 62:1426–1432.
- Ultsch, G. R. 2006. The ecology of overwintering among turtles: where turtles overwinter and its consequences. *Biological Reviews* 81:339–367.
- USHR (United States House of Representatives). 1976. Designation of Missouri River segment as a Wild and Scenic River. USHR, Subcommittee on National Parks and Recreation Report, Washington, D.C.
- Valenzuela, N. 2001. Maternal effects on life-history traits in the Amazonian giant river turtle *Podocnemis expansa*. *Journal of Herpetology* 35:368–378.
- Vogt, R. C. 1980. Natural history of the map turtles *Graptemys pseudogeographica* and *G. ouachitensis* in Wisconsin. *Tulane Studies in Zoology and Botany* 22:17–48.
- Vogt, R. C. 1997. Freshwater turtle nesting and reproduction in the neotropics. Abstract, p. 301. ASIH/HL/SSAR/AFS-ELHS/AES/GIS Joint Meetings, Washington.
- Vuke, S. M., K. W. Porter, J. D. Lonn, and D. A. Lopez. 2007. Geologic map of Montana. Montana Bureau of Mines and Geology. Geologic Map 62B, 1:500,000.
- Ward, J. V. 1989. The four-dimensional nature of lotic ecosystems. *Journal of the North American Benthological Society*, 8:2–8.

- Ward, J. V. and J. A. Stanford. 1983. The serial discontinuity concept of lotic ecosystems. pp. 29-42. *In* Dynamics of lotic ecosystems. T. D. Fontaine and S. M. Bartell (eds). Ann Arbor Science Publishers, Inc., Michigan.
- Webb, R. G. 1962. North American recent soft-shelled turtles (family Trionychidae). University of Kansas Publications Museum of Natural History 13:429–611.
- Webb, R. G. 1973. *Trionyx spiniferus*. Catalog of American Amphibians and Reptiles, 140:1–4.
- Weisrock, D. W., and F. J. Janzen. 1999. Thermal and fitness-related consequences of nest location in painted turtles (*Chrysemys picta*). Functional Ecology 13:94–101.
- Welcomme, R. L. 1979. Fisheries ecology of floodplain rivers. Longman, New York, New York.
- Werner, J. K., B. A. Maxell, P. Hendricks, and D. L. Flath. 2004. Amphibians and reptiles of Montana. Mountain Press, Missoula, Montana.
- White, G. C., and R. A. Garrott. 1990. Analysis of wildlife radio-tracking data. Academic Press, San Diego, California.
- Wildhaber, M. L., A. J. DeLonay, D. M. Papoulias, D. L. Galat, R. B. Jacobsen, D. G. Simpkins, P. J. Braaten, C. E. Korschgen, and M. J. Mac. 2011. Identifying structural elements needed for development of a predictive life-history model for pallid and shovelnose sturgeons. Journal Applied Ichthyology 27:462–469.
- Wilson, D. S. 1998. Nest-site selection: microhabitat variation and its effects on the survival of turtle embryos. Ecology 79:1884–1892.
- Witherington, B. E. 1995. Hatchling orientation. pp. 577–578. *In* Biology and Conservation of Sea Turtles. K. A. Bjorndal (Ed). Smithsonian Institution Press, Washington, D.C.
- Wood, D. W., and K. A. Bjorndal. 2000. Relation of temperature, moisture, salinity and slope to nest site selection in loggerhead sea turtles. Copeia 2000:119–128.
- Zuur, A. F., E. N. Ieno, N. J. Walker, A. A. Saveliev, and G. M. Smith. 2009. Mixed Effects Models and Extensions in Ecology with R. Springer Science+Business Media, LLC, New York.

APPENDICES

APPENDIX A

SPINY SOFTSHELL TURTLE MORPHOLOGY, MOVEMENT, HOME RANGE,
HABITAT SELECTION, AND MICROHABITAT TABLES

Table A.1. Mass, curved carapace length (CCL), monitoring period (Period) in days, number of point locations (Loc.), linear home range (LHR), and areal home range (AHR) of 46 female and 11 male telemetered *Apalone spinifera* in the Missouri River in Montana from 2009 through 2012. Number of point locations includes the total number of times each turtle was located by hand fixes and remote station fixes. The bottom table describes mean and standard deviation of mass, CCL, Period, Loc., LHR, and AHR for females and males and all turtles pooled.

Turtle no. (sex)	Mass (g)	CCL (mm)	Period	Loc.	LHR (km)	AHR (km ²)
40 (F)	1814	295	729	18	4.58	0.77
41 (F)	2466	354	955	23	7.49	1.35
43 (F)	2636	325	1006	23	5.33	0.71
44 (F)	2098	303	744	17	2.47	0.41
45 (F)	2551	310	955	29	5.63	0.71
46 (F)	2690	330	431	10	1.50	0.20
49 (F)	2198	301	342	7	13.16	1.58
50 (F)	3812	368	1064	88	67.32	4.71
51 (F)	3590	360	955	21	4.16	0.69
52 (F)	3186	350	1037	89	16.25	1.97
53 (F)	2610	315	812	23	2.96	0.49
54 (F)	2172	316	1022	24	5.36	0.75
55 (F)	1888	295	632	17	6.75	0.73
57 (F)	2498	319	1048	33	4.09	0.56
60 (F)	2486	320	1015	54	13.24	1.70
61 (F)	2710	331	743	30	16.52	3.15
62 (F)	2074	305	728	27	12.51	2.29
63 (F)	2760	331	429	33	6.63	0.48
64 (F)	2920	325	1035	29	6.98	1.01
65 (F)	3175	328	1022	27	5.38	0.89
69 (F)	3090	339	719	20	27.59	5.54
70 (F)	2807	320	350	9	2.86	0.44
71 (F)	2466	316	1022	27	2.51	0.37
72 (F)	4167	401	288	4	8.58	1.04
73 (F)	2268	306	811	22	58.73	8.41
74 (F)	2240	309	957	23	8.65	1.49
75 (F)	2324	309	454	13	4.46	0.64
76 (F)	2566	335	1064	26	50.48	8.92
77 (F)	1256	252	721	20	2.50	0.53
78 (F)	2439	300	1024	26	11.03	1.28
79 (F)	3530	351	709	15	2.57	0.49
80 (F)	2640	332	709	18	4.54	0.76
82 (F)	1726	293	759	25	2.43	0.42
83 (F)	1250	253	336	8	1.53	0.29

86 (F)	2294	322	1037	40	43.17	7.02
87 (F)	2580	322	396	26	86.85	16.95
88 (F)	3630	326	37	3	3.79	0.73
90 (F)	3044	346	1058	25	33.52	3.12
91 (F)	3230	349	707	16	12.30	2.72
92 (F)	3062	337	957	44	33.59	6.35
93 (F)	2270	334	779	27	51.88	9.02
94 (F)	3118	347	1054	49	4.27	0.85
95 (F)	3543	365	266	5	39.90	7.27
97 (F)	963	238	1021	27	1.75	0.30
98 (F)	2866	333	335	17	80.06	16.34
99 (F)	3600	370	811	21	8.45	1.60
42 (M)	652	192	273	3	16.13	2.46
47 (M)	408	166	811	15	3.34	0.46
48 (M)	486	181	811	21	5.57	0.68
56 (M)	598	190	812	29	9.40	1.63
58 (M)	464	178	351	10	0.85	0.08
59 (M)	502	181	343	5	12.76	2.15
66 (M)	652	189	957	22	5.38	0.85
67 (M)	737	185	688	21	23.39	2.93
68 (M)	652	180	758	22	6.54	0.74
81 (M)	344	163	43	1	20.34	1.41
96 (M)	453	178	759	29	53.17	6.36
Sex	Mass (g)	CCL (mm)	Period	Loc.	LHR (km)	AHR (km ²)
Females	2637.0 (676.4)	323.6 (30.3)			17.3 (22.1)	2.8 (3.9)
Males	561.6 (138.8)	180.5 (8.8)			14.3 (14.8)	1.8 (1.8)
Overall	2207.6 (1041.1)	294.0 (64.5)	720	24 (16)	16.7 (20.8)	2.6 (3.6)

Table A.2. Minimum, maximum, median, and standard deviation (SD) for seasonal linear and areal home ranges (LHR and AHR) of telemetered *Apalone spinifera* in the Missouri River in Montana from 2009 through 2012. Letters indicate significant differences in median LHR and AHR among seasons; seasons with the same letter are not significantly different. All seasons pooled are displayed in the row above each set of home range seasons.

Variable	Season	N turtles	Min.	Max.	Median	SD
Linear home range (km)	Pooled	57	0.85	86.85	6.98	20.76
	Spring ^a	53	0.01	54.78	1.58	12.98
	Summer ^b	57	0.76	76.84	4.99	16.88
	Autumn ^c	56	0.01	24.97	0.30	4.92
	Winter ^d	46	0.01	24.90	0.02	4.68
Areal home range (km ²)	Pooled	57	0.08	16.95	1.01	3.60
	Spring ^a	42	0.003	9.96	0.27	1.77
	Summer ^b	52	0.002	15.41	0.73	2.76
	Autumn ^a	50	0.002	4.49	0.06	0.77
	Winter ^c	39	0.002	4.49	0.01	0.94

Table A.3. Length, percent available and used, selection ratio, standard error for selection ratio, and lower and upper confidence intervals on the selection ratio for habitat units used by telemetered *Apalone spinifera* in the Missouri River in Montana from 2009 through 2012 by year. A selection ratio of 1 (i.e., no preference), values less than zero indicate a reach is used less than expected (i.e., avoidance), and values greater than zero indicate a reach is used more than expected (i.e., preference).

Variable	Season	Length (km)	% Available	% Used	Ratio	SE	LCI	UCI
Riffle	2010	13.24	0.10	0.09	0.92	0.27	0.27	1.58
	2011	13.24	0.10	0.11	1.06	0.32	0.30	1.82
	2012	13.24	0.10	0.00	0.00	0.00	0.00	0.00
Run Islands	2010	56.55	0.43	0.43	0.99	0.12	0.71	1.26
	2011	56.55	0.43	0.47	1.09	0.13	0.77	1.41
	2012	56.55	0.43	0.80	1.86	0.44	0.81	2.90
Run No island	2010	61.41	0.47	0.48	1.03	0.10	0.78	1.28
	2011	61.41	0.47	0.42	0.90	0.11	0.63	1.17
	2012	61.41	0.47	0.20	0.43	0.40	-0.54	1.39

Table A.4. Length, percent available and used, selection ratio, standard error for selection ratio, and lower and upper confidence intervals on the selection ratio for geomorphic reach types used by telemetered *Apalone spinifera* in the Missouri River in Montana from 2009 through 2012 by year. A selection ratio of 1 (i.e., no preference), values less than zero indicate a reach is used less than expected (i.e., avoidance), and values greater than zero indicate a reach is used more than expected (i.e., preference).

Variable	Season	Length (km)	% Available	% Used	Ratio	SE	LCI	UCI
Meander	2010	24.08	0.18	0.20	1.11	0.22	0.55	1.67
Island	2011	24.08	0.18	0.25	1.37	0.28	0.66	2.07
	2012	24.08	0.18	0.00	0.00	0.00	0.00	0.00
Meander	2010	42.21	0.32	0.38	1.17	0.16	0.77	1.58
No island	2011	42.21	0.32	0.32	0.99	0.17	0.55	1.42
	2012	42.21	0.32	0.20	0.62	0.58	-0.84	2.08
Straight	2010	38.61	0.29	0.27	0.91	0.15	0.53	1.29
Island	2011	38.61	0.29	0.28	0.96	0.19	0.49	1.44
	2012	38.61	0.29	0.60	2.04	0.75	0.17	3.91
Straight	2010	26.36	0.20	0.15	0.76	0.17	0.32	1.19
No island	2011	26.36	0.20	0.15	0.74	0.18	0.29	1.20
	2012	26.36	0.20	0.20	1.00	0.94	-1.35	3.34

Table A.5. Percent available and used, selection ratio, standard error for selection ratio, and lower and upper confidence intervals for bend types used by telemetered *Apalone spinifera* in the Missouri River in Montana from 2009 through 2012 by year. A selection ratio of 1 (i.e., no preference), values less than zero indicate a reach is used less than expected (i.e., avoidance), and values greater than zero indicate a reach is used more than expected (i.e., preference).

Variable	Season	% Available	% Used	Ratio	SE	LCI	UCI
Inside bend	2010	0.50	0.32	0.64	0.11	0.41	0.88
	2011	0.50	0.46	0.91	0.13	0.63	1.20
	2012	0.50	0.00	0.00	0.00	0.00	0.00
Outside bend	2010	0.50	0.68	1.36	0.11	1.12	1.59
	2011	0.50	0.54	1.09	0.13	0.80	1.37
	2012	0.50	0.00	0.00	0.00	0.00	0.00

Table A.6. Percent available and used, selection ratio, standard error, and lower and upper confidence intervals for substrate types used by telemetered *Apalone spinifera* in the Missouri River in Montana from 2009 through 2012 by year. A selection ratio of 1 (i.e., no preference), values less than zero indicate a reach is used less than expected (i.e., avoidance), and values greater than zero indicate a reach is used more than expected (i.e., preference).

Variable	Season	% Available	% Used	Ratio	SE	LCI	UCI
Cobble	2010	0.66	0.10	0.16	0.03	0.10	0.22
	2011	0.66	0.11	0.16	0.03	0.10	0.23
	2012	0.66	0.08	0.13	0.09	-0.09	0.34
Fines	2010	0.23	0.79	3.42	0.11	3.16	3.68
	2011	0.23	0.82	3.57	0.10	3.33	3.81
	2012	0.23	0.83	3.62	0.36	2.77	4.47
Gravel	2010	0.11	0.11	0.99	0.19	0.54	1.43
	2011	0.11	0.07	0.64	0.16	0.27	1.02
	2012	0.11	0.08	0.76	0.43	-0.27	1.78

Table A.7. Length, percent available and used, selection ratio, standard error for selection ratio, and lower and upper confidence intervals on the selection ratio for habitat units used by telemetered *Apalone spinifera* in the Missouri River in Montana from 2009 through 2012 by season. A selection ratio of 1 (i.e., no preference), values less than zero indicate a reach is used less than expected (i.e., avoidance), and values greater than zero indicate a reach is used more than expected (i.e., preference).

Variable	Season	Length (km)	% Available	% Used	Ratio	SE	LCI	UCI
Riffle	Spring	13.24	0.10	0.17	1.66	0.48	0.51	2.82
	Summer	13.24	0.10	0.08	0.80	0.22	0.28	1.32
	Autumn	13.24	0.10	0.06	0.61	0.30	-0.10	1.31
	Winter	13.24	0.10	0.09	0.87	0.39	-0.06	1.81
Run Island	Spring	56.55	0.43	0.48	1.11	0.15	0.74	1.48
	Summer	56.55	0.43	0.45	1.06	0.10	0.81	1.31
	Autumn	56.55	0.43	0.43	0.99	0.15	0.64	1.35
	Winter	56.55	0.43	0.35	0.82	0.16	0.44	1.20
Run No Island	Spring	61.41	0.47	0.35	0.76	0.14	0.43	1.08
	Summer	61.41	0.47	0.46	0.99	0.09	0.78	1.21
	Autumn	61.41	0.47	0.51	1.09	0.14	0.76	1.42
	Winter	61.41	0.47	0.56	1.19	0.15	0.83	1.56

Table A.8. Length, percent available and used, selection ratio, standard error for selection ratio, and lower and upper confidence intervals on the selection ratio for geomorphic reach types used by telemetered Apalone spinifera in the Missouri River in Montana from 2009 through 2012 by season. A selection ratio of 1 (i.e., no preference), values less than zero indicate a reach is used less than expected (i.e., avoidance), and values greater than zero indicate a reach is used more than expected (i.e., preference).

Variable	Season	Length (km)	% Available	% Used	Ratio	SE	LCI	UCI
Meander Island	Spring	24.08	0.18	0.27	1.47	0.31	0.69	2.26
	Summer	24.08	0.18	0.21	1.14	0.23	0.56	1.71
	Autumn	24.08	0.18	0.16	0.89	0.26	0.23	1.55
	Winter	24.08	0.18	0.15	0.80	0.28	0.11	1.50
Meander No Island	Spring	42.21	0.32	0.32	1.00	0.20	0.49	1.51
	Summer	42.21	0.32	0.32	0.99	0.13	0.65	1.32
	Autumn	42.21	0.32	0.41	1.28	0.21	0.76	1.79
	Winter	42.21	0.32	0.40	1.23	0.22	0.68	1.78
Straight Island	Spring	38.61	0.29	0.30	1.01	0.21	0.49	1.52
	Summer	38.61	0.29	0.29	0.98	0.15	0.60	1.36
	Autumn	38.61	0.29	0.27	0.91	0.20	0.42	1.40
	Winter	38.61	0.29	0.26	0.90	0.22	0.36	1.44
Straight No island	Spring	26.36	0.20	0.11	0.56	0.20	0.07	1.06
	Summer	26.36	0.20	0.19	0.92	0.19	0.46	1.39
	Autumn	26.36	0.20	0.16	0.78	0.22	0.22	1.34
	Winter	26.36	0.20	0.19	0.95	0.28	0.24	1.66

Table A.9. Percent available and used, selection ratio, standard error for selection ratio, and lower and upper confidence intervals for bend types used by telemetered *Apalone spinifera* in the Missouri River in Montana from 2009 through 2012 by season. A selection ratio of 1 (i.e., no preference), values less than zero indicate a reach is used less than expected (i.e., avoidance), and values greater than zero indicate a reach is used more than expected (i.e., preference).

Variable	Season	% Available	% Used	Ratio	SE	LCI	UCI
Inside bend	Spring	0.50	0.51	1.02	0.13	0.72	1.32
	Summer	0.50	0.47	0.95	0.09	0.74	1.15
	Autumn	0.50	0.24	0.49	0.14	0.17	0.80
	Winter	0.50	0.28	0.55	0.19	0.13	0.97
Outside bend	Spring	0.50	0.49	0.98	0.13	0.68	1.28
	Summer	0.50	0.53	1.05	0.09	0.85	1.26
	Autumn	0.50	0.76	1.51	0.14	1.20	1.83
	Winter	0.50	0.72	1.45	0.19	1.03	1.87

Table A.10. Percent available and used, selection ratio, standard error, and lower and upper confidence intervals for substrate types used by telemetered *Apalone spinifera* in the Missouri River in Montana from 2009 through 2012. A selection ratio of 1 (i.e., no preference), values less than zero indicate a reach is used less than expected (i.e., avoidance), and values greater than zero indicate a reach is used more than expected (i.e., preference).

Variable	Season	% Available	% Used	Ratio	SE	LCI	UCI
Cobble	Spring	0.66	0.01	0.02	0.02	-0.03	0.07
	Summer	0.66	0.10	0.16	0.04	0.07	0.24
	Autumn	0.66	0.14	0.21	0.06	0.08	0.35
	Winter	0.66	0.11	0.16	0.08	-0.02	0.35
Fines	Spring	0.23	0.96	4.16	0.10	3.91	4.41
	Summer	0.23	0.76	3.29	0.15	2.93	3.64
	Autumn	0.23	0.65	2.84	0.24	2.26	3.41
	Winter	0.23	0.86	3.76	0.24	3.18	4.34
Gravel	Spring	0.11	0.03	0.26	0.18	-0.18	0.70
	Summer	0.11	0.14	1.28	0.29	0.59	1.97
	Autumn	0.11	0.21	1.88	0.41	0.90	2.86
	Winter	0.11	0.03	0.25	0.24	-0.33	0.82

Table A.11. Minimum, maximum, median, and standard deviation (SD) for microhabitat characteristics at point locations of telemetered *Apalone spinifera* in the Missouri River in Montana from 2009 through 2012. Letters indicate significant differences in median monthly microhabitat characteristics; months with the same letter are not significantly different. All months pooled are displayed in the row above each set of habitat characteristic months.

Variable	Period	N turtles	n obs.	Min.	Max.	Median	SD
Distance to shore (m)	Pooled	57	576	0.00	132.00	3.00	15.76
	April ^a	43	71	4.00	80.50	13.70	11.39
	May ^b	36	61	0.00	47.50	2.00	8.79
	June ^b	50	106	0.00	95.10	1.50	17.76
	July ^b	52	139	0.00	132.00	1.20	16.05
	August ^b	47	94	0.00	92.80	2.00	22.24
	October ^a	33	47	4.00	44.00	14.00	7.45
	November ^a	40	58	5.00	27.00	14.00	5.00
Depth (m)	Pooled	57	638	0.00	4.15	0.86	0.79
	April ^a	45	76	0.40	2.99	1.71	0.55
	May ^b	36	60	0.10	2.40	0.54	0.54
	June ^b	50	107	0.00	3.40	0.55	0.59
	July ^b	52	140	0.00	2.80	0.50	0.52
	August ^b	47	94	0.06	2.20	0.61	0.41
	October ^a	53	99	0.50	4.15	1.90	0.59
	November ^c	41	62	1.20	3.30	2.30	0.45
Relative Depth (m)	Pooled	57	510	0.00	1.00	0.37	0.29
	April ^a	33	45	0.20	1.00	0.72	0.23
	May ^b	31	45	0.06	1.00	0.14	0.23
	June ^c	50	99	0.00	1.00	0.30	0.27
	July ^d	52	122	0.00	1.00	0.20	0.22
	August ^c	45	92	0.06	1.00	0.30	0.19
	October ^a	46	59	0.20	0.99	0.80	0.19
	November ^a	33	48	0.45	0.96	0.82	0.13
Velocity (m/sec)	Pooled	53	425	0.00	1.69	0.10	0.30
	April ^a	28	36	0.11	0.99	0.54	0.19
	May ^{b,c}	36	61	0.00	1.30	0.02	0.34
	June ^b	46	77	0.00	1.69	0.02	0.28
	July ^{c,d}	50	114	0.00	1.39	0.15	0.29
	August ^d	47	95	0.00	1.51	0.20	0.34
	October ^{a,c,d}	5	7	0.11	0.62	0.42	0.19
	November ^a	26	35	0.25	0.93	0.49	0.14

Bottom Velocity (m/sec)	Pooled	53	425	0.00	1.56	0.08	0.26
	April ^a	28	36	0.07	0.95	0.46	0.18
	May ^{b,c}	36	61	0.00	1.21	0.01	0.31
	June ^b	46	77	0.00	1.56	0.01	0.23
	July ^c	50	114	0.00	1.19	0.09	0.23
	August ^c	47	95	0.00	1.17	0.10	0.26
	October ^{a,c}	5	7	0.08	0.48	0.27	0.15
	November ^a	26	35	0.17	0.84	0.38	0.15
Relative Velocity (m/sec)	Pooled	46	259	0.00	1.00	0.16	0.28
	April ^a	27	35	0.10	1.00	0.55	0.20
	May ^{b,c}	34	52	0.00	1.00	0.02	0.27
	June ^{b,c}	15	20	0.00	0.85	0.00	0.20
	July ^b	40	69	0.00	0.91	0.11	0.20
	August ^c	31	52	0.00	0.98	0.13	0.22
	October	0	0				
	November ^a	25	31	0.33	0.84	0.58	0.15

Table A.12. Minimum, maximum, median, mean, and standard deviation (SD) for depth, velocity, and bottom velocity by habitat type at point locations of telemetered spiny softshell turtles in the Missouri River above Fort Peck reservoir, Montana, from 2009–2012. Letters indicate significant differences in median microhabitat characteristics among habitat types; habitat types with the same letter are not significantly different. All habitat types pooled are displayed in the row above each set of habitat characteristics.

Variable	Period	N		Min	Max	Median	SD
		turtles	n obs.				
Depth (m)	Pooled	50	509	0.00	3.40	0.68	0.71
	Tributaries ^a	33	72	0.00	1.70	0.42	0.40
	Floodplains ^{b,c}	19	29	0.29	2.20	0.70	0.46
	Main channel ^b	50	312	0.00	3.40	0.83	0.79
	Backwaters ^c	19	22	0.05	1.10	0.57	0.40
	Side channels ^{a,c}	32	74	0.00	1.40	0.53	0.40
Velocity (m/sec)	Pooled	53	425	0.00	1.69	0.10	0.30
	Tributaries ^{a,b}	30	63	0.00	0.52	0.00	0.08
	Floodplains ^a	17	27	0.00	1.09	0.01	0.22
	Main channel ^c	50	260	0.00	1.69	0.31	0.32
	Backwaters ^b	13	15	0.00	0.17	0.00	0.04
	Side channels ^c	31	60	0.00	0.99	0.14	0.30
Bottom Velocity (m/sec)	Pooled	53	425	0.00	1.56	0.08	0.26
	Tributaries ^{a,b}	30	63	0.00	0.53	0.00	0.08
	Floodplains ^a	17	27	0.00	1.08	0.01	0.22
	Main channel ^c	50	260	0.00	1.56	0.20	0.28
	Backwaters ^b	13	15	0.00	0.10	0.00	0.03
	Side channels ^c	31	60	0.00	0.85	0.10	0.22

APPENDIX B

SPINY SOFTSHELL TURTLE MOVEMENT FIGURES

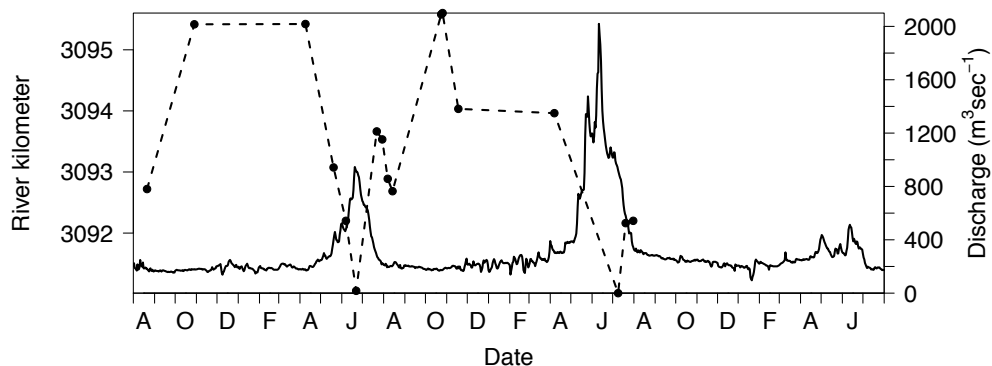


Figure B.1. Movements of spiny softshell turtle 40 (female, N=17; dotted line) plotted against mean daily discharge (solid line) from August 2009 through July 2012 in the Missouri River, Montana.

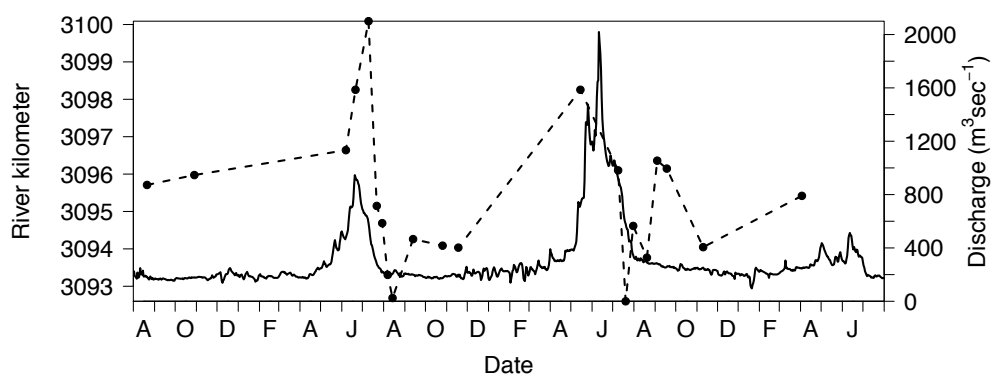


Figure B.2. Movements of spiny softshell turtle 41 (female, N=21) plotted against mean daily discharge from August 2009 through July 2012 in the Missouri River, Montana.

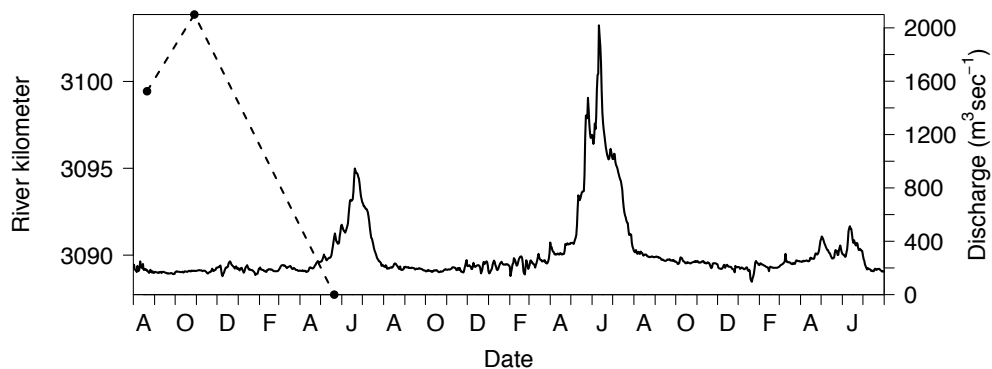


Figure B.3. Movements of spiny softshell turtle 42 (male, N=3) plotted against mean daily discharge from August 2009 through July 2012 in the Missouri River, Montana.

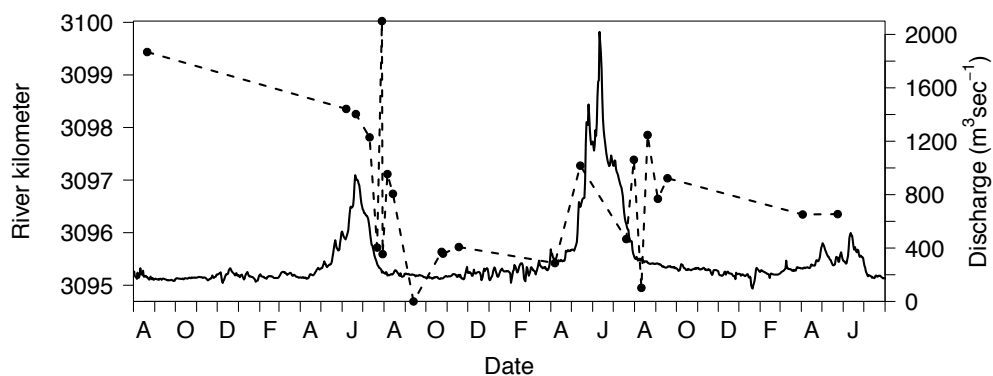


Figure B.4. Movements of spiny softshell turtle 43 (female, N=23) plotted against mean daily discharge from August 2009 through July 2012 in the Missouri River, Montana.

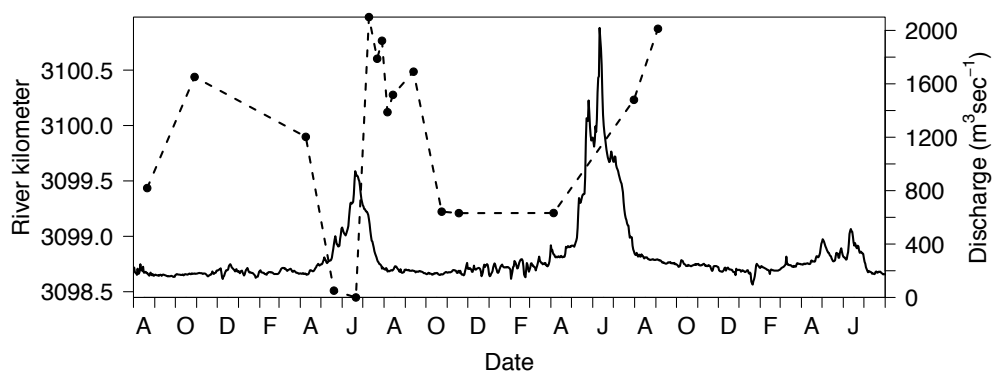


Figure B.5. Movements of spiny softshell turtle 44 (female, N=16) plotted against mean daily discharge from August 2009 through July 2012 in the Missouri River, Montana.

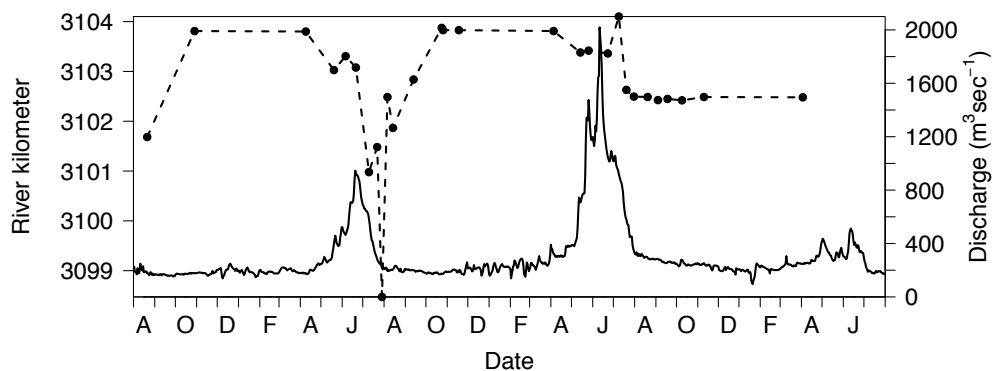


Figure B.6. Movements of spiny softshell turtle 45 (female, N=28) plotted against mean daily discharge from August 2009 through July 2012 in the Missouri River, Montana.

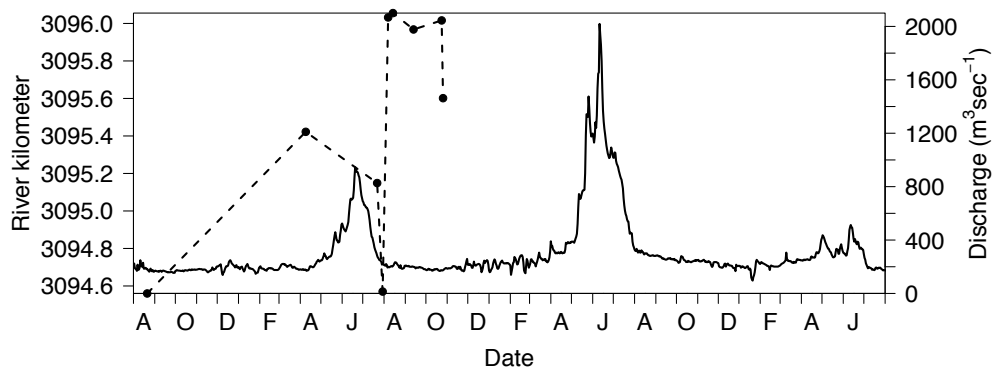


Figure B.7. Movements of spiny softshell turtle 46 (female, N=9) plotted against mean daily discharge from August 2009 through July 2012 in the Missouri River, Montana.

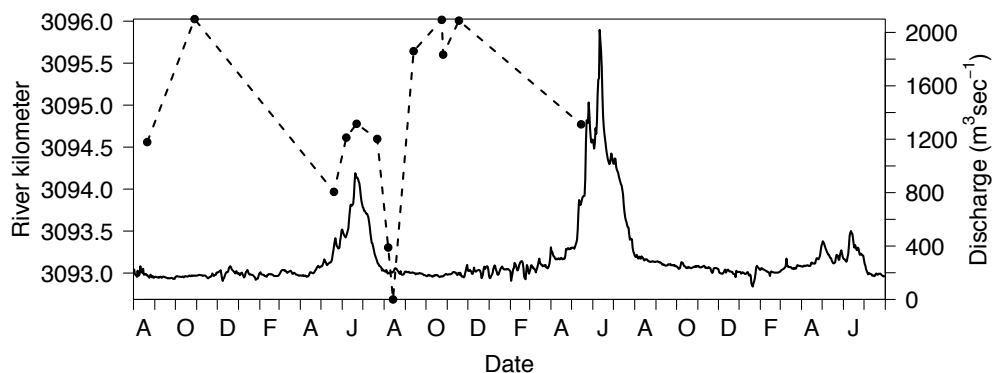


Figure B.8. Movements of spiny softshell turtle 47 (female, N=13) plotted against mean daily discharge from August 2009 through July 2012 in the Missouri River, Montana.

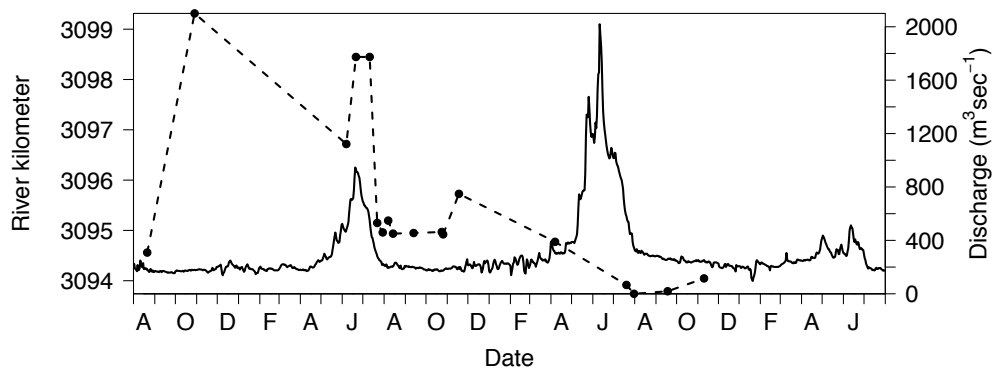


Figure B.9. Movements of spiny softshell turtle 48 (male, N=18) plotted against mean daily discharge from August 2009 through July 2012 in the Missouri River, Montana.

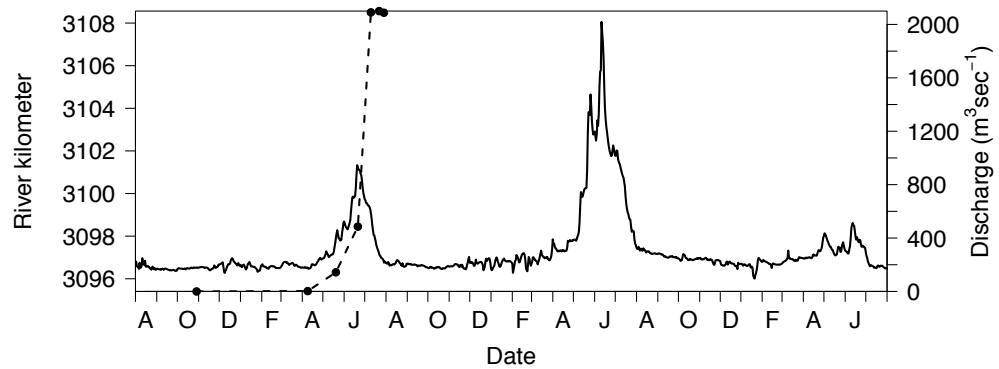


Figure B.10. Movements of spiny softshell turtle 49 (female, N=7) plotted against mean daily discharge from August 2009 through July 2012 in the Missouri River, Montana.

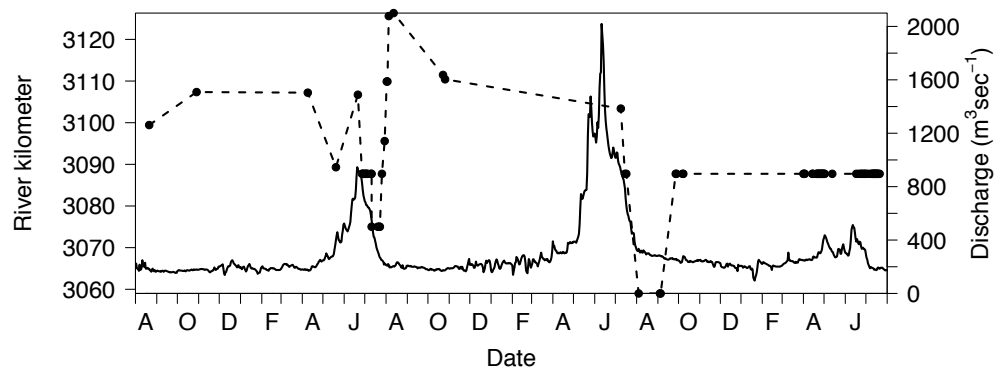


Figure B.11. Movements of spiny softshell turtle 50 (female, N=75) plotted against mean daily discharge from August 2009 through July 2012 in the Missouri River, Montana.

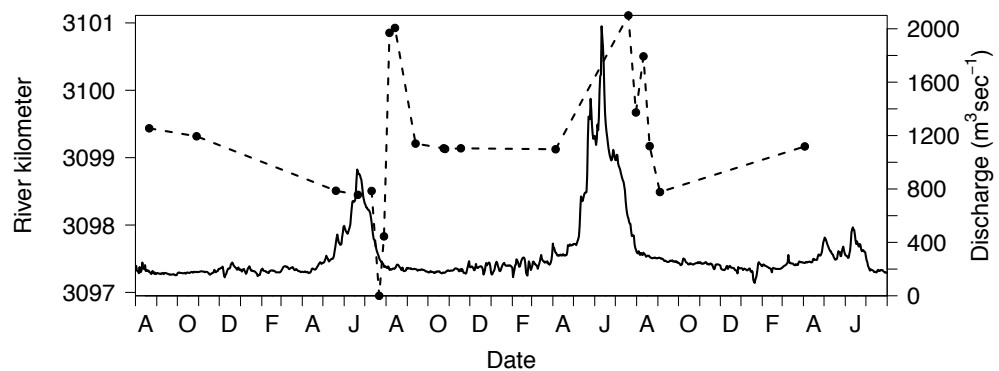


Figure B.12. Movements of spiny softshell turtle 51 (female, N=20) plotted against mean daily discharge from August 2009 through July 2012 in the Missouri River, Montana.

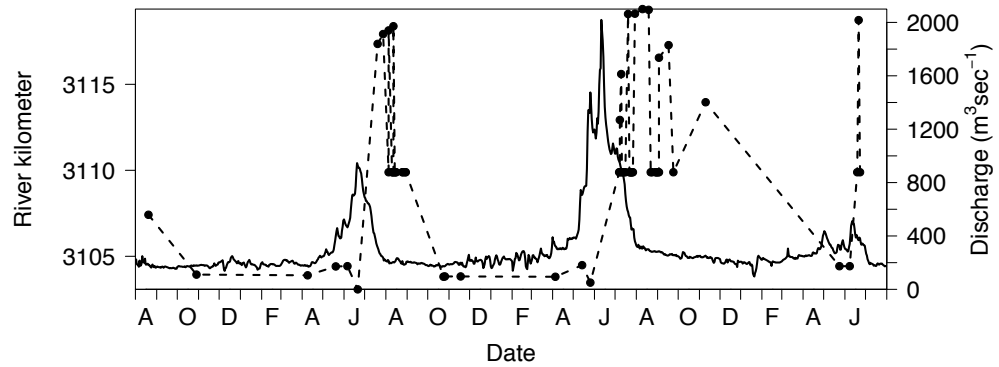


Figure B.13. Movements of spiny softshell turtle 52 (female, N=61) plotted against mean daily discharge from August 2009 through July 2012 in the Missouri River, Montana.

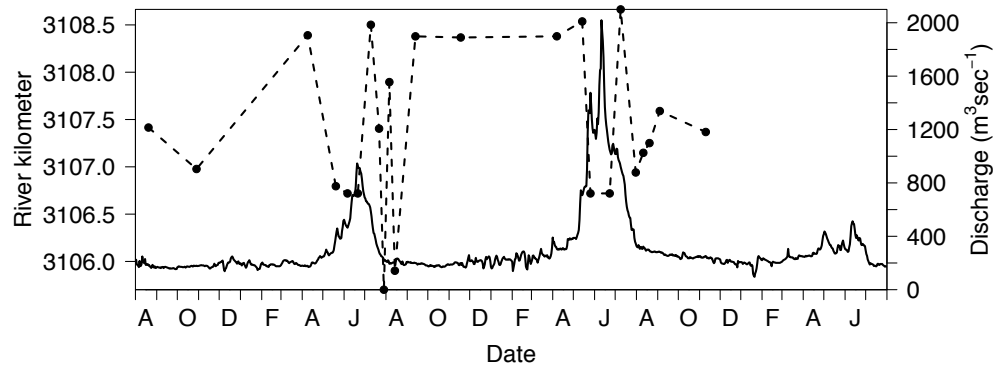


Figure B.14. Movements of spiny softshell turtle 53 (female, N=23) plotted against mean daily discharge from August 2009 through July 2012 in the Missouri River, Montana.

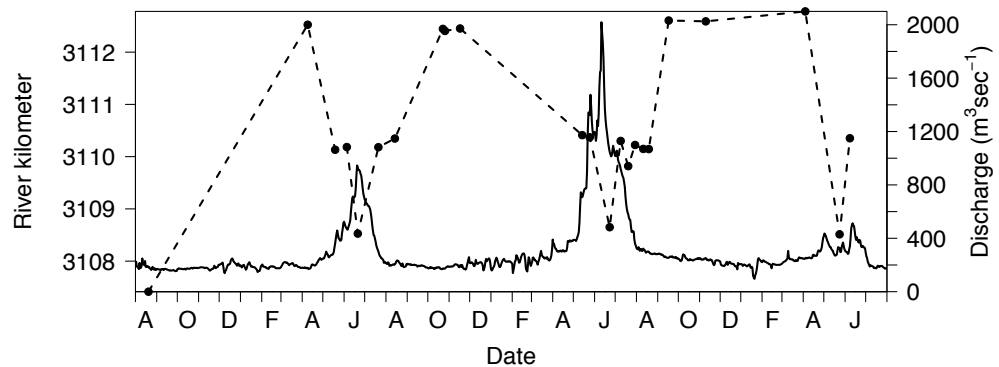


Figure B.15. Movements of spiny softshell turtle 54 (female, N=23) plotted against mean daily discharge from August 2009 through July 2012 in the Missouri River, Montana.

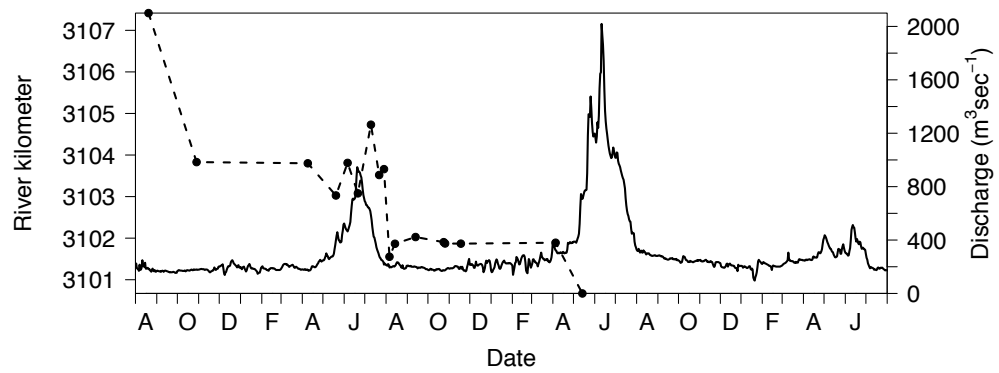


Figure B.16. Movements of spiny softshell turtle 55 (female, N=17) plotted against mean daily discharge from August 2009 through July 2012 in the Missouri River, Montana.

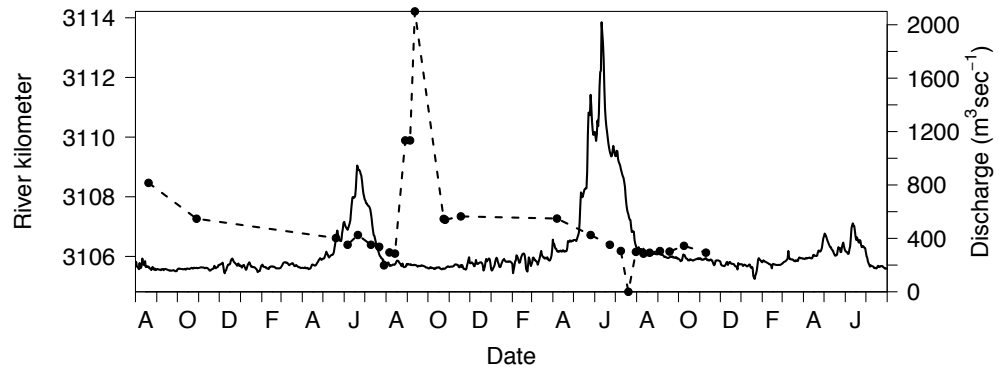


Figure B.17. Movements of spiny softshell turtle 56 (male, N=28) plotted against mean daily discharge from August 2009 through July 2012 in the Missouri River, Montana.

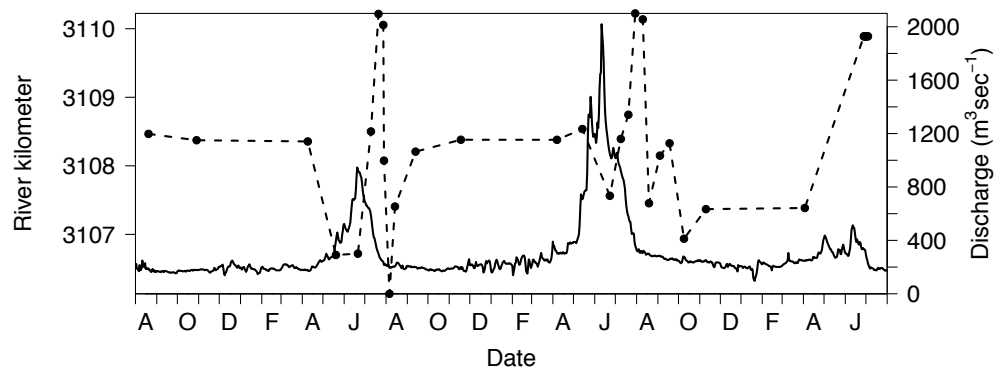


Figure B.18. Movements of spiny softshell turtle 57 (female, N=32) plotted against mean daily discharge from August 2009 through July 2012 in the Missouri River, Montana.

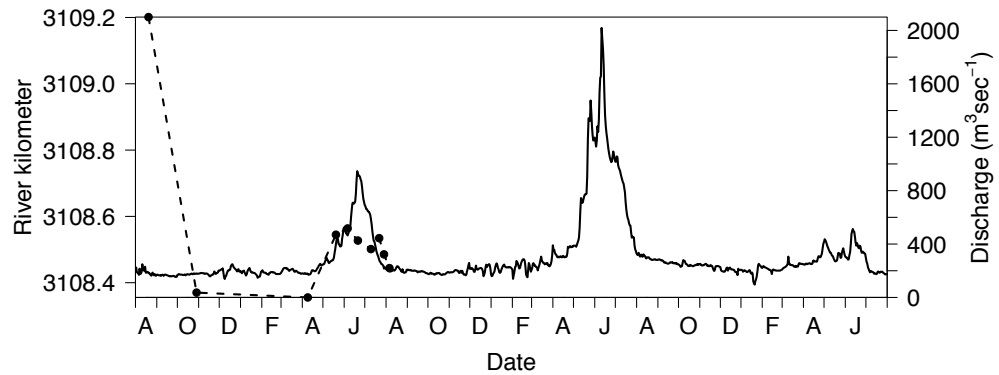


Figure B.19. Movements of spiny softshell turtle 58 (male, N=10) plotted against mean daily discharge from August 2009 through July 2012 in the Missouri River, Montana.

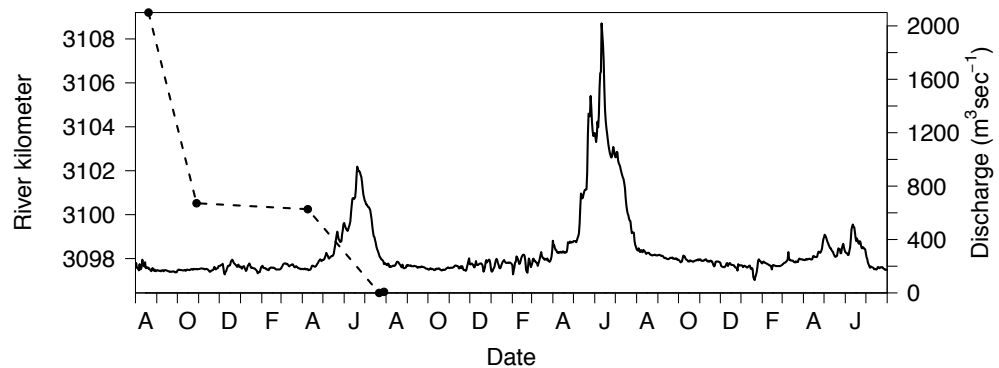


Figure B.20. Movements of spiny softshell turtle 59 (male, N=5) plotted against mean daily discharge from August 2009 through July 2012 in the Missouri River, Montana.

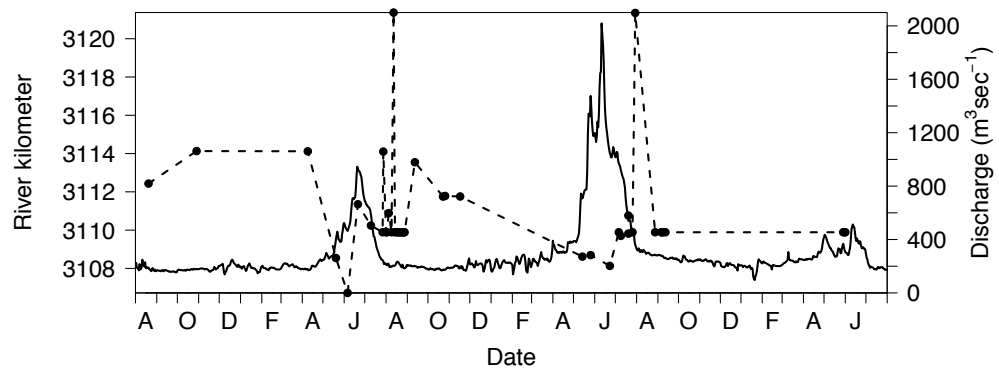


Figure B.21. Movements of spiny softshell turtle 60 (female, N=45) plotted against mean daily discharge from August 2009 through July 2012 in the Missouri River, Montana.

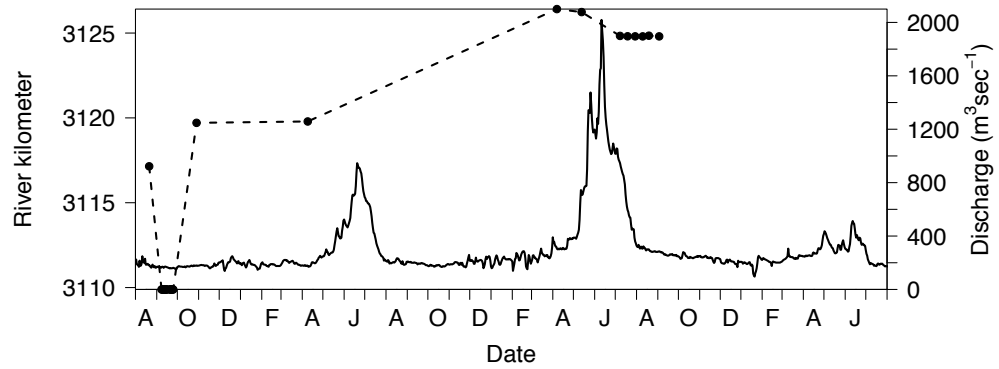


Figure B.22. Movements of spiny softshell turtle 61 (female, N=26) plotted against mean daily discharge from August 2009 through July 2012 in the Missouri River, Montana.

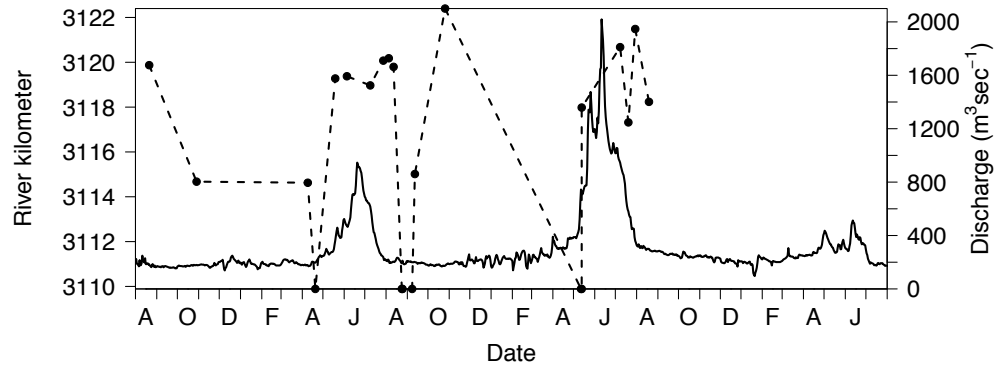


Figure B.23. Movements of spiny softshell turtle 62 (female, N=22) plotted against mean daily discharge from August 2009 through July 2012 in the Missouri River, Montana.

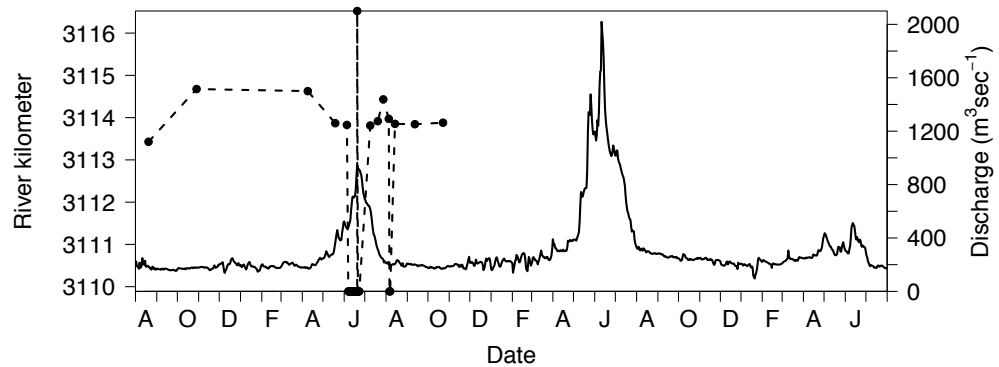


Figure B.24. Movements of spiny softshell turtle 63 (female, N=32) plotted against mean daily discharge from August 2009 through July 2012 in the Missouri River, Montana.

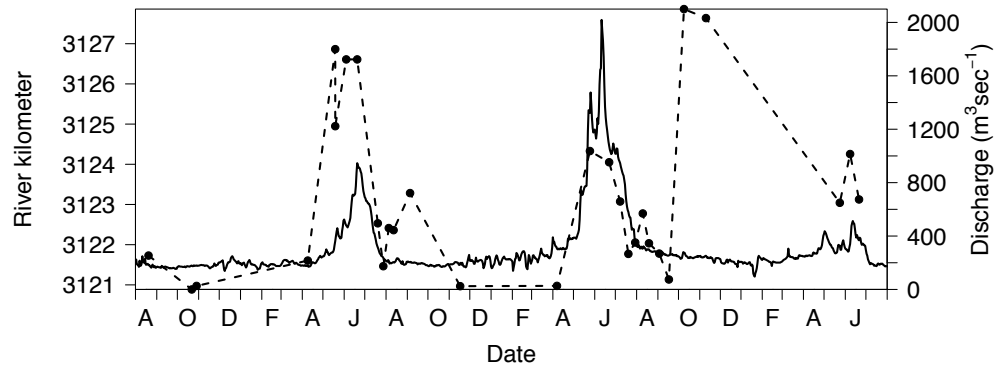


Figure B.25. Movements of spiny softshell turtle 64 (female, N=29) plotted against mean daily discharge from August 2009 through July 2012 in the Missouri River, Montana.

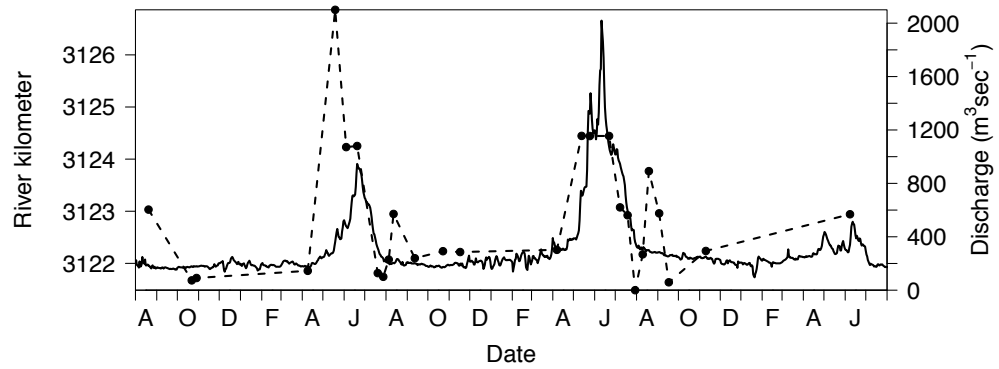


Figure B.26. Movements of spiny softshell turtle 65 (female, N=27) plotted against mean daily discharge from August 2009 through July 2012 in the Missouri River, Montana.

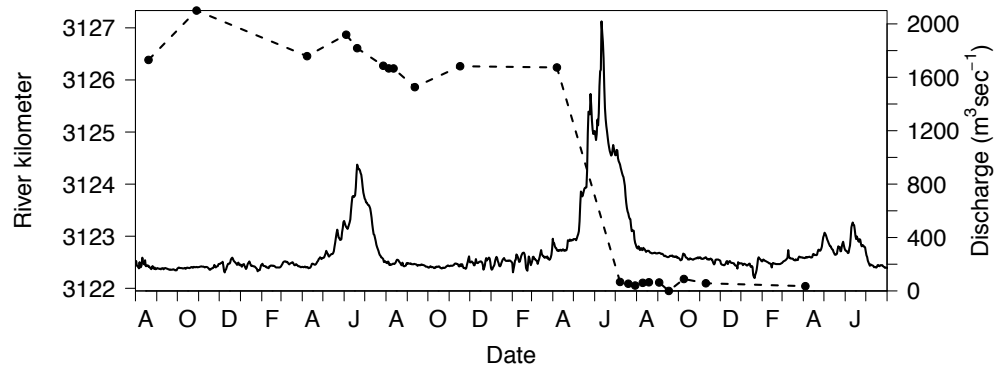


Figure B.27. Movements of spiny softshell turtle 66 (male, N=21) plotted against mean daily discharge from August 2009 through July 2012 in the Missouri River, Montana.

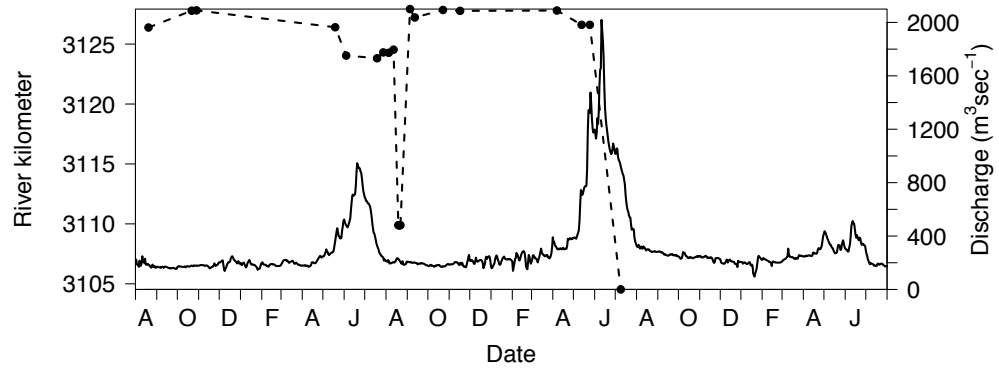


Figure B.28. Movements of spiny softshell turtle 67 (male, N=21) plotted against mean daily discharge from August 2009 through July 2012 in the Missouri River, Montana.

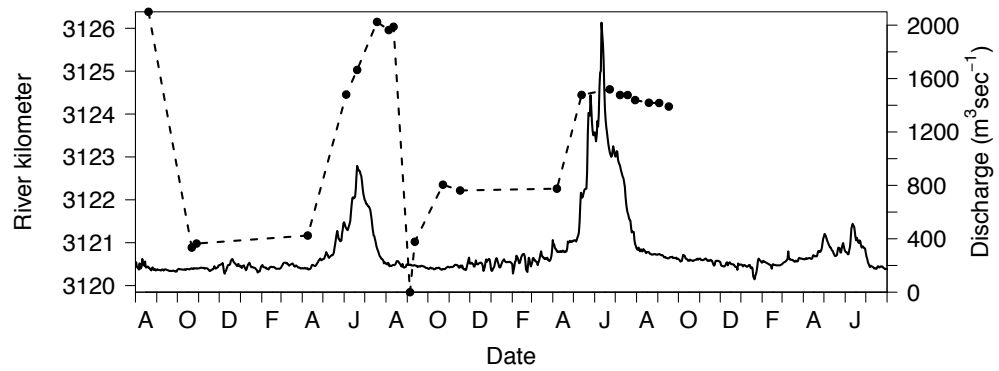


Figure B.29. Movements of spiny softshell turtle 68 (male, N=22) plotted against mean daily discharge from August 2009 through July 2012 in the Missouri River, Montana.

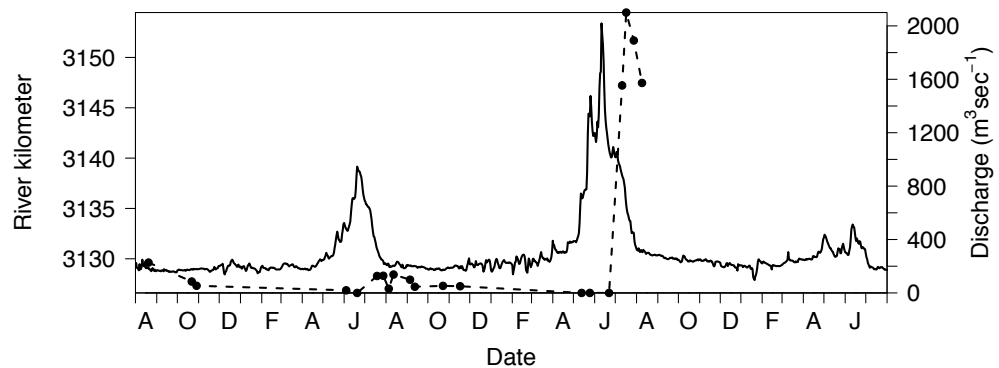


Figure B.30. Movements of spiny softshell turtle 69 (female, N=20) plotted against mean daily discharge from August 2009 through July 2012 in the Missouri River, Montana.

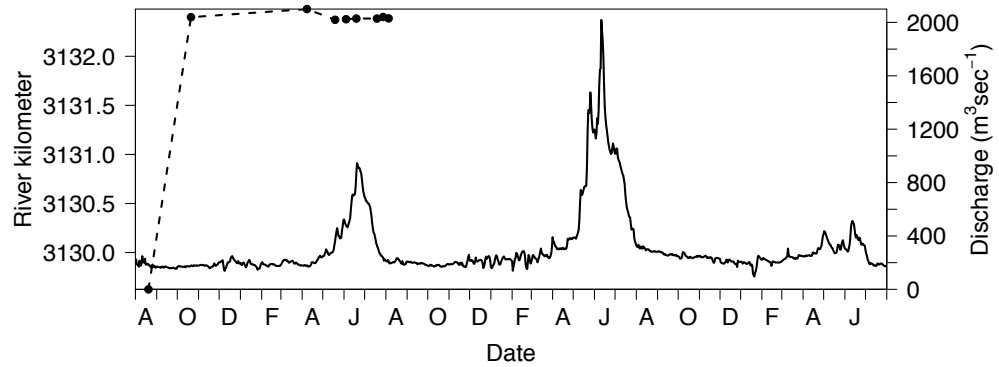


Figure B.31. Movements of spiny softshell turtle 70 (female, N=9) plotted against mean daily discharge from August 2009 through July 2012 in the Missouri River, Montana.

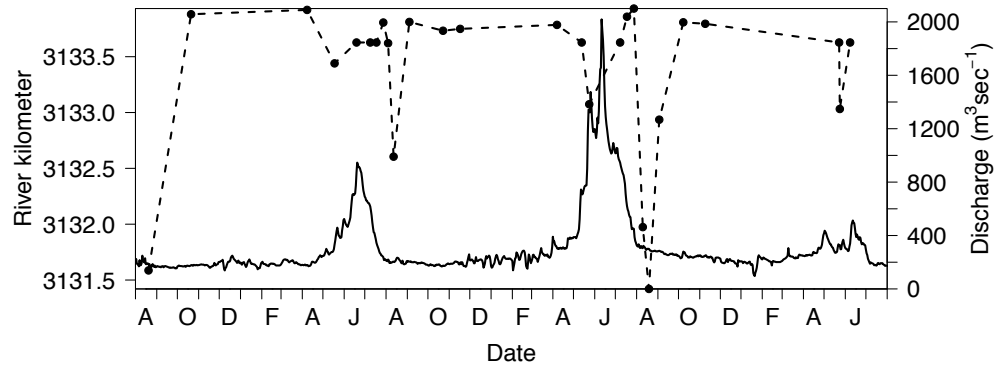


Figure B.32. Movements of spiny softshell turtle 71 (female, N=27) plotted against mean daily discharge from August 2009 through July 2012 in the Missouri River, Montana.

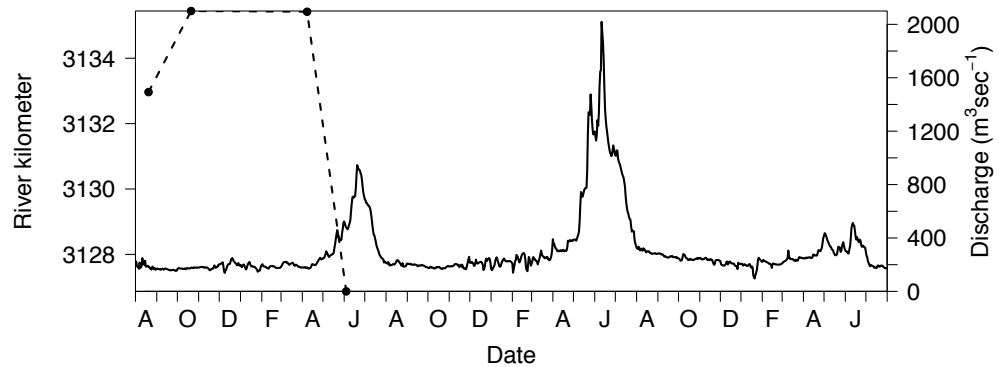


Figure B.33. Movements of spiny softshell turtle 72 (female, N=4) plotted against mean daily discharge from August 2009 through July 2012 in the Missouri River, Montana.

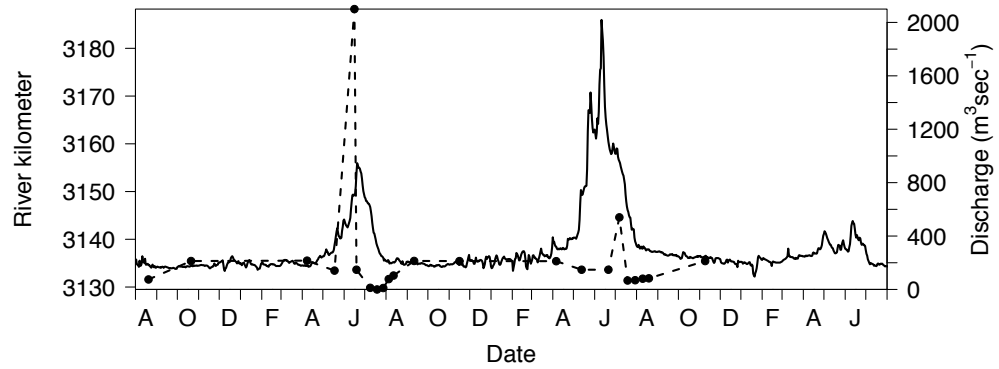


Figure B.34. Movements of spiny softshell turtle 73 (female, N=22) plotted against mean daily discharge from August 2009 through July 2012 in the Missouri River, Montana.

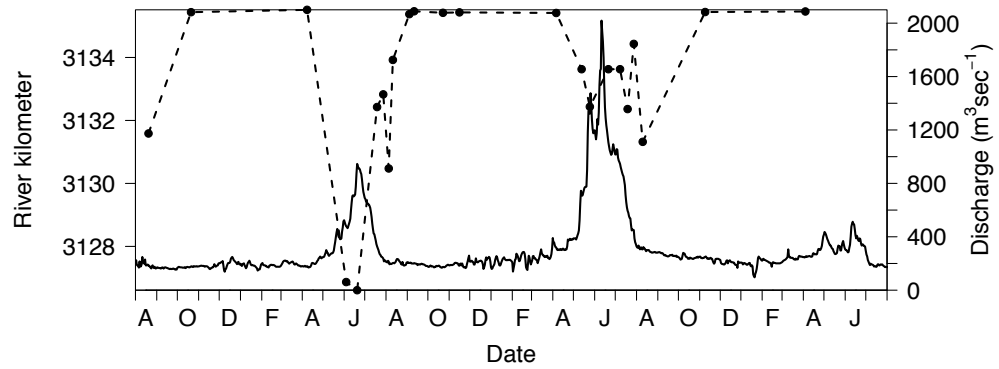


Figure B.35. Movements of spiny softshell turtle 74 (female, N=23) plotted against mean daily discharge from August 2009 through July 2012 in the Missouri River, Montana.

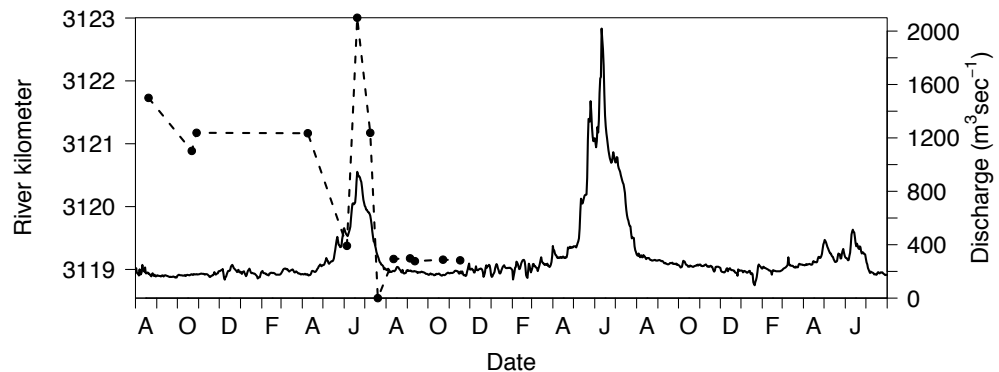


Figure B.36. Movements of spiny softshell turtle 75 (female, N=13) plotted against mean daily discharge from August 2009 through July 2012 in the Missouri River, Montana.

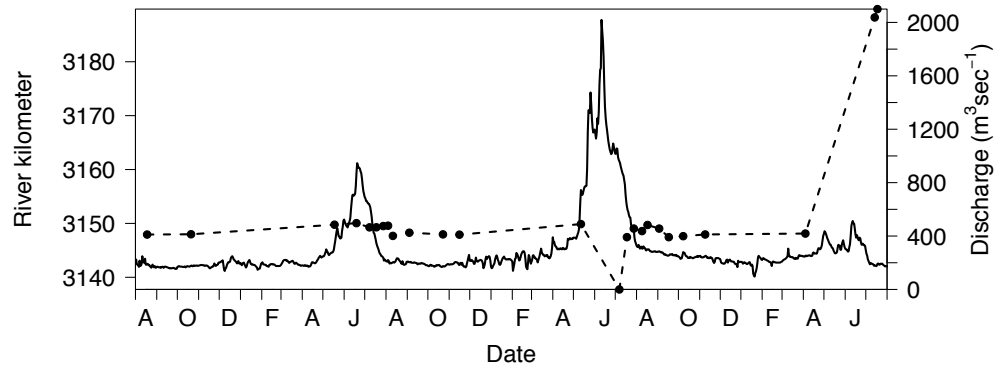


Figure B.37. Movements of spiny softshell turtle 76 (female, N=25) plotted against mean daily discharge from August 2009 through July 2012 in the Missouri River, Montana.

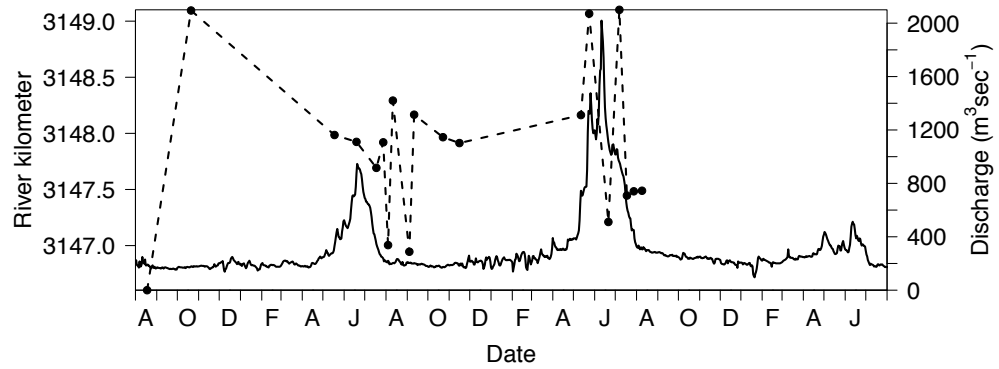


Figure B.38. Movements of spiny softshell turtle 77 (female, N=19) plotted against mean daily discharge from August 2009 through July 2012 in the Missouri River, Montana.

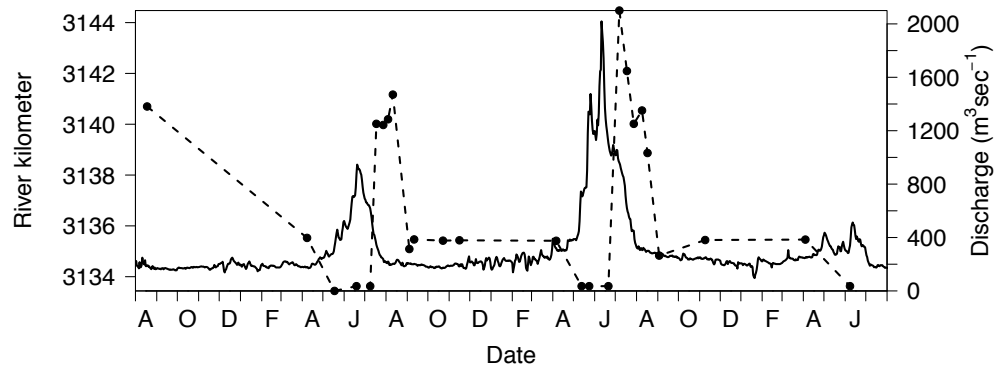


Figure B.39. Movements of spiny softshell turtle 78 (female, N=26) plotted against mean daily discharge from August 2009 through July 2012 in the Missouri River, Montana.

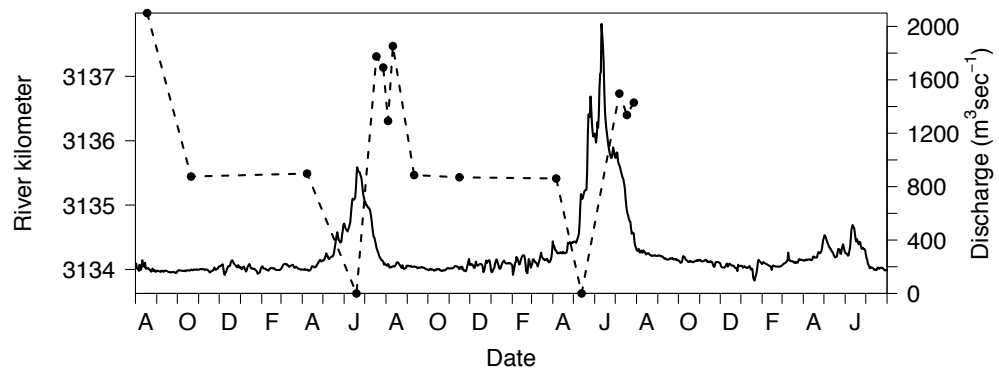


Figure B.40. Movements of spiny softshell turtle 79 (female, N=15) plotted against mean daily discharge from August 2009 through July 2012 in the Missouri River, Montana.

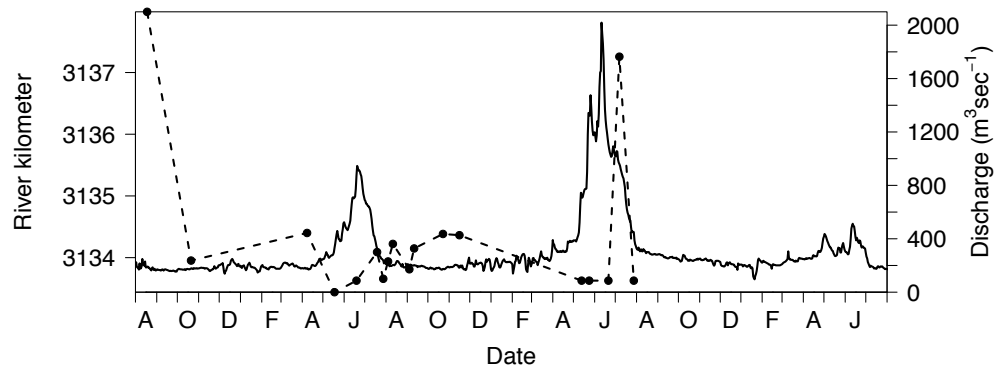


Figure B.41. Movements of spiny softshell turtle 80 (female, N=18) plotted against mean daily discharge from August 2009 through July 2012 in the Missouri River, Montana.

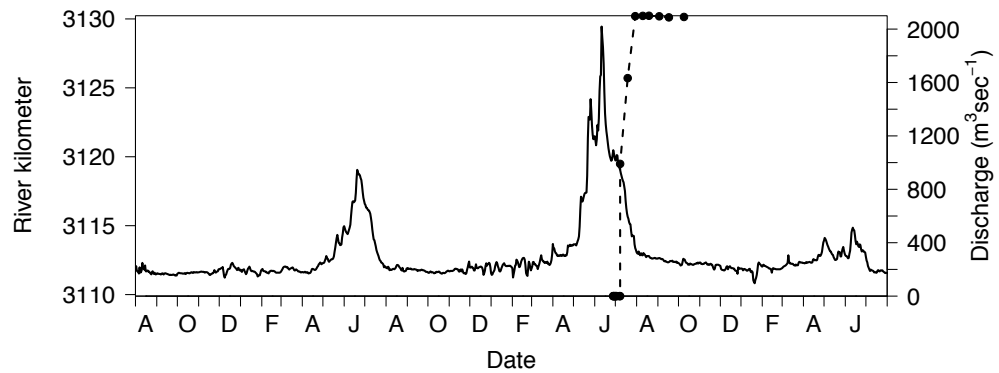


Figure B.42. Movements of spiny softshell turtle 81 (male, N=17) plotted against mean daily discharge from August 2009 through July 2012 in the Missouri River, Montana.

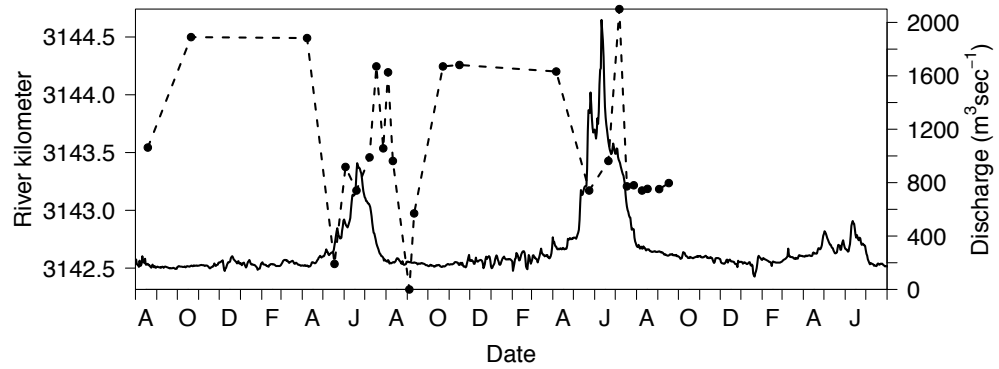


Figure B.43. Movements of spiny softshell turtle 82 (female, N=25) plotted against mean daily discharge from August 2009 through July 2012 in the Missouri River, Montana.

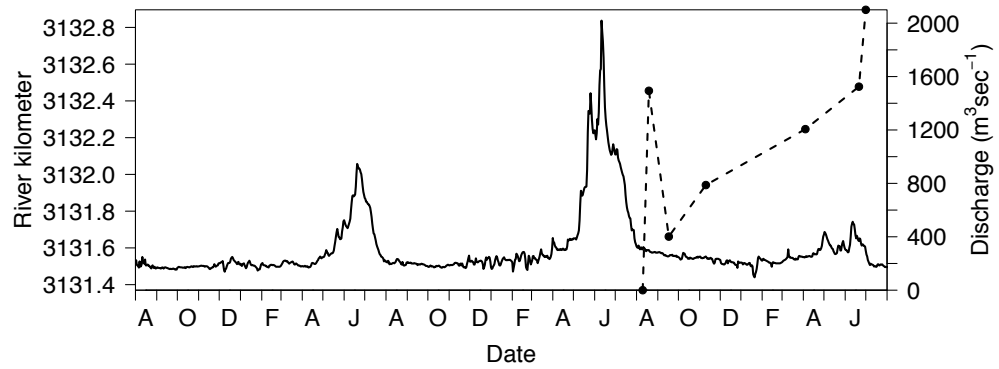


Figure B.44. Movements of spiny softshell turtle 83 (female, N=7) plotted against mean daily discharge from August 2009 through July 2012 in the Missouri River, Montana.

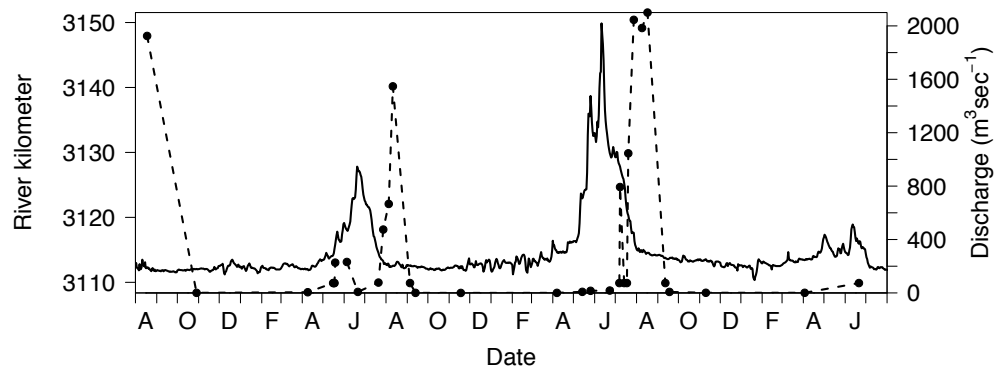


Figure B.45. Movements of spiny softshell turtle 86 (female, N=33) plotted against mean daily discharge from August 2009 through July 2012 in the Missouri River, Montana.

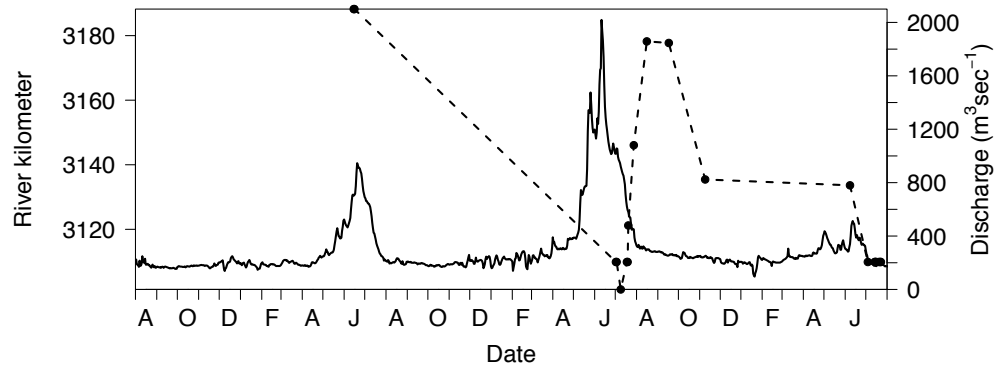


Figure B.46. Movements of spiny softshell turtle 87 (female, N=20) plotted against mean daily discharge from August 2009 through July 2012 in the Missouri River, Montana.

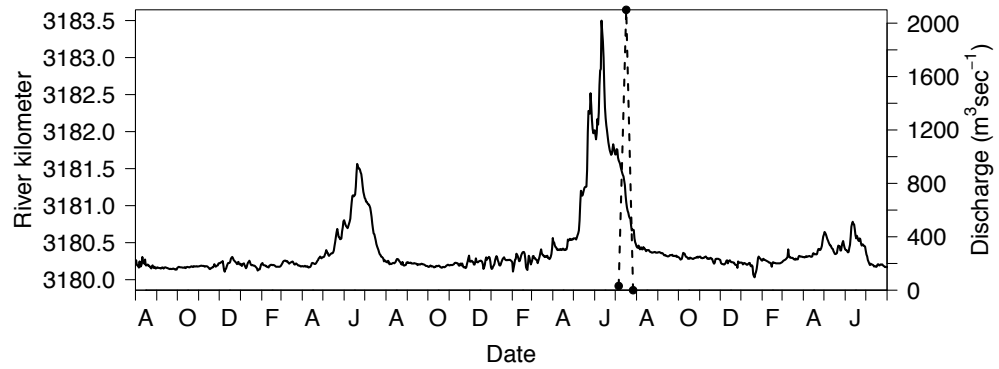


Figure B.47. Movements of spiny softshell turtle 88 (female, N=3) plotted against mean daily discharge from August 2009 through July 2012 in the Missouri River, Montana.

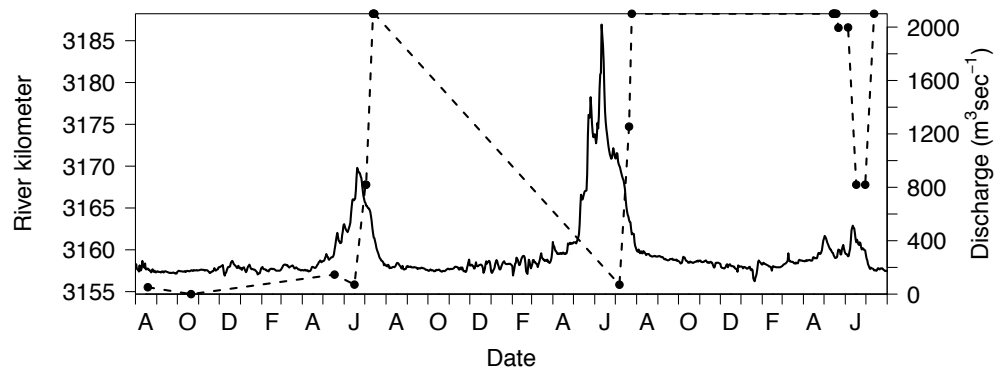


Figure B.48. Movements of spiny softshell turtle 90 (female, N=22) plotted against mean daily discharge from August 2009 through July 2012 in the Missouri River, Montana.

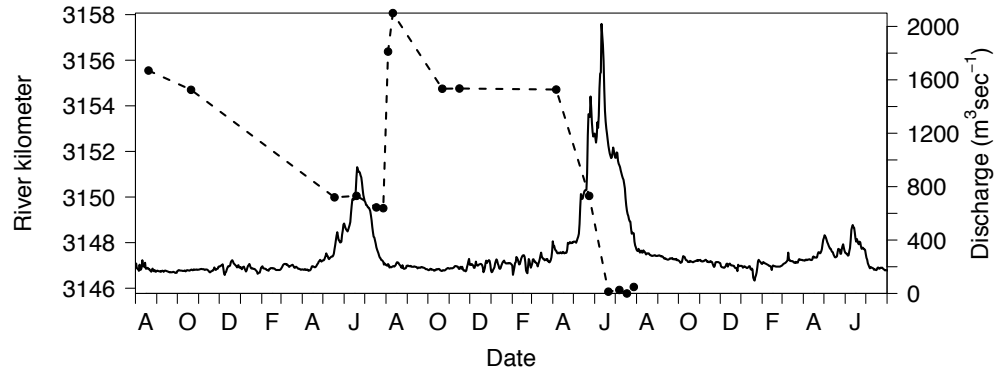


Figure 49. Movements of spiny softshell turtle 91 (female, N=16) plotted against mean daily discharge from August 2009 through July 2012 in the Missouri River, Montana.

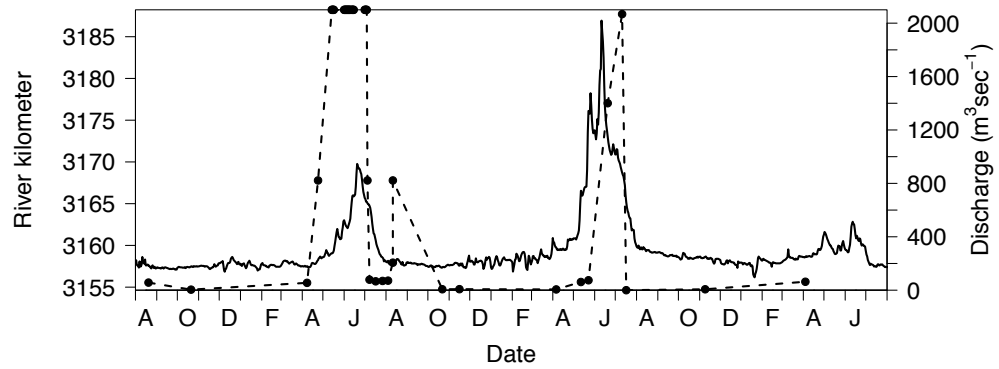


Figure B.50. Movements of spiny softshell turtle 92 (female, N=43) plotted against mean daily discharge from August 2009 through July 2012 in the Missouri River, Montana.

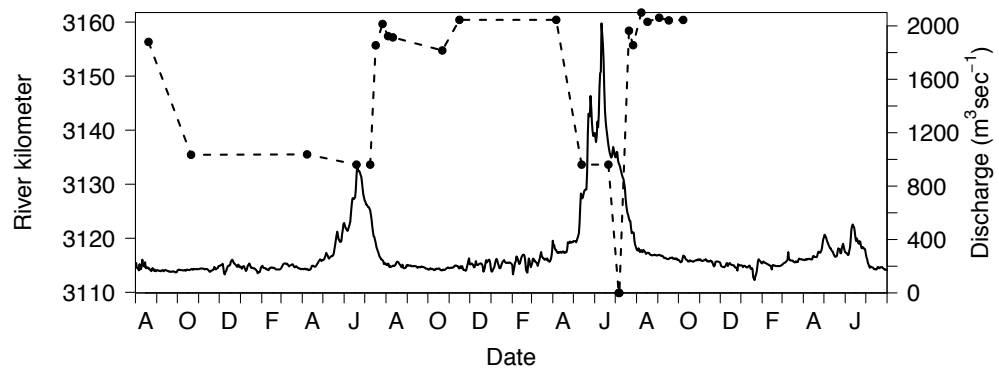


Figure B.51. Movements of spiny softshell turtle 93 (female, N=23) plotted against mean daily discharge from August 2009 through July 2012 in the Missouri River, Montana.

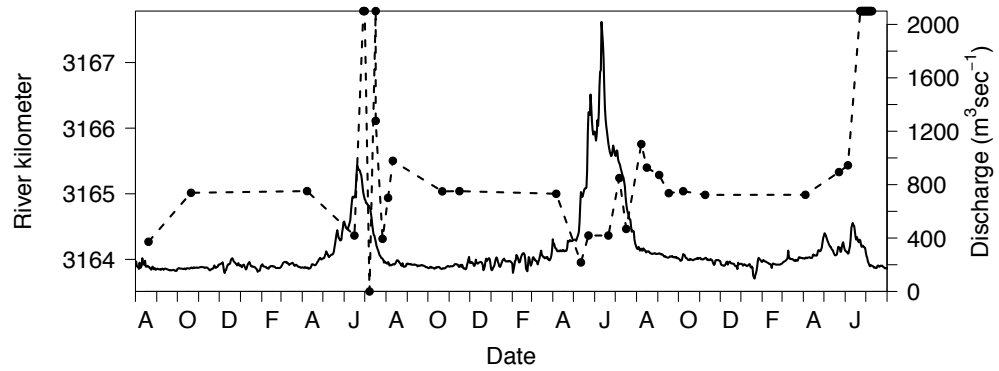


Figure B.52. Movements of spiny softshell turtle 94 (female, N=48) plotted against mean daily discharge from August 2009 through July 2012 in the Missouri River, Montana.

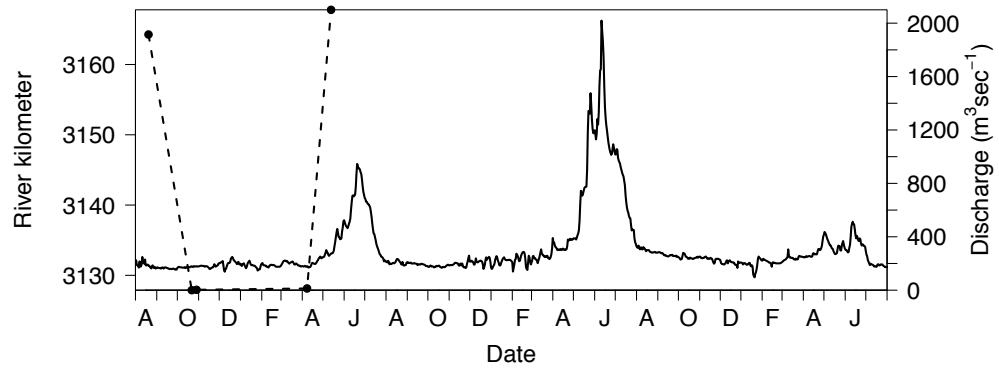


Figure B.53. Movements of spiny softshell turtle 95 (female, N=5) plotted against mean daily discharge from August 2009 through July 2012 in the Missouri River, Montana.

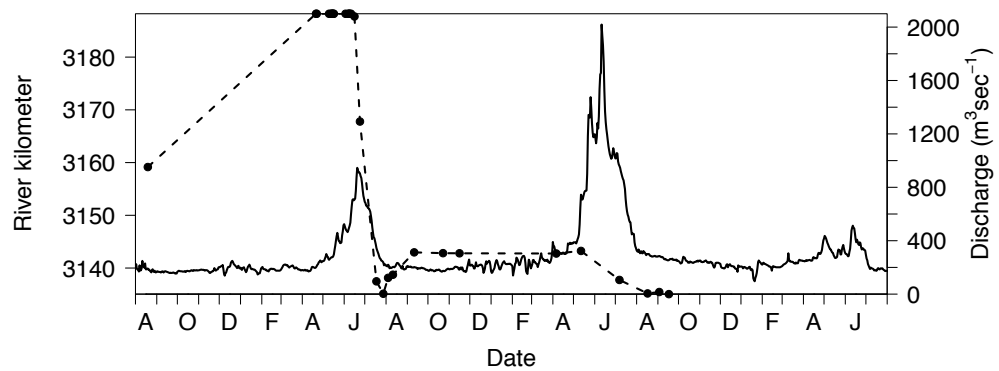


Figure B.54. Movements of spiny softshell turtle 96 (male, N=29) plotted against mean daily discharge from August 2009 through July 2012 in the Missouri River, Montana.

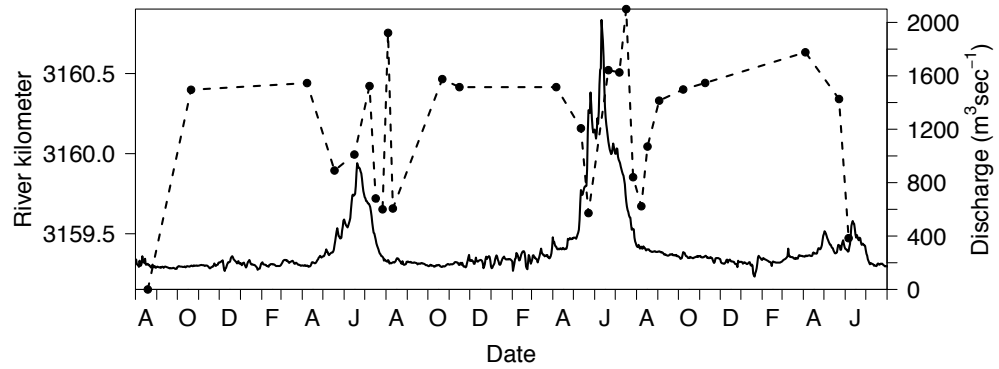


Figure B.55. Movements of spiny softshell turtle 97 (female, N=27) plotted against mean daily discharge from August 2009 through July 2012 in the Missouri River, Montana.

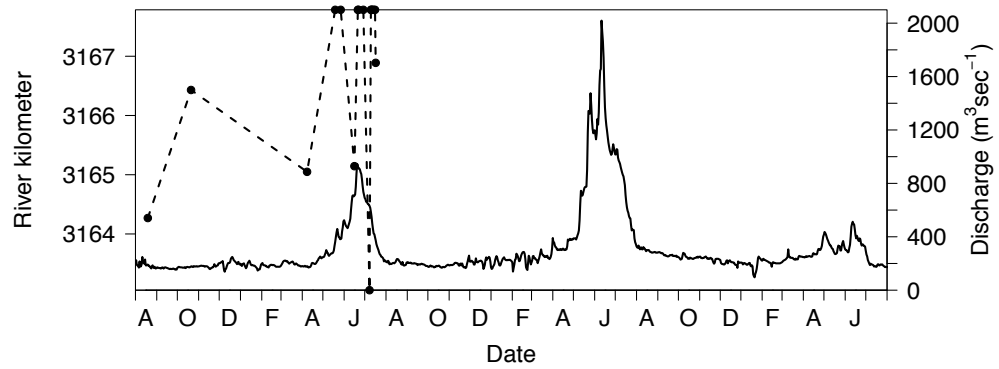


Figure B.56. Movements of spiny softshell turtle 98 (female, N=16) plotted against mean daily discharge from August 2009 through July 2012 in the Missouri River, Montana.

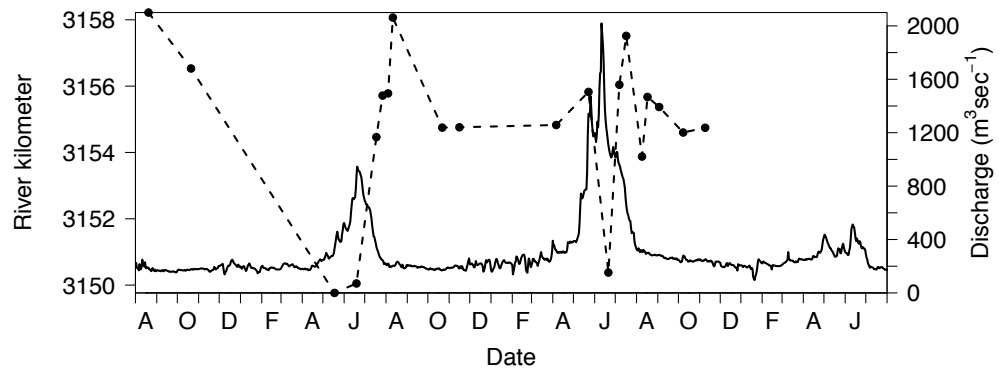


Figure B.57. Movements of spiny softshell turtle 99 (female, N=20) plotted against mean daily discharge from August 2009 through July 2012 in the Missouri River, Montana.