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Population Structure of the Spiny Softshell Turtle (*Apalone spinifera*) in Five Montana Rivers

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Abstract. – To conserve or restore riverine turtles, managers need baseline information on subpopulation structure and abundance in multiple rivers across large geographic areas. Assessing the demographics and morphological characteristics of different subpopulations can increase our understanding of how anthropogenic factors influence mortality and reproduction. We examined spiny softshell turtles (*Apalone spinifera*) in 5 rivers at the western edge of the species' range in southcentral Montana, where no commercial harvest is allowed. Over 4 yrs, we captured 637 spiny softshell turtles with fish-baited hoop traps. Our objective was to compare the subpopulation demographics in the Yellowstone River—considered one of the most intact rivers in the conterminous United States—to 3 Yellowstone River tributaries (Bighorn and Clarks Fork rivers and Pryor Creek) and the adjacent Musselshell River. Subpopulations differed significantly based on the demographic metrics we examined (e.g., mean sizes and sex ratios), and we documented limited numbers of males (4%–15%). Reproductive potential and mortality of adults among rivers appeared distinct based on juvenile and size class distribution of length-frequency histograms. This information from unharvested populations illustrates the variability in subpopulation demographics of riverine turtles.

Key Words. – demographics; river hydrology; commercial harvest; size classes; sex ratios; oil spill; Yellowstone River; Bighorn River

Anthropogenic changes in rivers, such as pollution (Luiselli and Akami 2003; Basile et al. 2011; Yu et al. 2011), temperature changes (Du and Ji 2003; Snover et al. 2015), hydroperiod (Moll and Moll 2004), and fluvial dynamics (Bodie 2001; Usuda et al. 2012), threaten turtles in lotic ecosystems. As long-lived animals, riverine turtles are particularly vulnerable to catastrophic mortality events (Moll and Moll 2004) and commercial harvest (Mali et al. 2014b; Shaffer et al. 2017). Changes in hydrology may exacerbate mortality events by impeding metapopulation connectivity or recolonization after extirpation (Dodd 1990; Plummer and Mills 2008; Reinersten et al. 2016). Environmental variables, such as 1) availability of sand and gravel bars, 2) presence of predators, and 3) water temperature and flow regimes, are primary determinants of turtle population viability (Bodie 2001; Moll and Moll 2004; Dixon 2009). The life-history strategies of riverine turtles incorporate terrestrial and aquatic habitats (Bodie 2001; Moll and Moll 2004), making them ideal ecological indicators of intact rivers with natural flow regimes (Galois et al. 2002; Usuda et al. 2012; Tornabene 2014). However, the demographics of turtles between intact and impaired rivers have rarely been examined to understand the potential influence of anthropogenic activities (Reese and Welsh 1998; Ashton et al. 2015; Snover et al. 2015). Population viability related to natural or anthropogenic factors can be assessed with demographic metrics, such as overall abundance, sex ratios, sexual size dimorphism (Lovich and Gibbons 1992), size cohorts, juvenile-to-adult ratios, growth dynamics, and mean sizes (Dodd 1990; Moll and Moll 2004; Plummer and Mills 2008; Melancon et al. 2013).

Of all habitat modifications, dams may have the most critical influence on riverine turtles by reducing connectivity, altering sediment mobilization, modifying timing and consistency of ice cover, and changing peak flow volumes, timing, and temperature (Bodie 2001; Bunn and Arthington 2002; Lenhart et al. 2013; Tornabene et al. 2017). Flow regimes and water temperature are critical for maintaining body temperature, influencing hatchling and adult growth rates, survival, nesting success, and reproduction (Sajwaj and Lang 2000; Selman 2012; Lazure et

Table 1. Characteristics of the rivers surveyed. Years river surveyed (Years); kilometers surveyed per river (km); flow in mean cubic meters per second calculated as an average from available US Geological Survey data (Flow); undammed, dammed, or off-river[a] (Dammed); low-head diversion dams (Barriers); general channel morphology (Morphology); primary terrestrial ownership classified as rural, subdivided (smaller properties 20–160 acres), or mixed category (Ownership).

River	Years	km	Flow ($m^3/s \pm$ SD)	Dammed	Barriers	Morphology	Ownership
Bighorn	2015–2018	109	81 ± 28	Yes	3	Single channel	Rural
Clarks Fork	2016, 2018	57	28 ± 7	No	4	Single channel	Subdivided
Musselshell	2015–2017	231	4 ± 3	Off-river	8	Single channel	Rural
Pryor Creek	2015–2018	107	2 ± 1	No	1	Single channel	Rural
Yellowstone	2015–2018	118	183 ± 54	Off-river	2[b]	Multichannel	Mixed

[a] Off-river impoundments operate differently on the Musselshell and Yellowstone rivers. On the Musselshell River, impoundments capture winter and spring water for release back to the river to maintain summer flows for irrigation. The off-river impoundments on the Yellowstone River capture spring runoff to sustain irrigation canal releases during the summer.
[b] Both of these are low-head diversion dams that span 1 channel of a multichannel site.

al. 2019). Turtle subpopulations in different rivers, upstream or downstream of dams or experiencing habitat fragmentation, can vary in their reproductive potential, growth rates, mortality rates, and resilience to population declines (Dodd 1990; Germano and Bury 2009; Melancon et al. 2013). Metapopulation structure and integrity are mostly unknown, mainly because studies on a large geographic scale are rarely undertaken (Burke et al. 1995; Plummer and Mills 2008).

Assessing population demographic differences in multiple aquatic systems with various anthropogenic modifications is essential for understanding population persistence threats (Moll and Moll 2004; Ashton et al. 2015; Tornabene et al. 2019). For many turtle species, poorly understood demographic structure are problematic not only for conservation but also for assessing the influence of harvesting and the effects of catastrophic events, such as large-scale floods, droughts, or oil pipeline spills (Dodd 1990; Galois and Ouellet 2007; Selman 2012; Plummer and Mills 2015). Germano and Bury (2009) recommend landscape-scale studies that examine differences in body size and growth rates of turtles to understand what factors influence demographics.

Even though state agencies are beginning to restrict commercial harvest (Luiselli et al. 2016), over 216,000,000 freshwater turtles have been exported (2002–2012) from the United States (Mali et al. 2014b). Spiny softshell turtles (*Apalone spinifera*) are among the leading commercial trade species (Moll and Moll 2004; Zimmer-Shaffer et al. 2014). Across North America, managers list spiny softshell turtles as a species of concern due to harvest rates and habitat loss (Galois et al. 2002; Moll and Moll 2004; Montana Field Guide 2016). Limited information on subpopulation status, distribution, and potential threats means that managers often set statewide rather than watershed-level regulations (Tornabene 2014; Colteaux 2017). Montana prohibits commercial harvest, but personal-use regulations (consumption or pet ownership) do not exist. Often, minimum size limits guide turtle harvest practices, resulting in demographic changes and reduced population viability because elasticity analysis has demonstrated that larger adults are the most critical demographic element (Zimmer-Schaffer et al. 2014; Colteaux 2017).

Understanding spiny softshell turtle demographics and abundance in a population with no commercial harvest in a mostly unaltered river will help managers better understand this species' natural population structure. As the longest undammed river in the conterminous United States, the Yellowstone River serves as a model of how natural spring pulses influence river morphology and the life history of many species (Reinhold et al. 2018; Tornabene et al. 2019). Identifying differences in spiny softshell turtle demographics in rivers with different flow regimes or anthropogenic impacts (dams and irrigation diversions) may help managers set harvest regulations or restore hydrology more suitable to conserving riverine species (Bodie 2001; Bunn and Arthington 2002; Tornabene et al. 2019). Therefore, our goal was to assess the overall distribution and abundance of spiny softshell turtles at the western edge of their range in south-central Montana. Once we identified distinct subpopulations in different rivers, our primary objective was to compare the demographic structure in the Yellowstone River (a highly dynamic and intact system) to 3 of its more modified tributaries and the Musselshell River (a Missouri River tributary).

METHODS

Study Area. — We surveyed spiny softshell turtles on 118 km of the Yellowstone River from approximately Billings to Custer, Montana (Table 1). In this reach, we surveyed another 271 km on 3 Yellowstone River tributaries (Bighorn River, the Clarks Fork of the Yellowstone River [hereafter, Clarks Fork River], and Pryor Creek). We surveyed 231 km on the Musselshell River (for comparative purposes), which is not part of the Yellowstone River watershed (Fig. 1). The surrounding landscape for all rivers was generally arid, with a small riparian zone along the river corridor interspersed with agriculture, ranching, and rural development. Flow dynamics included an early spring pulse (lowland melting and runoff) followed by a larger peak in late spring or early summer from melting snowpack. Historically, spring

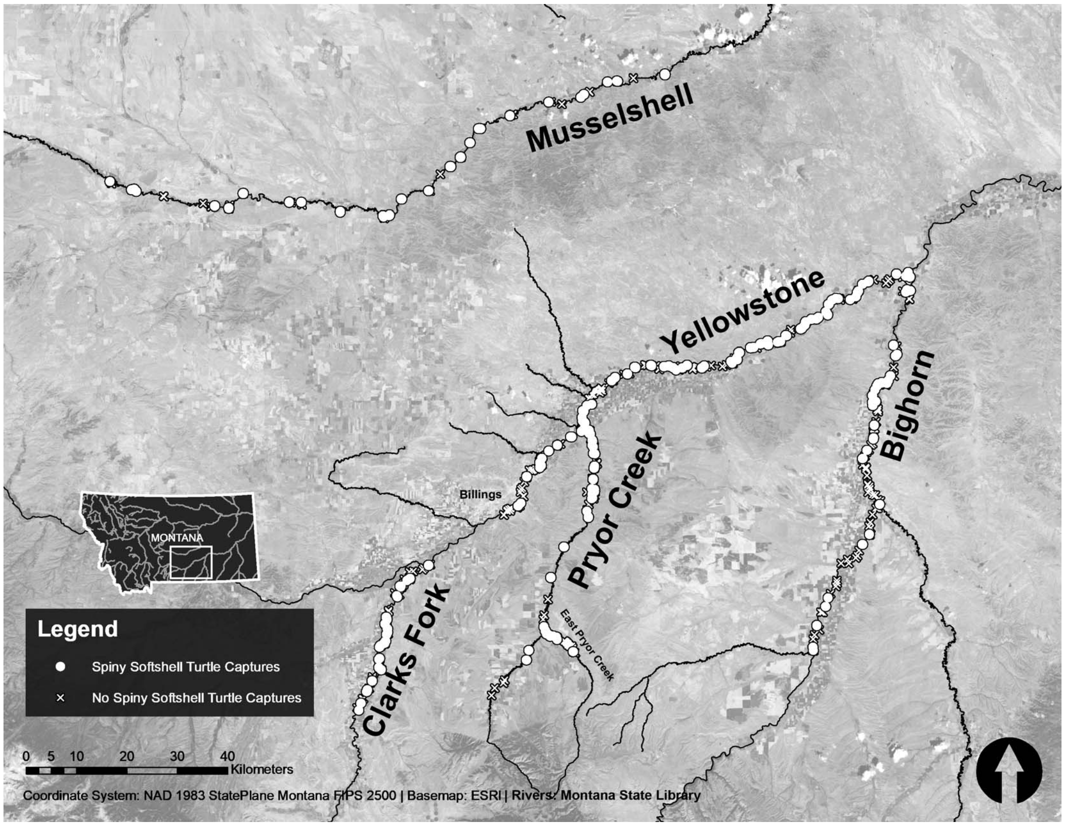

Figure 1. All trap locations (n = 582) on the 5 rivers (622 km) surveyed in south-central Montana (East Pryor Creek included as part of the Pryor Creek analysis).

pulse flows created meandering, braided channels, sand and gravel bars, and islands; however, these features have declined in some rivers because of anthropogenic modifications. The rivers had vastly different hydrologic regimes and anthropogenic influences, which we anticipated would manifest in differences in the spiny softshell turtle population structure (Table 1).

The Yellowstone River has 2 low-head diversion dams within the study area (Huntley and Waco diversion dams) and a multichannel low-head diversion dam 4.25 km below the study area. There are also 3 oil refineries (one pipeline spill in 2011), sewage effluent from Montana's largest city (Billings; over 109,000 people), and, until 2015, a coal-fired power plant. Historically, the Bighorn River was a highly dynamic system until Yellowtail and Afterbay dams were built in 1967. These dams changed this river into a system regulated for flood control, irrigation, and hydroelectricity. Pryor Creek and the Bighorn, Clarks Fork, and Musselshell rivers all have several low-head diversion dams (Table 1). Overall, the ecological integrity of all 5 rivers remains vulnerable to ongoing changes, including bank armoring to prevent erosion (Reinhold et al. 2018), irrigation modifications, road building, and development in the floodplain (Bodie 2001; Lenhart et al. 2013; Table 1).

Sampling Techniques. — We trapped spiny softshell turtles with baited hoop traps in June, July, and August 2015–2018. We placed traps approximately 2 km apart for rivers that were accessed by boat (Yellowstone and Bighorn rivers) and in pairs roughly 100–200 m apart (in fast and slow water) every 3–8 km when accessed by foot (Pryor Creek and Musselshell and Clarks Fork rivers). Due to various factors (limited crews, access to boats, high water, and flooding), we did not sample all rivers simultaneously or every year. We sampled the Yellowstone and Bighorn rivers and Pryor Creek in 2015–2018, the Clarks Fork River in 2016 and 2018, and the Musselshell River in 2015–2017. Sampling months occurred as follows: Bighorn River (August), Clarks Fork River (July and August), Yellowstone River (July and August), and the Musselshell River and Pryor Creek (June–August). Preferred trapping locations were side channels or tributary confluences and inside bends or point bars. We used single-throated, single-opening hoop nets (90-cm diameter with 2.5- or 7.5-cm^2 mesh) baited with local fishes (usually family Catostomidae). We set traps to allow turtles to surface and with the openings facing downstream (Plummer and Mills 1997; Mali et al. 2014a).

Trap set duration was generally 2 d (range, 0.8–5.1 d), with traps checked for captures after 2 nights. Each turtle was placed inside a bag and weighed using a hanging digital scale to 0.01 kg and measured with a flexible millimeter tape to record curved carapace length (CCL), curved carapace width, and plastron length (2017–2018). We used multiple characteristics to distinguish males (longer and thicker tail, cloacal position beyond the carapace edge, and rough texture and ocelli pattern on the carapace) and are confident sexes were identified accurately. To document potential tag loss, we tagged each turtle with an external and internal tag. Internal 8- or 12.5-mm passive integrated transponder (PIT) tags (Biomark) were implanted in the right inguinal area of loose skin using a Biomark Implanter (McDonald and Dutton 1996; Buhlmann and Tuberville 1998). External 2.5-cm (2016–2018) and 4-cm (2015) Monel tags (National Band and Tag Company) containing a unique identifying number, as well as contact information, were applied through the back-right edge of the carapace between the hind limb and tail.

Data Analysis. — To assess spiny softshell turtle movements, we compared the original capture location to recaptures and then used ArcGIS to calculate total river kilometers moved (Environmental Systems Research Institute 2019). We assessed mass (kg) and CCL (mm) data separately for males and females because of sexual dimorphism in this species (Ernst and Lovich 2009). We calculated a size dimorphism index (SDI; Lovich and Gibbons 1992) for each river from the mean CCL of the larger sex divided by the mean CCL of the smaller sex. To assess minimum size at sexual maturity, we used reported plastron sizes for sexual maturity (180 and 80 mm for females and males, respectively; Webb 1962; Robinson and Murphy 1978; Plummer and Mills 2015). We used these plastron lengths to calculate CCL at sexual maturity. Based on a subset of our data with both plastron and CCL measurements, we developed conversion factors (plastron length to CCL) of 1.42 for females and 1.50 for males. The conversion resulted in a CCL $\geq$ 256 mm and $\geq$ 120 mm as the cutoff for sexually mature (hereafter adult) females and males, respectively. This method does not account for the potential variability of minimum reproductive size among subpopulations in different regions. We used 1-way analysis of variance to determine if mean CCL differed among rivers; if $p < 0.05$, we examined all pairwise comparisons with Tukey's honest significance difference (HSD) post hoc tests. To assess female CCL distribution, we grouped individuals in 10-mm increment size classes and plotted length-frequency histograms by river.

We examined relationships among mass and CCL, sex, and river with multiple linear regression. We used an initial model including interactions among all independent variables and a backward elimination procedure using extra-sum-of-squares F-statistic to select an inferential model. We removed coefficients with the smallest F-statistic in a stepwise fashion and an F-statistic of 4 or greater for the retention of variables to select an inferential model (Ramsey and Schafer 2012). The strength of statistical evidence for covariates within the inferential model was examined with extra-sum-of-squares F-tests by comparing the inferential model to the model without the covariate of interest (Ramsey and Schafer 2012). Due to a lack of independence, we did not include recapture data in the analysis of mass or length data.

We calculated catch per unit effort (CPUE) to estimate relative abundance in each river. CPUE equals the total number of captures per river (catch) divided by the total number of trap days (effort). For CPUE calculations, we excluded hand captures ($n = 2$) and traps that were ineffective due to holes created by mammals, such as raccoons (*Procyon lotor*) and mink (*Neovison vison*). Additionally, we examined the relative frequency of zero captures, a less biased index that is more responsive to changes in abundance than CPUE in marine fisheries (Bannerot and Austin 1983).

We used chi-square analyses to compare the percentages of males to females and juvenile females to adult females among rivers. To assess assumptions of equal variance, normality, and linearity, we used boxplots, histograms, residual versus fitted plots, normal probability plots, and plots of response variables versus continuous explanatory variables. All analyses were conducted in R 3.5.0 (R Core Team 2018) and the Real Statistics Resource Pack software 6.8 (Zaiontz 2020) with $\alpha = 0.05$.

RESULTS

A total of 1167 trap days with 582 different trap sites resulted in 637 captures of spiny softshell turtles, 39 snapping turtles (*Chelydra serpentina*), and 12 painted turtles (*Chrysemys picta*). We did not conduct additional analyses of snapping and painted turtle captures. Of the total number of spiny softshell turtles captured, 570 were new individuals, 67 were recaptures, 506 were females, 60 were males, and 4 were small unsexed juveniles. We captured the 4 juveniles (based on our size cutoff) in the Musselshell River during the first month of sampling in 2015 (Table 2). Of the recaptured individuals, only 2 females moved between rivers (individual 1 moved 39.12 km, and individual 2 moved 3.96 km), both moving from the Yellowstone River into Pryor Creek. No turtle movement was documented between the Clarks Fork and Bighorn River tributaries and the Yellowstone River. The mean distance moved for all recaptured females was 4.73 km (standard deviation [SD] = 8.74 km), and no males were recaptured. We documented 6 external tags lost (9%) on recaptured turtles. No PIT tags were lost, and all external tag losses occurred with the larger tags, which were used only in 2015.

There were more females than males in each river ($\chi^2_4 = 9.40$, $p = 0.05$). Overall, there were 11% males and 89% females, with the Yellowstone River having the highest percentage of males (15%) and Pryor Creek the lowest (4%). The overall SDI based on CCL was 1.93 (Table 2).

Thirty-five females were classified as juveniles using the 256-mm CCL cutoff for categorizing sexual maturity. The percentages of juvenile females to adult females differed among rivers ($\chi^2_4 = 11.86$, $p = 0.02$). The

Table 2. Number of captured individuals (n; excluding recaptures); size dimorphism index (SDI) calculated from mean curved carapace length (CCL) females/mean CCL males; frequency of males, females, and juvenile females classified by length ($\leq$ 256 mm); and mass, CCL, and curved carapace width (CCW) presented as the mean $\pm$ SD with the range in parentheses.[a]

River	n	SDI	Percent males	Percent females	Percent juvenile females	Mass (kg) Female	Mass (kg) Male	CCL (mm) Female	CCL (mm) Male	CCW (mm) Female	CCW (mm) Male
Bighorn	78	1.99	9	91	1	4.88 ± 1.26 (0.24–7.06)	0.69 ± 0.20 (0.49–0.98)	395 ± 45 (140–464)	198 ± 14 (183–219)	309 ± 33 (122–349)	170 ± 13 (154–193)
Clarks Fork	47	2.11	6	94	4	4.62 ± 1.47 (0.16–6.64)	0.54 ± 0.19 (0.34–0.72)	384 ± 66 (128–449)	182 ± 20 (159–196)	298 ± 48 (112–346)	157 ± 17 (138–167)
Musselshell	128	1.84	10	87	12	2.60 ± 1.07 (0.16–4.66)	0.45 ± 0.12 (0.27–0.63)	313 ± 56 (124–397)	170 ± 16 (145–190)	252 ± 41 (113–310)	152 ± 15 (130–173)
Pryor Creek	84	2.19	4	96	7	3.19 ± 1.23 (0.16–5.77)	0.36 ± 0.13 (0.23–0.49)	337 ± 64 (118–439)	154 ± 24 (130–177)	267 ± 47 (102–331)	135 ± 12 (123–147)
Yellowstone	233	1.95	15	85	5	4.32 ± 1.64 (0.17–8.39)	0.63 ± 0.12 (0.41–0.82)	379 ± 62 (129–504)	194 ± 12 (169–220)	301 ± 46 (116–376)	167 ± 9 (150–188)

[a] Juvenile females included in presented mass, CCL, and CCW.

percentage of juvenile females classified by length was highest in the Musselshell River (12%) and lowest in the Bighorn River (1%; Table 2). The mean CCL for juvenile females was 186 mm (SD = 49.17), and the mean mass was 0.59 kg (SD = 0.37). All males captured were larger than the cutoff calculated for adults, 120 mm (all $\geq$ 130 mm).

The representation of size class frequency (10-mm increments) is demonstrated in the length-frequency histogram by river (Fig. 2). Most of the females with the largest CCL were captured in the Yellowstone, Clarks Fork, and Bighorn rivers. The Yellowstone River had the most size classes (n = 32) distributed more evenly than any other river. There were fewer size classes for the Bighorn (n = 16) and Clarks Fork (n = 13) rivers, with few small females and juveniles recorded. The size classes for the Musselshell River (n = 25) and Pryor Creek (n = 20) included more small size classes but few large turtles over 400 mm. The Musselshell River had the most (n = 11) juvenile size classes ($\leq$ 256 mm), followed by the Yellowstone River (Fig. 2).

Mean CCL of adult females ($F_{4,466}$ = 53.8, $p < 0.0001$) and adult males ($F_{4,55}$ = 12.5, $p < 0.0001$) differed among rivers. Tukey HSD post hoc tests indicated that adult female CCL differed between all pairs of rivers except the Yellowstone, Clarks Fork, and Bighorn rivers ($p \geq 0.42$; Table 3), with the largest difference between the Musselshell and Bighorn rivers. Maximum CCL for the largest female in the Yellowstone River was 504 mm, which was similar in length to the largest female (464 mm) in the Bighorn River (Table 2) but 13%–21% larger than the largest females in the Musselshell and Clarks

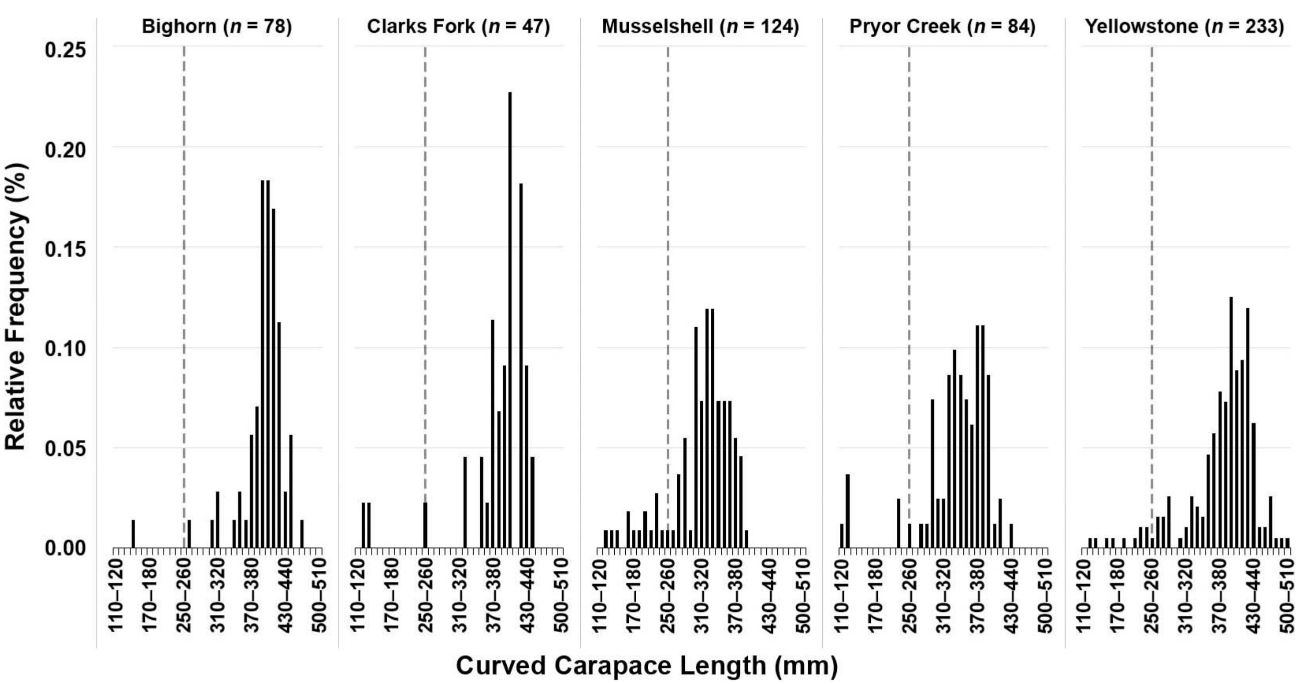

Figure 2. Relative frequency histogram (10-mm intervals) for female spiny softshell turtle curved carapace length for each of the 5 rivers. Vertical dashed bars indicate the 256-mm cutoff for classifying juvenile vs. adult females.

Table 3. Adult CCL (mm) post hoc Tukey honest significance difference pairwise comparisons for each river (females and males).

River	*n*	Mean	SD	Bighorn	Clarks Fork	Musselshell	Pryor Creek	Yellowstone
Females[a]								
Bighorn	70	398.3	33.49		1	< 0.0001	< 0.0001	0.42
Clarks Fork	42	395.9	36.72			< 0.0001	< 0.0001	0.85
Musselshell	96	331.7	30.04				0.008	< 0.0001
Pryor Creek	75	351.5	36.55					< 0.0001
Yellowstone	188	389.3	44.24					
Males								
Bighorn	7	198.4	13.75		0.44	0.0005	0.0002	0.94
Clarks Fork	3	182.0	20.07			0.65	0.12	0.61
Musselshell	13	169.9	16.14				0.42	< 0.0001
Pryor Creek	3	154.3	23.54					0.0001
Yellowstone	34	194.0	11.63					

[a] Females $\leq$ 256 mm excluded from analysis; classified as juveniles.

Fork rivers and Pryor Creek. Post hoc tests indicated that mean CCL for adult males differed between Pryor Creek and the Yellowstone and Bighorn rivers and between the Musselshell and the Yellowstone and Bighorn rivers ($p < 0.0001$; Table 3). The largest difference in mean CCL was between Pryor Creek and the Bighorn River. Mean body mass also differed among rivers for adult females ($F_{4,466} = 50.6$, $p < 0.0001$) and adult males ($F_{4,55} = 7.3$, $p < 0.0001$; Table 2). The heaviest female from the Yellowstone River weighed 8.39 kg, which was 19%–80% heavier than the heaviest females captured in the Musselshell, Clarks Fork, and Bighorn rivers and Pryor Creek. The largest difference in body mass was between the Yellowstone and the Musselshell rivers (Table 2).

We observed an exponential relationship between mass and CCL, both of which were natural log-transformed (ln) prior to multiple regression to meet assumptions of linearity. Turtles without sex determination ($n = 4$) were not included in the mass–length analysis. Relations among mass and CCL, sex, and river (i.e., 3-way interaction; $F_{4,545} = 1.6$, $p = 0.17$), length and sex ($F_{1,549} = 0.5$, $p = 0.49$), and river and sex ($F_{4,550} = 1.1$, $p = 0.37$) were not supported and were removed from the inferential model. There was strong evidence for a relationship between mass and sex ($F_{1,554} = 19.4$, $p < 0.0001$), and the relation between mass and length depended on the river (2-way interaction; $F_{9,554} = 2560.0$, $p < 0.0001$; Table 4). The significance of the sex coefficient indicated that males are 1.09 times heavier (95% confidence interval: 1.05–1.14) at a given length than females. There was strong evidence that turtles in Pryor Creek had a different ($p < 0.0001$) mass $\times$ length relationship than observed in all other rivers (Fig. 3). There was no evidence that the relationship between mass and length differed among the Yellowstone, Bighorn, Clarks Fork, and Musselshell rivers ($p \geq 0.29$).

The CPUE values of the 2 rivers surveyed by boat (Yellowstone = 0.68 and Bighorn = 0.37) were substantially different. Of the other 3 rivers surveyed by foot, the Musselshell River (CPUE = 0.66) had the highest CPUE (Table 5). The percentage of trap days without captures was highest for the Bighorn River (67%) and lowest for Pryor Creek (42%). The 3 highest numbers of captures per trapping event occurred on the Yellowstone River, with 12, 10, and 9 turtles captured, respectively.

DISCUSSION

Other researchers have examined Trionychidae or spiny softshell turtle population demographics in isolated systems (Barko and Briggler 2006; Munscher et al. 2015; Plummer and Mills 2015), and Tornabene et al. (2019) examined spiny softshell turtle habitat use in 2 large rivers in Montana. However, most of these studies had small sample sizes over a limited geographic range. We found significant demographic differences in subpopulations of spiny softshell turtles in south-central Montana when examined at a large scale across multiple rivers. We

Table 4. Regression coefficients (β), standard error (SE), and *p*-values for the inferential regression model examining relationships among the natural log of mass and the natural log (ln) of curved carapace length (CCL), sex, and river. Females are the reference level for sex, and Pryor Creek is the reference level for river (i.e., coefficients represent differences in comparison to females and Pryor Creek).

Parameter	β	SE	*p*	Parameter	β	SE	*p*
Intercept	−14.65	0.22	< 0.0001	Bighorn	−1.46	0.36	< 0.0001
ln(CCL)	2.72	0.04	< 0.0001	Musselshell × ln(CCL)	0.22	0.05	< 0.0001
Male	0.09	0.02	< 0.0001	Yellowstone × ln(CCL)	0.20	0.05	< 0.0001
Musselshell	−1.25	0.29	< 0.0001	Clarks Fork × ln(CCL)	0.26	0.06	< 0.0001
Yellowstone	−1.19	0.36	< 0.0001	Bighorn × ln(CCL)	0.25	0.06	< 0.0001
Clarks Fork	−1.50	0.36	< 0.0001				

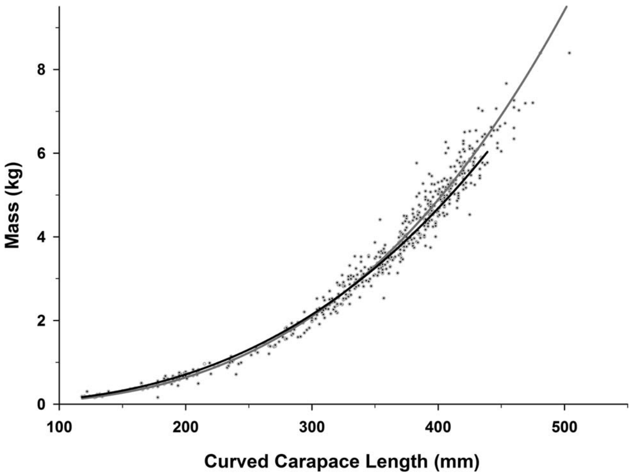

Figure 3. Relationship and fitted regression curve between mass (kg) and curved carapace length (mm) for female turtles. The gray line is representative of the mass–length relationship for the Musselshell, Yellowstone, Bighorn, and Clarks Fork rivers (n = 486), whereas the black line is representative of Pryor Creek (n = 84).

suspect that anthropogenic modifications, such as dams, influence the observed subpopulation differences. However, we did not assess this relationship beyond our knowledge of which rivers were dammed and undammed and the number of low-head diversion dams.

Subpopulation Connectivity Between Rivers. — Home range sizes for spiny softshell turtles differ considerably across studies and aquatic systems (Graham and Graham 1997; Plummer and Mills 1997; Galois et al. 2002). A lack of suitable habitat may result in increased turtle movements (Galois et al. 2002; Tornabene et al. 2019). Based on our recapture data, both the Bighorn and the Clarks Fork river subpopulations appear isolated from the Yellowstone River, although we suspect that some exchange occurs. Both of these rivers have multiple low-head diversion dams (1 within 6 km of the Yellowstone and Bighorn confluence), which could explain the degree of subpopulation isolation.

Tornabene et al. (2019), using radiotelemetry, also noted little movement from the Yellowstone River to tributaries. A lack of connectivity related to habitat fragmentation, such as dams, can limit the rescue effect from neighboring subpopulations, eventually affecting population resilience and persistence (Dodd 1990). Interestingly, we recorded movements of 2 turtles from the Yellowstone River into lower Pryor Creek. After flood damage in 2011, a 2.5-m-high low-head diversion dam (built in 1906) washed out at the confluence with the Yellowstone River. We documented the first turtle passage in 2015 after the Yellowstone Conservation District rebuilt the site to allow fish passage.

CPUE Comparisons. — The CPUE metric is often used in fisheries and sometimes with freshwater turtles (e.g., Melancon et al. 2013) as a relative indicator of abundance. However, variables such as calculation methods, exact survey areas, and flow rates can complicate comparisons. Our CPUE values for the Yellowstone River

Table 5. Number of captures, trap days, catch per unit effort (CPUE) = captures/trap days, and percentage of trap days (mean duration of trap sets = 2.0 days) without captures.

River	Captures	Trap days	CPUE	% Trap days without captures
Bighorn	82	222.7	0.37	67
Clarks Fork	52	146.5	0.36	56
Musselshell	145	219.5	0.66	50
Pryor Creek	101	200.3	0.50	42
Yellowstone	257	378.2	0.68	49

(0.68) offer the only possible historical comparison (Dood et al. 2009; CPUE = 0.40) on a river reach that included similar study areas. These CPUE numbers provide a baseline of turtle abundance for assessing future catastrophic events, such as oil spills (2 on the Yellowstone River in the past decade), or habitat modifications, such as low-head diversion dams.

Sexual Size Dimorphism and Sex Ratios. — The SDI values we report are similar to the value Plummer and Mills (2015) reported in Arkansas (SDI = 2.13). With such dimorphism, it is not surprising that female aggression occurs, resulting in competitive displacement and trap avoidance by males (Underwood et al. 2013). We attributed 2 male mortality incidents (in traps) to females with evidence of multiple bite marks on males. The rougher carapace of male spiny softshell turtles may serve as protection when mating, as with skin thickness in elasmobranchs (Kajiura et al. 2000).

Spiny softshell turtles have genetic sex determination, and equal sex ratios of hatchlings have been documented (Vogt and Bull 1982). Reported male-to-female ratios vary widely, but none approached the degree of bias we documented (1.00:1, Vogt and Bull 1982; 1.00:1, Graham and Graham 1997; 2.83:1, Rizkalla and Swihart 2006; 0.49:1, Barko and Briggler 2006; 2.00–2.50:1, Plummer and Mills 2008; 1.91:1, Mahoney and Lindeman 2016). Potential factors for skewed sex ratios include sampling bias of certain thermal conditions (Feltz and Tamplin 2007; Tornabene 2014), niche partitioning (Webb 1962; Galois et al. 2002), capture techniques (Gibbons 1983; Swannack and Rose 2003; Munscher et al. 2015), and endocrine-disrupting chemicals (Willingham 2005; Basile et al. 2011; Mizoguchi and Valenzuela 2016). Due to the distinct SDI, dietary niche separation and ontogenetic dietary shifts may bias catch rates during specific periods (Congdon et al. 1992; Mahoney and Lindeman 2016).

Generally, spiny softshell turtles are considered thermoconformers with some ability to thermoregulate by basking (Plummer et al. 2005). We suspect that thermal factors influence male habitat use and distribution. Temperature profiles of dammed and undammed rivers may result in range edges unsuitable for male occupancy (Plummer and Burnley 1997; Feltz and Tamplin 2007). Plummer et al. (2005) recorded body temperatures (12.8°C–34.0°C) of females, but temperature ranges remain unknown for wild males. With significantly smaller body size than females, males should be more sensitive to lower critical temperatures for metabolism.

Reproductive Success as Indicated by Juvenile Size Classes. — Differences in the number of size classes in rivers indicate variable nesting success (Litzgus and Brooks 1998; Germano and Bury 2009). Limited nest success on the Bighorn River may be due to flow regimes altered by dams. Free-flowing rivers are essential for creating gravel and sandbar nesting habitat (Vandewalle and Christiansen 1996; Lenhart et al. 2013; Tornabene et al. 2018).

Changes to river hydrology, such as the timing and degree of peak flows, can result in inundation and failure of nests or increased sandbar submergence duration, impeding nesting activity (Bodie 2001; Lenhart et al. 2013; Tornabene et al. 2018). Spiny softshell turtle hatchlings appear unable to overwinter in nests in their northern range (Costanzo et al. 1995; Tornabene et al. 2018). On the dam-regulated Bighorn River, we observed delayed peak flows, which could inundate nests or delay the onset of nesting, thus increasing hatchling mortality related to freezing (Tornabene et al. 2018).

Decreased formation and inundation of islands related to dam operations might further increase nest failure and nest depredation (Bodie 2001; Moll and Moll 2004). Spiny softshell turtle nest depredation rates were three times greater on mainland areas than on islands in the Missouri River, Montana (Tornabene et al. 2018). Relatively low numbers of islands and high nest depredation rates potentially explain the lack of juvenile size classes observed in the Bighorn River (Melancon et al. 2013). Suitable habitat for adult female turtles appears to exist on the Bighorn River, yet the flow dynamics related to a dam-regulated system could create a population sink, with reproductive success and juvenile recruitment occurring infrequently (Dodd 1990; Germano and Bury 2009; Melancon et al. 2013; Lazure et al. 2019).

Growth Rates and Size Classes. — Countergradient growth related to latitude or colder temperatures occurs in fish (Pegg and Pierce 2001) and turtles (Litzgus and Brooks 1998; Snover et al. 2015). In colder environments, turtles have slower growth rates and take longer to reach sexual maturity (King et al. 1998; Litzgus and Brooks 1998; Snover et al. 2015). It is unknown how carapace size correlates with age, sexual maturity, or growth rates in Montana. Latitude and colder water temperatures may explain why none of the males we captured fell within reported juvenile male size ranges (Webb 1962; Plummer and Mills 2015).

We caught some of the largest turtles on the Bighorn River. However, the low CPUE and limited numbers of males and juveniles indicate long-term persistence challenges for this subpopulation. Reese and Welsh (1998) hypothesized that colder water associated with dam-regulated rivers could reduce juvenile survival and growth rates in western pond turtles (*Actinemys marmorata*). We suspect that hypolimnetic dam releases on the Bighorn River create unsuitable thermal conditions for juveniles and males yet allow adult female survival (Ashton et al. 2015).

Yellowstone River length-frequency histograms indicate missing size cohorts (290–320 mm) not apparent in the Musselshell River and Pryor Creek (the other 2 rivers with successful juvenile recruitment). The missing cohorts represent young, sexually mature turtles based on the growth data of Plummer and Mills (2015). It appears a mortality event may have occurred, possibly associated with the Yellowstone River ExxonMobil Silvertip pipeline rupture (1 July 2011, 63,000 gal; Montana Department of Environmental Quality 2017). In Montana, spiny softshell turtles initiate nesting just after peak flows (Tornabene 2014; Tornabene et al. 2018), so nesting probably occurred on oil-coated sites. Polycyclic aromatic hydrocarbon exposure affects both embryonic development and juvenile survival (Milton et al. 2003; Bell 2005; Van Meter et al. 2006; Mitchelmore et al. 2017). We are unaware of other large-scale factors resulting in significant nesting failure or juvenile mortality. Even with little documented acute mortality, population-level effects may occur in the Yellowstone River as this cohort moves into reproductive life-history stages (Hinkeldey et al. 2001; Michel et al. 2001).

The length-frequency histograms also indicate that spiny softshell turtles in the Musselshell River and Pryor Creek have limited growth or longevity. Spiny softshell turtles use extrapulmonary extraction of dissolved oxygen but are particularly anoxia intolerant, requiring larger rivers and lakes for hibernacula (Reese et al. 2003). In some years, the Musselshell River has reduced winter flows due to water diversions for reservoir filling, and Pryor Creek had the lowest flow of all systems. Pryor Creek and the Musselshell River appear to have marginally suitable winter flows to prevent anoxic conditions and possibly lack sufficient structural habitat (bluff or alluvial pools) secure from ice scour (Tornabene et al. 2019).

Intraspecific and Sympatric Species Competition. — Habitat overlap and resource competition can affect population demographics (Gibbons and Lovich 1990; Fuselier and Edds 1994; Selman 2012). Intraspecific competition and ontogenetic dietary shifts can reduce male survival due to female displacement (Congdon et al. 1992; Swannack and Rose 2003), dietary preferences, and prey availability. Similarly, competition with adults or sympatric species in rivers with limited prey availability can limit juvenile growth rates (Avery et al. 1993; Selman 2012). Pryor Creek was unique as the only river with sympatric snapping turtles, which, as dietary competitors, may be a factor in the different scaling of mass to length.

Management Considerations. — Of the demographic differences we documented, 4 concerning observations were identified: 1) the degree of subpopulation isolation, 2) the female-biased sex ratios, 3) the lack of juveniles in the Bighorn and Clarks Fork rivers and missing cohorts in the Yellowstone River, and 4) the limited numbers of large turtles in the Musselshell River and Pryor Creek. Further research should identify specific challenges to long-term persistence in subpopulations to help managers develop conservation and management actions (Bodie 2001; Tucker et al. 2012; Lenhart et al. 2013; Tornabene et al. 2018).

This population is not harvested, which provides a unique opportunity for demographic comparisons with harvested populations. Habitat conditions and anthropogenic changes affect discrete subpopulations, warranting specific regulations rather than general statewide plans often implemented for turtles. Although we suspect that no harvest occurs, we receive fishing bycatch reports of tagged turtles (3–4 annually) and realize that recreational fishing (Galois and Ouellet 2007) results in some mortality (B. Tornabene, *pers. comm.*, February 2020). To monitor harvest and bycatch, we recommend implementing reporting requirements to understand potential impacts on subpopulations. Our findings indicate that subpopulations have variable population potential. Therefore, different regulations for different rivers or reaches are warranted when managers develop regulations.

By further studying the demographic differences and vital habitat parameters in these rivers, we can better understand crucial elements for population viability. We plan to continue this study to examine environmental or resource-driven changes in demographics and abundance. This knowledge is critical to assess subpopulation status and highlights the importance of ongoing monitoring for long-lived species. Anthropogenic influences and management are constantly changing; without recurring studies, we will not understand how changes affect spiny softshell turtles. Mortality events (Yellowstone River oil spill) and impaired recruitment (Bighorn River) demonstrate the importance of population connectivity for recovery. Further evaluating barriers to movement and the impact of dam-regulated systems will help determine metapopulation resilience (Tucker et al. 2012; Ashton et al. 2015). It is essential to understand the fluvial conditions necessary to maintain dynamic riverine ecosystems to conserve and manage spiny softshell turtles and other species with similar life-history strategies.

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