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Abundance and harvest proportion of river turtles in Missouri

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ABSTRACT
Freshwater turtle populations are declining worldwide, yet managers have little information about the effects of commercial turtle harvests. In Missouri, the snapping turtle (*Chelydra serpentina*), smooth softshell (*Apalone mutica*), and spiny softshell (*Apalone spinifera*) are harvested commercially in the Missouri River. In 2011 and 2012, we conducted mark–recapture of these species to estimate abundance on the Missouri River and two unharvested tributaries, the Osage and Gasconade Rivers. We conducted mock harvests, applying capture methods of the state's primary commercial harvester, to estimate plausible expected harvest proportions. Snapping turtle abundance per 2 km was lower at harvested units ($\overline{X}$ = 15; SE = 7.1; unharvested: $\overline{X}$ = 90; SE = 40.3). Smooth softshell abundance was greater at harvested units ($\overline{X}$ = 59; SE = 7.9; unharvested: $\overline{X}$ = 14; SE = 28.1), although the difference was not significant. Mean unique spiny softshell captures were similar at harvested ($\overline{X}$ = 18; SE = 4.3) and unharvested ($\overline{X}$ = 17; SE = 9.7) units. Expected harvest proportions averaged 23% across species (SE = 5%; range = 6%–79%), exceeding sustainable rates reported for turtles. Our results suggest that on a small scale, using these methods, harvesters can remove a substantial portion of river turtle populations.

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Abundance estimation; *Apalone mutica*; *Apalone spinifera*; *Chelydra serpentina*; commercial turtle harvest; harvest proportion; Missouri

Introduction

Freshwater turtle populations are declining worldwide as a result of multiple factors, which include the harvest of wild populations for food and pet markets (Klemens and Thorbjarnarson 1995; Gibbons et al. 2000). Commercial turtle harvest is an important cause of population declines (Ceballos and Fitzgerald 2004; Moll and Moll 2004; Schlaepfer et al. 2005). Worldwide, the US is among the major exporters of turtle species (Luiselli et al. 2016) and turtle populations within the US have been increasingly targeted within the past few decades (Mali et al. 2014). Where harvesting is permitted, regulations often place few restrictions on harvesters (Congdon et al. 1994). For example, prior to 2002 in Minnesota, commercial harvesters were only limited to the number and type of traps used, but there were no limits on the number of turtles that could be removed (Gamble and Simons 2003, 2004). Additionally, the national and international commercial turtle markets have been largely under-regulated, which contributes to population declines (Gibbons et al. 2000; Ceballos and Fitzgerald 2004; Schlaepfer et al. 2005; Cheung and Dudgeon 2006). Regulations that are in place may be outdated or inconsistent throughout a region (e.g. Sigouin et al. 2017).

More than 9.3 million reptiles, 8.9 million of which were turtles and tortoises, were exported from the US in 1997 alone (Telecky 2001), though within the past decade, commercial turtle harvest in a

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number of US states have been closed (e.g. Florida, Alabama) or restricted through changes to harvest regulations such as bag or slot limits (e.g. Texas, Georgia; Mali et al. 2014; Colteaux and Johnson 2017). Mali et al. (2014) report that the overall number of native freshwater turtle species (including wild-caught and farmed turtles) exported out of the US exceeded 216 million individuals between 2002 and 2012, and while the number of individuals exported has declined yearly since 2002, the harvest of wild turtle populations has increased in states where regulations remain loose (e.g. Louisiana). This shift in harvest pressure may be a result of increased harvest regulation or closure of harvest in neighboring states, driving commercial harvesters to collect turtles from states where harvest is still permitted (Mali et al. 2014). Concurrent to the overall decline in the number of individual turtles exported from the US reported by Mali et al. (2014), Colteaux and Johnson (2017) report that specifically for snapping turtles (*Chelydra serpentina*), the number exported from the US from 1999 to 2014 has increased. These numbers include both wild-caught and farmed individuals, though the proportion of wild-caught turtles compared to farmed turtles has declined (Colteaux and Johnson 2017).

As long-lived species with delayed reproduction, low hatchling survival, and for many species, no known density-dependent responses to increased mortality rates, turtles are a challenging group to harvest sustainably at a commercial scale (Crouse et al. 1987; Brooks et al. 1991; Crouse and Frazer 1995; Galbraith et al. 1997; Heppell 1998; Zhou and Jiang 2008; Zimmer-Shaffer et al. 2014). Natural annual survival estimates for adult female snapping turtles range from 0.88 to 0.97 (Galbraith and Brooks 1987; Congdon et al. 1993, 1994). Maintaining this high level of survivorship is considered necessary for long-term population stability (Congdon et al. 1994; Galbraith et al. 1997). For snapping turtles, low rates of commercial harvest can have long-term effects on harvested populations. For example, life table analysis of 18 consecutive years of demographic data collected from a snapping turtle population in Michigan showed that a 10% increase in adult mortality resulted in a 50% decrease in the total population size within 20 years (Congdon et al. 1994). Other turtle species may be equally sensitive to relatively small increases in mortality. For example, population modeling for painted turtles (*Chrysemys picta*) indicated that populations are susceptible to the effects of overharvest when 4%–5% of females are removed (Gamble and Simons 2003). Although all turtle size classes have value in the turtle trade, adult turtles may be specifically targeted by commercial harvesters because they are worth the most money when sold by weight (Brown et al. 2011). Further, this has important implications considering the sexual dimorphism exhibited by softshell species where females reach greater maximum size than their male counterparts (Johnson 2000). Because of low hatchling survivorship and late maturity, adults lost to increased mortality cannot be replaced quickly enough to sustain the population (Brooks et al. 1991; Congdon et al. 1994).

In Missouri, three turtle species are commercially harvested: the snapping turtle, the smooth softshell (*Apalone mutica*), and the spiny softshell (*Apalone spinifera*). These species may be harvested from the Missouri River, the St. Francis River (along the Missouri/Arkansas border), and the Mississippi River. Commercial turtle harvest is closed in the tributaries of the Missouri River, as well as within 300 m of tributary confluences on the Missouri River. Commercial turtle harvest is covered under commercial fishing harvest permits, which must be obtained (and renewed) annually. Harvesters are required to report monthly the total number of turtles harvested of each species and from which river they were removed. Currently, Missouri commercial turtle harvest regulations do not limit the number of turtles that may be taken, trapping may take place year-round, and there are no size limits. However, the federal law prevents sale, holding, and distribution of all turtles less than four inches in carapace length (USFDA 2015). Analysis of historical population data from 1969 and 1980 indicated population declines of northern map turtles (*Graptemys geographica*) in Missouri, and suggested that illegal collection may have been an influence on population declines, as evidenced by reduced numbers of large mature females and thus, a decline in fecundity leading to reduced numbers of hatchlings (Nickerson and Pitt 2012). Still, no research has assessed the abundance of turtle populations currently known to be harvested in Missouri. A Missouri Department of Conservation (J. Briggler, personal communication) report showed an increase in the total numbers of turtles harvested in Missouri from less than 100 turtles in 1993 to more than 2000 in 2007; approximate harvest was reported to be 400 individuals in both 2009 and 2012. Despite an overall increase in the number of turtles removed, the number of commercial turtle harvesters reporting captures decreased from 17 in 1994 to 6 in 2012, implying that individual harvester activity or effectiveness has increased.

In light of the limited availability of abundance estimates of harvested river turtle populations and the possible effects the activity has on these populations, the objective of this study was to estimate the abundance and determine plausible expected harvest proportions for the three commercially harvested turtle species (snapping turtles, smooth softshells, and spiny softshells) in Missouri. Field work took place in the Missouri River, which is open to commercial harvest, and in the Osage, and Gasconade Rivers, which are Missouri River tributaries closed to commercial harvest. We used mark–recapture sampling to estimate the abundance and compared the abundance among the three rivers. To estimate the plausible harvest proportions, we carried out mock harvests within our study sites based on methods used by Missouri's leading commercial turtle harvester to simulate commercial turtle harvest. This study is the first in Missouri to estimate the abundance of harvested large-river turtle populations; further, we are not aware of other research estimating plausible harvest proportions for river turtle populations.

Methods

Study area

Our study was conducted in the Missouri River (nineth stream order) and within the lower reaches of two major tributaries, the Osage River and the Gasconade River. These tributaries were chosen as comparable unharvested reference sites because they are both high order, and the lower reaches of each have similar stream characteristics with the Missouri River. This includes attributes such as high turbidity and the presence of sandbars and other habitat appropriate for the target species, all three of which are present in these rivers.

We conducted our field work during the summers of 2011 and 2012 between river miles 154 and 80 of the Missouri River in central Missouri ('River mile', hereafter RM, is used as a standard geographic designation [e.g. see USACE 2014] and the reason why we do not convert these to metric units throughout). The confluences of the Osage and Gasconade Rivers occur within this region. This portion of the Missouri River is characterized by a high number of modifications (i.e. wing dikes) along both sides of the bank (Galat and Lipkin 2000; Pegg et al. 2003). A visual assessment of aerial imagery indicated that many of the RMs within our study area contain at least four wing dikes, which channelize the river and disrupt the flow along the banks. Within our study region, sand bars and large, gradually sloping banks are commonly formed in the shallow, slow-current areas found on the downstream side of the dikes, which provide optimal basking and nesting areas for both softshell species. Muddy substrate and floating debris (i.e. stumps, root masses) also accumulate in these areas, creating appropriate habitat for snapping turtles, as well as the habitat for prey species. Private development is limited along the Missouri River throughout this region, and much of the river within this area is bordered by agricultural fields.

As the two largest tributaries of the Missouri River in central Missouri, the lower reaches of the Osage River and the Gasconade River have similar habitat to the Missouri River within our study area. Recreational use within and along the banks of the Osage River is common, as is development. Availability of appropriate sand or mud banks was limited, particularly at times of high water, though submerged woody debris and root masses that create appropriate snapping turtle habitat were abundant. In contrast to the Osage River, there is wide availability of gravel bars and sandy banks within the Gasconade River with relatively little development and recreational use.

River characteristics differed between 2011 and 2012 due to major differences in precipitation. Total rainfall from May through August in central Missouri was 45.85 cm in 2011 vs. 16.28 cm in 2012 (USDA 2015). On 2 July 2011, the Missouri River at the Jefferson City river depth gauge recorded a yearly maximum height of approximately 8.23 m. On the same date in 2012, the same gauge recorded a height of approximately 2.13 m. The yearly maximum river height in 2012 was approximately 2.59 m, occurring on 23 March (USGS 2015). High amounts of precipitation in 2011 caused flood-like conditions throughout the field season, and storms and high water levels resulted in limited trap site availability in the Missouri and Osage Rivers, though we were still able to find a sufficient number of suitable locations (i.e. containing habitat appropriate for the target species) within each trap site to place turtle traps. In contrast, low water levels in 2012 greatly increased the availability of appropriate river turtle habitat components such as slow, backwater areas and sand bars, as well as increasing river bank size.

Site selection

Based on power and precision analyses using pilot data collected in 2010 (Zimmer 2013), we randomly selected six 1-km sites on the Missouri River and three 1-km sites on both the Osage and Gasconade Rivers for the 2011 and 2012 field seasons. We selected Missouri River sites by first stratifying a 120.7-km (75 RM) stretch of the river in central Missouri into three 40.2-km (25 RM) units: RMs 80–104 (Hermann unit), 105–129 (Mokane unit), and 130–154 (Jefferson City unit). Because the Osage–Missouri confluence (at approx. RM 130) and Gasconade–Missouri confluence (at approx. RM 105) are within this 120.7-km stretch, the Missouri River was stratified into these three units to account for any potential variation in turtle density upstream and downstream of the two tributaries. We excluded eight RM from each of the three units for one or more of the following reasons: the river miles contained disturbances that could affect our results such as housing, docks, or other development; the river miles overlapped tributary confluences with the Missouri River; or the river miles did not contain any of the habitat components used by the three target species (i.e. sand bars and banks, shallow backwater areas, root masses, submerged debris). Finally, we randomly selected 2 RM from the remaining sites at each of the three Missouri River units. We defined 1-km trap sites as the downstream-most 1000 m of each selected RM.

We limited selection of trapping sites in the Osage and Gasconade Rivers to within the first 17.7 km (11 RM) of the confluence due to the placement of a dam structure on the Osage River at approximately 18.5 km upstream, which may restrict the movement of turtles, and which is impassable by boat. In addition, habitat similarity to the Missouri River on both the Osage and the Gasconade Rivers decreases rapidly as one moves further upstream. We removed RM's from consideration where housing, docks, and other riverside development was present. We also eliminated RM 1 from each tributary to avoid trapping in the vicinity of the confluence. We randomly selected three river miles from those that remained within each tributary. We defined 1-km trap sites as the downstream-most 1000 m of each selected RM.

Across all three rivers, locations which were eliminated from our random selection process (e.g. confluence sites, RMs containing development or docks) left us with potential sites that were suitable for successful turtle trapping, contained suitable habitat for the three target species, and were representative of the types of areas from which commercial turtle harvesters would likely select trapping locations. We selected our final trap sites from these areas using simple random sampling on each river, and our inference applies to locations such as these.

Mark–recapture

In 2011 and 2012, we conducted a mark–recapture study and a mock harvest within 10 of the randomly selected sites: six sites on the Missouri River, and two sites each on the Gasconade and Osage Rivers (Figure 1). On the Missouri River, the Hermann unit (sites at RM103 and RM94) was trapped in both 2011 and 2012; the Mokane unit (sites at RM128 and RM122) was trapped in 2011; the Jefferson City unit (sites at RM137 and RM134) was trapped in 2012. The Mokane unit could not be trapped again in 2012 due to theft and vandalism of our equipment during sampling, requiring us to move sampling to the Jefferson City unit in that year. On the Osage River, RM5 and RM7 were

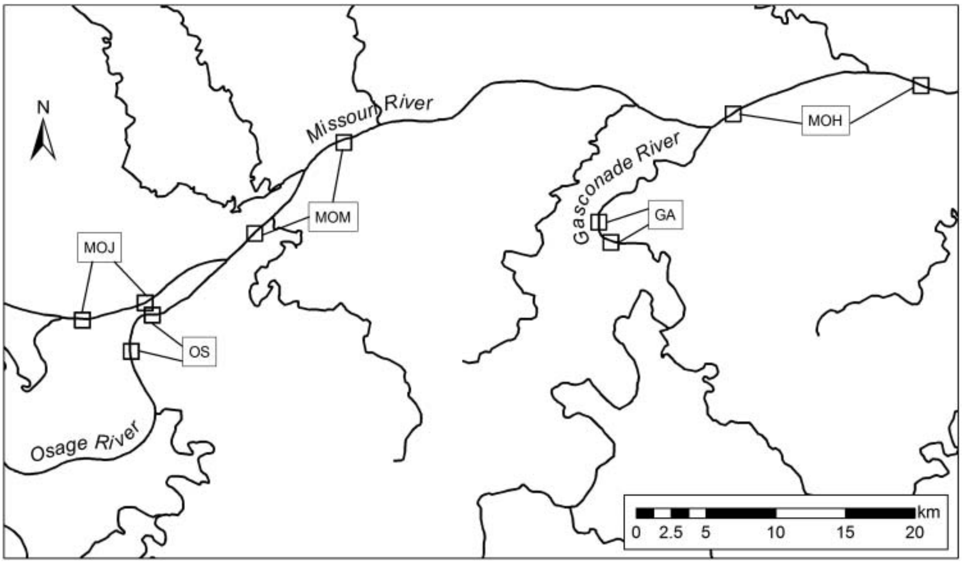

Figure 1. Map of the five units (10 1-km sites in total, indicated with squares) trapped for mark–recapture and mock harvest during the 2011 and 2012 field seasons on the Missouri, Osage, and Gasconade Rivers in central Missouri. MOJ = Missouri River at Jefferson City unit (river mile [RM] 137 and RM 134, trapped in 2012); MOM = Missouri River at Mokane unit (RM 128 and RM 122, trapped in 2011); MOH = Missouri River at Hermann unit (RM 103 and RM 94, trapped in 2011 and 2012); OS = Osage River unit (RM 5 and RM 7, trapped in 2011 and 2012); GA = Gasconade River unit (RM 9 and RM 10, trapped in 2011 and 2012).

trapped in 2011 and 2012. On the Gasconade River, RM9 and RM10 were trapped in 2011 and 2012. Trapping took place from 6 May to 8 September in 2011 and from 19 April to 18 August in 2012. Each year, we trapped sites for a single eight-day period, followed by a four-day mock harvest.

We used three types of traps to capture turtles during the mark–recapture: round-frame 3-hoop nets, mini-fyke nets, and custom D-frame 3-hoop nets. Pilot work indicated that trap types may differ in their effectiveness by habitat type. Additionally, the habitat preferences of snapping turtles and softshells, as well as between male and female softshells, vary (Barko and Briggler 2006; Ernst and Lovich 2009); so we utilized different types of traps to minimize habitat-biased trapping. To minimize turtle mortality and bycatch, traps most frequently were placed in relatively shallow, slow-current areas of the river. We placed all nets to avoid their spinning, collapsing, or becoming completely inundated. We placed 20 total nets at each site. When traps were lost due to theft or flooding (three in total lost in 2011 during mark–recapture, none lost in 2012), they were replaced the day they were noticed missing to maintain the intended trap effort per session. Round-frame 3-hoop nets were the predominant type of trap that we used based on the available trap locations, though we used custom-made D-hoop and mini-fyke nets to accommodate varying habitat types available within trap sites. For example, in areas of high current where round-frame nets were prone to rolling, we used the D-frame 3-hoop nets, which are less prone to shifting in the current. We placed these nets in rocky, sandy, gravelly, muddy, or debris-filled areas along the banks. We used mini-fyke nets in shallow areas of the river with little to no current, typically found only behind dikes on the Missouri River or on gravel bars or banks within the Gasconade River. All nets were set in contact with the ground, staked in place, and partially submerged, allowing access to the surface of the water for captured animals. Traps were baited using fresh or frozen-thawed fish (typically either invasive carp species [*Hypophthalmichthys molitr*, *Hypophthalmichthys nobilis*] or gizzard shad [*Dorosoma cepedianum*]) attached inside the trap. When fresh or frozen-thawed fish were not available, we used an approximate 1:4 mixture of canned sardines and cracked corn or a mixture of chicken gizzards and hearts. Both the sardine mixture and chicken gizzards were packed into plastic bottles, perforated to allow the scent to disperse throughout the water. We recorded GPS coordinates (Universal Transverse Mercator) at each trap location.

Each trap was set for eight trap nights and checked daily. We checked all captured turtles for previous marks and tags and recorded all instances of recaptures. New individuals of all three target species were injected with an AVID (American Veterinary Identification Devices, Norco, California) passive integrated transponder (PIT) tag (12 mm, 125 kHz), each encrypted with a unique nine-digit code for individual identification. We injected PIT tags subcutaneously in the left inguinal region. Softshell turtles less than approximately 90 mm in carapace length and hatchling snapping turtles were not injected with PIT tags because of issues with body size and fragile skin; in these cases, we used scissors to give turtles unique clips along the posterior margin of their carapace. Because snapping turtles have defined scutes, individuals of this species were also given a daily cohort mark by filing marginal scutes according to an alphabetical system that assigns a unique letter code per day. For all turtles, we determined the sex of mature individuals based on the species-specific sexually dimorphic physical characteristics (e.g. Johnson 2000); sex was not determined for non-mature juvenile turtles or hatchlings since they do not typically exhibit such characteristics until maturity. Stage (hatchling, juvenile, or adult) was determined according to stage-specific straight carapace length measurements described by Johnson (2000); straight carapace length and straight plastron length were measured using calipers. Once processed, each turtle was released at the capture location.

Mock harvest

At each of the sampling sites, we conducted a mock harvest within one to six days of completing the mark–recapture work. Our mock harvests followed methods used by one of Missouri's most active commercial turtle harvesters (i.e. this individual's contribution to the total number of legally harvested turtles reported in Missouri from 2008 to 2013 ranged from 33% to 45%). In a personal interview with this harvester, we learned the type of traps used, approximate number of nights that traps were set per location, approximate distance between traps, types of habitat utilized for trapping, and the type of bait used. Following these methods as closely as possible, our study design was as follows: we used D-frame hoop nets manufactured to the exact specifications of the traps used by this commercial turtle harvester. We set 20–25 traps within each 1-km trap site (depending on availability of appropriate habitat) and we trapped two sites simultaneously for four consecutive trap nights. Within each site, we placed four to five traps together within 30 m of one another in areas of prime turtle habitat (e.g. in a shallow backwater, or along a sandbar behind a dike) to optimize trapping success. This trap density was selected to best simulate methods used by the commercial turtle harvester. Traps were baited using carp species as with the mark–recapture portion of the sampling. We processed all captured turtles using the same methods used during the mark–recapture sampling. To simulate the removal (harvest) of the target species, all captured snapping turtles, spiny softshells, and smooth softshells were placed in closed nets within their river of origin at least 20 m from other active nets and held for the duration of the mock harvest. The mesh size of the mock harvest turtle traps (5.08 cm, which stretches to approximately 10.16 cm at its fullest extent) limited our capture of turtles to adults and larger juveniles unable to escape the nets. We checked and provided bait fish daily to all nets containing the captive turtles. After completion of the mock harvest, all turtles were released at their capture locations.

Though commercial turtle harvesters may not remove all size classes when harvesting turtles (i.e. may only remove larger individuals, or individuals within a certain size range according to regulations; e.g. Close and Seigel 1997; Mali et al. 2014), our removal of every individual of the target species during mock harvests was based on estimating the overall potential for turtle removal by commercial harvesters (i.e. our estimated plausible harvest rates). Our capture methods were approved by the University of Missouri Animal Care and Use Committee Protocol #6744.

Table 1. Sites sampled during the 2011 and 2012 field seasons on the Missouri, Osage, and Gasconade Rivers in central Missouri. Unit represents the pairs of sites grouped by location. Numbers in the 'Site' column represent the randomly selected river mile one each river within which each 1-km trap site was located. Year(s) sampled represents the year or years when each site was sampled. Unit codes are defined as follows: MOH = Missouri River at Hermann; MOM = Missouri River at Mokane; MOH = Missouri River at Hermann; MOJ = Missouri River at Jefferson City; OS = Osage River; GA = Gasconade River.

River	Unit	Site (River mile)	Year(s) sampled
Missouri	MOH	94	2011, 2012
		103	2011, 2012
	MOM	122	2011
		128	2011
	MOJ	134	2012
		137	2012
Osage	OS	5	2011, 2012
		7	2011, 2012
Gasconade	GA	9	2011, 2012
		10	2011, 2012

Analysis: abundance estimates

Due to sparse captures within some sites, for analysis, we grouped the 1-km sites into pairs (pairs hereafter referred to as units) based on location and pooled the captures within each unit by year for analysis (Table 1). This resulted in the analysis of four total unharvested units: Gasconade 2011 (GA11), Gasconade 2012 (GA12), Osage 2011 (OS11), Osage 2012 (OS12), and four total harvested units: Missouri at Hermann 2011 (MOH11), Missouri at Hermann 2012 (MOH12), Missouri at Mokane 2011 (MOM11), and Missouri at Jefferson City 2012 (MOJ12; Figure 1; Table 1). Samples from these units were treated independently among years for analysis due to the time (approximately one year) between trapping sessions at each location and major differences in environmental conditions and available habitat (i.e. due to differences in water levels) between the two years.

We estimated abundance per unit (i.e. per 2 km) using mark–recapture data from the first eight trap nights and from the subsequent four-night mock harvests; the 12 total trap nights each year at each unit were treated as single 12-occasion closed-population mark–recapture sample, with separate analyses conducted for each unit each year. Because we 'harvested' turtles during mock harvests (i.e. temporarily removed them from the trappable population), these individuals were denoted as no longer available for capture during subsequent trap nights when estimating abundance.

For snapping turtles, we used program MARK (White and Burnham 1999) to estimate the abundance within each of these 2-km units, using two closed capture models: Model M_0, which assumes no temporal, behavioral, or trap-response heterogeneity in detectability, and Model M_t, which incorporates temporal heterogeneity, allowing detectability to vary for each trap night. For groups of turtles that contained no recaptures (i.e. both species of softshells on the Osage River in both 2011 and 2012), mark–recapture abundance estimation was not feasible.

We treated each abundance estimate per unit per year as an independent data point, and compared year-unit-level abundance between harvested and unharvested sites. Using two-sample t tests of equal log-scale average captures, we compared the abundance estimates between the harvested (treatment, T) and unharvested (C) populations (Skalski and Robson 1992:121, 5.3). This analysis of differences between treatments on the log-scale assumes multiplicative (proportional) effects of harvesting on the absolute abundance compared to the no-harvest reference sites (Skalski and Robson 1992:120, 5.2).

For both softshell species, we based comparisons between harvested and unharvested units on relative abundances (i.e. the number of unique turtles captured) rather than the abundance estimates because very low captures and lack of recaptures precluded mark–recapture abundance estimation for some harvested units. For these two species, we analyzed log-capture counts with t-tests parallel to the approach described above. The accuracy of this comparison, as in most analyses of capture counts unadjusted for detectability, depended on the assumption that differences in capture rates reflected the differences in true abundance rather than systematic differences in susceptibility to trapping (e.g. Skalski and Robson 1992).

Analysis: plausible harvest proportions

For each unit in each year, we estimated daily capture probabilities for the 12 trap nights of the trap session with model M_t in program MARK. The final four nights of each session made up the mock harvest trapping; thus, these four nightly detectability parameters were estimates of the 'harvest' proportion, and the estimated overall probability that a turtle would be detected during the four-night mock harvest was also an estimate of the expected probability of harvest during each year's mock harvest of a unit. Therefore, to estimate the expected proportion of the population that was removed during the mock harvest, we used the estimated daily capture probabilities of the four trap nights of mock harvest. Our plausible harvest proportion (H) was calculated as

$$H = 1 - (1 - p_1) \times (1 - p_2) \times (1 - p_3) \times (1 - p_4),$$

where $p_i$is the estimated nightly capture rate for each night (i) of the mock harvest. Harvest proportions were not calculated when no recaptures were obtained or captures were too low to support the mark–recapture estimation.

We used the Delta Method (Powell 2007) to estimate the variance of the plausible harvest proportion. The variance estimate is of the form

$$\mathrm{var}(H) = \mathrm{var}[f(p_1, p_2, p_3, p_4)],$$
$$= \sum_{i=1}^{4} \mathrm{var}(p_i)\left[\frac{\partial f}{\partial p_i}\right]^2 + 2\sum_{i=1}^{4}\sum_{j=1}^{4} \mathrm{cov}(p_i, p_j)\left[\frac{\partial f}{\partial p_i}\right]\left[\frac{\partial f}{\partial p_j}\right],$$

where H is the plausible harvest proportion over all nights of the mock harvest, which is a function of the capture rate (p_i) for each trap night, each with its own estimate of variance; $\left[\frac{\partial f}{\partial p_i}\right]$ and $\left[\frac{\partial f}{\partial p_j}\right]$are the partial derivatives with respect to each nightly capture probability. All variance and covariance estimates were obtained from the MARK output for Model M_t.

Results

Abundance estimates

For snapping turtles, we calculated the abundance per 2 km at each of the four harvested units, and at each of the four unharvested units. Abundance was lower at the Missouri River units (Table 2; $\overline{X}$= 15 turtles; SE = 7.1) than at the unharvested units ($\overline{X}$ = 90 turtles; SE = 40.3; $t_6 = -2.96$, $P = 0.03$). For smooth softshells, the greatest abundance estimates and highest capture counts occurred at the harvested units (Table 2), yet these results, based on counts of unique smooth softshell turtles captured per session, were non-significant ($t_6 = 2.12$, $P = 0.08$) when comparing the harvested (capture count $\overline{X}$ = 59 turtles; SE = 7.9) and unharvested units ($\overline{X}$ = 14 turtles; SE = 28.1). For spiny softshells, the mean unique captures on the Missouri River sites ($\overline{X}$ = 18 turtles; SE = 4.3) were similar to the mean captures at the unharvested sites ($\overline{X}$ = 17 turtles; SE = 9.7; $t_6 = 0.77$, $P = 0.47$). The total number of captures across both 2011 and 2012 per species by stage and sex were summarized within each of the three rivers (Figure 2).

Table 2. Abundance estimates ($\hat{N}$) per 2 km of river for snapping turtles (*Chelydra serpentina*, CSNT), smooth softshell turtles (*Apalone mutica*, SMSS), and spiny softshell turtles (*Apalone spinifera*, SPSS) in harvested (Missouri River) and unharvested (Osage River, Gasconade River) trapping units in central Missouri. Unit = 2-km trapping units. Trap nights = number of nights spent at each site (number of traps per unit multiplied by the total number of nights spent per unit); *n* = number of individual turtles caught within each unit. Proportion recaptures = proportion of individuals that had been recaptured at least one time following initial capture. Mean capture probability = the mean nightly probability that an individual will be captured during a given trap night. Capture proportion = expected proportion of the population captured at least once during the span of each trap run. Unit codes are defined as follows: MOH11 = Missouri River at Hermann 2011; MOM11 = Missouri River at Mokane 2011; MOH12 = Missouri River at Hermann 2012; MOJ12 = Missouri River at Jefferson City 2012; OS11 = Osage River 2011; GA11 = Gasconade River 2011; OS12 = Osage River 2012; GA12 = Gasconade River 2012. An asterisk (*) indicates units where estimation of $\hat{N}$ was not feasible due to lack of recaptures.

Species	River status	Unit	Trap nights	*n*	Proportion recaptures	Mean capture probability	$\hat{N}$	SE	LCI	UCI	Capture proportion
CSNT	Harvested	MOH11	482	5	0.375	0.116	5	1.44	5.01	14.88	0.86
		MOM11	482	5	0.444	0.146	5	1.09	5.00	10.08	0.90
		MOH12	502	11	0.214	0.031	35	21.11	16.91	118.50	0.34
		MOJ12	480	6	0.143	0.038	14	11.78	7.09	70.85	0.40
	Unharvested	OS11	601	31	0.184	0.031	70	21.14	45.64	136.50	0.44
		GA11	547	41	0.406	0.09	55	6.32	46.93	73.49	0.74
		OS12	492	32	0.059	0.014	208	137.90	77.48	714.80	0.15
		GA12	480	12	0.143	0.045	27	14.84	14.93	87.81	0.44
SMSS	Harvested	MOH11	482	140	0.235	0.044	300	36.50	242.70	388.60	0.47
		MOM11	482	39	0.114	0.023	148	58.72	79.22	332.00	0.26
		MOH12	502	45	0.151	0.030	136	41.33	83.77	257.50	0.33
		MOJ12	480	11	0.000		*				
	Unharvested	OS11	601	8	0.000		*				
		GA11	547	4	0.000		*				
		OS12	492	5	0.000		*				
		GA12	480	37	0.362	0.098	51	6.68	42.47	70.81	0.99
SPSS	Harvested	MOH11	482	10	0.474	0.155	10	1.10	10.00	17.40	0.94
		MOM11	482	12	0.294	0.073	18	5.54	13.43	39.76	0.64
		MOH12	502	29	0.293	0.065	49	10.09	36.64	79.73	0.59
		MOJ12	480	19	0.000		*				
	Unharvested	OS11	601	4	0.000		*				
		GA11	547	19	0.000		*				
		OS12	492	2	0.000		*				
		GA12	480	44	0.279	0.074	72	11.82	56.69	106.00	0.61

No traps were lost during the mark–recapture periods in 2012, but three traps in total were lost during two mark–recapture periods in 2011. Two of these three were lost on the OS5 trap site one, between 17 and 18 May 2011, and one between 18 and 19 May 2011. The third trap was lost from the MO94 trap site between 10 and 11 July 2011. Each of these traps were replaced the day they were found missing.

Plausible harvest proportions

During mock harvests, our estimated plausible harvest proportions ranged from 6.7% to 56.8% of the snapping turtle population (Table 3). In most cases, the plausible harvest proportions were lower at the unharvested units than at the harvested units. For smooth softshells at units for which harvest proportion could be estimated, the proportion removed ranged from 8.8% to 33.6% of the marked population and was greatest at the unharvested unit. For spiny softshells, the proportion removed ranged from 6.2% to 79.2% of the population and harvest proportions were greater at the harvested units than at the unharvested units (Table 3).

Throughout all mock harvests, no active or closed traps were lost and we saw no evidence indicating that our traps had been tampered with (e.g. turtles removed). During a mock harvest, a single trap set for capture on the Gasconade River contained a turtle mortality event for a trap set on 29 July 2012, in which one live adult female spiny softshell along with two dead adult male spiny

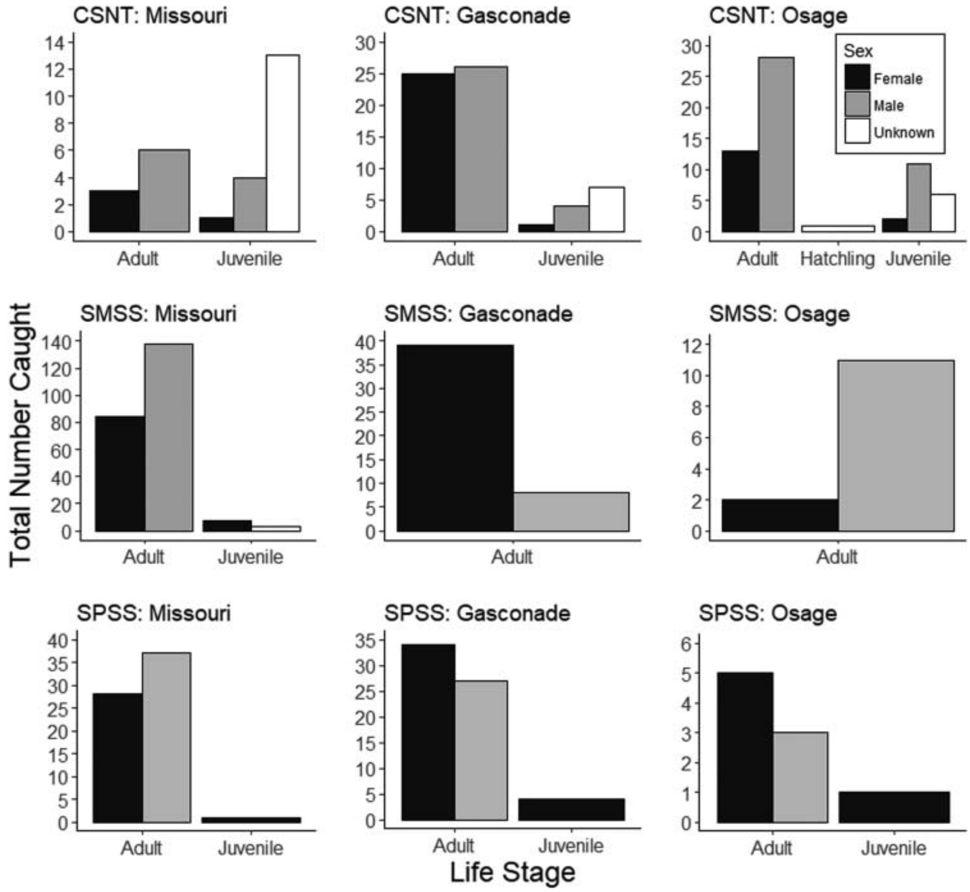

Figure 2. Histograms showing the distribution of the total number of individual turtles, not including recaptures, caught during mark–recapture periods and mock harvest periods during the 2011 and 2012 field seasons in central Missouri. Plots are broken down by sex (female, male, unknown) and by life stage (adult, juvenile, hatchling; designations based on Johnson [2000]), for each species (CSNT = snapping turtle, *Chelydra serpentina*; SMSS = smooth softshell turtle, *Apalone mutica*; SPSS = spiny softshell turtle, *Apalone spinifera*), and river of capture (Missouri River, Gasconade River, Osage River).

softshells were found within the trap when it was checked on 30 July 2012. No cause of these mortalities was evident.

Discussion

This study offers the first available estimates of the proportion of wild turtle populations that commercial harvesters are capable of removing: all of our harvest proportions exceeded 6%, and half exceeded 20% (Table 3). Harvest proportions estimated in this study indicate that commercial turtle harvesters can remove a sizeable proportion of harvestable turtle populations, at least on small spatial scales within the Missouri River. Because our methods closely followed the methods used by Missouri's leading commercial turtle harvester, these rates represent a plausible estimate of removal rates in trapped regions under the state's current regulations using these methods.

Natural mortality rates for adult turtles are generally low, which is important to maintain population stability (Galbraith et al. 1997). Yet, our lowest estimate of plausible harvest proportions results in harvest mortality above 5%, the level for total mortality, which has been reported to be detrimental in the long term to the viability of other turtle populations (Gamble and Simons 2003). Our own research, which involved modeling population growth rates of river turtles at these harvest estimates

Table 3. Expected harvest proportions for snapping turtles (*Chelydra serpentina*, CSNT), smooth softshell turtles (*Apalone mutica*, SMSS), and spiny softshell turtles (*Apalone spinifera*, SPSS) in harvested (Missouri River) and unharvested (Osage River, Gasconade River) trapping units in central Missouri. Harvest proportion represents the expected proportion of each population that was captured ('harvested') during each mock harvest (see Table 2). Unit = 2-km trapping unit. Trap nights = total number of nights spent at each site (total number of traps per unit multiplied by the total number of nights spent per unit); *n* = total number of turtles caught within each unit. Proportion recaptures = proportion of the total number of captured individuals that had been recaptured at least one time following initial capture. Variance was estimated using the Delta Method (Powell 2007). Unit codes are defined as follows: MOH11 = Missouri River at Hermann 2011; MOM11 = Missouri River at Mokane 2011; MOH12 = Missouri River at Hermann 2012; MOJ12 = Missouri River at Jefferson City 2012; OS11 = Osage River 2011; GA11 = Gasconade River 2011; OS12 = Osage River 2012; GA12 = Gasconade River 2012. An asterisk (*) indicates units where estimation of harvest proportion was not feasible due to lack of recaptures.

Species	River status	Unit	Trap nights	*n*	Proportion recaptures	Harvest proportion	SE
CSNT	Harvested	MOH11	164	3	0.333	0.568	0.27
		MOM11	163	1	1.000	0.249	0.23
		MOH12	176	3	0.667	0.086	0.07
		MOJ12	160	2	1.000	0.139	0.15
	Unharvested	OS11	144	14	0.214	0.199	0.08
		GA11	147	7	0.571	0.128	0.05
		OS12	172	14	0.071	0.067	0.04
		GA12	160	7	0.143	0.260	0.17
SMSS	Harvested	MOH11	164	35	0.229	0.117	0.02
		MOM11	163	13	0.231	0.088	0.04
		MOH12	176	12	0.167	0.088	0.03
		MOJ12	160	4	0.000	*	
	Unharvested	OS11	144	0	0.000	*	
		GA11	147	3	0.000	*	
		OS12	172	3	0.000	*	
		GA12	160	17	0.529	0.336	0.08
SPSS	Harvested	MOH11	164	8	0.500	0.792	0.15
		MOM11	163	4	0.250	0.219	0.12
		MOH12	176	3	0.667	0.062	0.04
		MOJ12	147	6	0.000	*	
	Unharvested	OS11	144	0	0.000	*	
		GA11	160	5	0.000	*	
		OS12	172	1	0.000	*	
		GA12	160	17	0.529	0.236	0.06

indicated that our lowest estimated harvest proportions for softshell turtles (6%) and snapping turtles (7%) were unsustainable when considering the average demographic rates for these species (Zimmer-Shaffer et al. 2014). Thus, our research supports other work indicating that under most conditions, these species cannot sustain annually our estimated harvest proportions. To be sustainable, commercial harvest rates must be conservative (Congdon et al. 1994; Ceballos and Fitzgerald 2004) but this may be difficult where there are few restrictions controlling the level of harvest and areas that are harvested (e.g. Mali et al. 2014). Further, the largest turtles (e.g. adults) may be specifically targeted by commercial harvesters as evidenced by the reduced numbers of larger individuals (Close and Seigel 1997; Shipman and Riedle 2008; Nickerson and Pitt 2012); and for species where females reach greater length and mass than males, this selection could have an influence on fecundity in affected populations (Nickerson and Pitt 2012). Findings such as these outline the importance of determining the population structure when quantifying the long-term effects of commercial turtle harvest on populations. For example, for populations of red-eared sliders (*Trachemys scripta elegans*) exposed to varying harvest conditions, Close and Seigel (1997) detected differences in the mean body size for both adult males and females though they were unable to determine the precise influence that harvest activity had on these populations. Likewise, Nickerson and Pitt (2012) found that within a harvested population of northern map turtles, the number of larger mature females present declined over time.

Our research is one of the few studies to estimate the abundance or report on the abundance (as number of individuals) for these freshwater turtle species in any system (e.g. Barko and Briggler

2006; Aresco and Gunzburger 2007). Estimates of abundance for snapping turtles in non-riverine systems are available (e.g. Decker Major 1975), but comparisons with these studies are difficult because of habitat differences. For long-lived species such as turtles, appropriate abundance estimates are important for informing management decisions. Our estimates indicated that snapping turtle abundance was lower at our Missouri River sites than at the unharvested tributaries. These differences could be due to harvest or to broader differences in habitat conditions among the three rivers sampled. Similarly, flooding in 2011 may have had an impact on trapping success, though environmental stochasticity such as this is unavoidable in such studies. Though results were non-significant, smooth softshell abundance estimates were considerably higher on the Missouri River compared to both spiny softshells and snapping turtles, and these findings are not necessarily an indication that the population can sustain added mortality from harvest pressure. Because our comparisons for both softshell species are based on raw capture data (i.e. unique captures), these abundance estimates do not account for potential variation in detectability among populations and movement of turtles within rivers, and therefore may be considered exploratory. For units where we could estimate the abundance of smooth softshells, we estimated high abundance on the Missouri River. This does not necessarily mean that smooth softshells are not being affected by harvesting, particularly at localized scales. Still, smooth softshells are typically smaller-bodied compared to spiny softshells and snapping turtles, thus making an individual smooth softshell less valuable on the market when sold by weight. Finally, differences in habitat preference among species should be considered when examining our findings. For example, smooth softshells are large river (e.g. the Missouri River) specialists based on the availability of sand bar habitats, which are less commonly found within the smaller tributaries; spiny softshells, on the other hand, are not limited by sand bar availability and can be found across a much broader range of habitat types in water bodies of varying sizes (Johnson 2000; Barko and Briggler 2006; Ernst and Lovich 2009; Powell et al. 2016). Because it was beyond the scope of the study to examine the influence that habitat variations, environmental conditions, trap effectiveness, or turtle movements may have had on our abundance estimates, it is difficult to tease out whether or not our abundance estimates were affected by these factors or by commercial harvest activity. As such, our abundance estimates are best used as a basis for our plausible harvest rates.

Our Missouri River trapping sites were randomly selected from approximately 121 consecutive kilometer of river that is open to commercial turtle harvest (excluding tributary areas), and it is unknown if commercial harvest took place within any of our randomly selected sites at any point during 2011 or 2012. Even so, no traps aside from our own were observed in any part of any of the three rivers where sampling for this study took place and we are confident that no commercial turtle harvester activity was taking place concurrently at any site where our research was being conducted. Additionally, the commercial harvester that we interviewed informed us of the reaches of river he typically traps within, and we purposely avoided these areas to reduce disturbance of the traps.

Because commercial turtle harvest probably occurs at a small scale, considering the number of harvesters reporting turtles, and because it is likely restricted to specific areas of the river, it can be difficult to detect the effects of this activity on the harvested populations. Life history traits for many reptile species (i.e. large home range, limited congregational behavior such as annual migration, and low population density; Gibbons et al. 2000) can also create difficulty in observing large-scale trends within the population. Additionally, many turtle populations have not been subjected to long-term research (but see Galbraith et al. 1989; Congdon et al. 1994; Reid et al. 2016), which creates difficulties in detecting shifts in demographic rates (Gibbons et al. 2000). Because collection of life history information for such long-lived species needs to occur over long time periods (i.e. decades), and because of specific demographic characteristics such as high adult survivorship and low fecundity, the effects of commercial turtle harvest could go undetected in the short term (Gamble and Simons 2004). Thus, we expect given the current turtle harvester numbers, methods of take, and the expected harvest proportions we observed, effects of commercial harvest occur at a local scale. This hypothesis is supported by commercial turtle harvesters who have indicated that after trapping in one area, turtle numbers decline for a period of time following harvest activity; Breckenridge (1955) reported periods lasting up to three to four years. Additionally, because individual harvester activity is likely restricted to relatively small scales (i.e. depending on boat ramp availability and ease of access to the river or trapping locations), population declines may be difficult to detect in areas that are not commonly harvested and shifts in overall population trends may go unnoticed in the short term.

The current commercial turtle harvest regulations in Missouri place few restrictions on commercial harvesters and allow for potentially substantial harvests. Considering the current known decreases in wild turtle populations worldwide, the non-restrictive regulations should be evaluated in light of harvest and population objectives. In response to these concerns and potential impacts of commercial turtle harvest, the collection of turtles for commercial purposes has been banned in multiple states (e.g. Illinois, Indiana, Michigan, Nebraska, Kansas, Florida, Alabama, and South Dakota). Additionally, states that continue to issue commercial turtle harvest permits have recently moved forward to enforce more restrictive limits on these activities (e.g. South Carolina, Georgia) due to observed negative effects on harvested turtle populations (i.e. Minnesota; Gamble and Simons 2003, 2004). Based on our plausible harvest proportions, commercial turtle harvesters have the potential to remove a considerable proportion of turtle populations at a local scale. While the long-term impacts of increased mortality due to commercial harvest of Missouri River turtle populations are unknown, precautionary management of these species is warranted.

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