IMPLICATIONS OF COMMERCIAL HARVEST OF RIVER TURTLES IN MISSOURI

A Thesis

presented to

the Faculty of the Graduate School

at the University of Missouri-Columbia

In Partial Fulfillment

of the Requirements for the Degree

Master of Science

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by

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July 2013

The undersigned, appointed by the dean of the Graduate School, have examined the thesis entitled

IMPLICATIONS OF COMMERCIAL HARVEST

OF RIVER TURTLES IN MISSOURI

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and hereby certify that, in their opinion, it is worthy of acceptance.

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ACKNOWLEDGEMENTS

I would like to thank the University of Missouri and my committee members for assisting me throughout this research. I would especially like to thank my adviser, Dr. Joshua Millspaugh, for the constant confidence, trust, support, and knowledge that he provided throughout this research. I also thank Dr. Jeffrey Briggler for his interest in this project and for his guidance and trust. I wish thank Dr. Craig Paukert for his helpful input and interest, and Dr. Robert Gitzen for his assistance and knowledge which greatly benefitted this work.

I wish to thank the Missouri Department of Conservation (MDC) and the University of Missouri for financial support of this work. I thank Dr. Robert DiStefano and Rochelle Renken for arranging the use of boats in order to conduct my field work. I also thank Norman Murray and Daniel Zekor for their logistical assistance. I thank Phil Pitts for his constant support and assistance, and for his interest in this project. I wish to thank Randy White and Kevin Hempen for assisting with mechanical issues with the boats and trucks. I also thank all MDC and United States Geologic Survey employees who kindly provided me with the bait fish needed to catch turtles on many instances. For their expertise, knowledge, advice, and support, I thank Dr. Gregory Whitledge at Southern Illinois University-Carbondale, and Dr. Alan Shiller at University of Southern Mississippi.

A number of individuals provided their assistance both in the field and in the lab for this project. I thank Cathy Bodinof for her assistance in getting this project started,

and for her research expertise, knowledge, and turtle-handling techniques. I also thank fellow graduate students who assisted with field work including Amy Bleisch, Michael Burfield, Dr. David Jachowski, and Dr. Christopher Rota. I thank Jaymi LeBrun, Alicia Fremgen, Dr. Barb Keller, and Leslie Schreiber for their helpful input and advice on specific aspects of this project. I would also like to thank Preston Feltrop as a fellow technician during the pilot season of this research, and for his assistance in developing field methods. For their patience, work ethic, and sense of humor, I would like to thank Vincent Belfiore, Elizabeth Cantrell, and Kathryn Woods in their assistance as field technicians on this project, and I am grateful for their additional help with lab work. I would also like to thank Tom Bonnot for his assistance with statistical software and analysis, Kathryn Womack for her instruction on laboratory techniques, and Roy Lowery for his advice and for providing me the use of his lab and equipment. I thank Dr. Michael Shaffer for his constant support and his assistance in the field and lab, and my family for their encouragement and confidence in me.

Finally, I extend my special thanks to James Harding, whose fine ethical attitude toward reptiles and amphibians greatly influenced my interest in the field of herpetology, and to Dr. Matthew Douglas for inspiring my interest in biology, and for helping me find the will to go after it.

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ABSTRACT

Commercial turtle harvest is cited as being a major influence of turtle population declines. In Missouri, little is known about the demographics of harvested turtle populations. The three species open to harvest in the state are the common snapping turtle (*Chelydra serpentina*), smooth softshell (*Apalone mutica*), and spiny softshell (*Apalone spinifera*). In order to assess the impacts of harvest on these populations, we completed a mark-recapture study of these species in 2011 and 2012 on the Missouri River and two of its tributaries where harvesting is not legal, the Osage and Gasconade rivers. Using mark-recapture data, we compared turtle abundance in harvested versus unharvested rivers. We then conducted mock harvests at the same sites which were based on capture methods used by Missouri's primary commercial harvester, in order to estimate plausible commercial harvest rates. In both years, snapping turtle abundance was lower in the Missouri River than the Osage and Gasconade tributaries. Due to low capture rates, we were unable to estimate abundance at all sites for either softshell species, and we were unable to test for differences using mark-recapture data. Alternatively, we ran significance tests using raw capture data, which detected no difference in population size for harvested vs. unharvested sites for either softshell species. Mock harvest rates for all turtles averaged removal of 23% of the harvested population (SE = 5%; 6-79%), based on the abundance estimates for each site. Our results suggest that a substantial portion of a population can be harvested on a small scale using the methods we applied. These abundance estimates and harvest rates were used to model population growth of these three species.

In order to assess the potential impacts of harvest on harvested turtle populations, we gathered demographic rates from the literature for the three harvestable turtle species in Missouri, and developed deterministic, density independent, stage-based matrix models to assess turtle population response to our estimated harvest rates. We developed one model for snapping turtles and another for both softshell species combined due to the lack of available species-specific demographic data for either softshell species. Snapping turtle populations had a growth rate of $\lambda = 1.030$ using average vital rate data for survival and fecundity. Minimum demographic rates resulted population declines at $\lambda = 0.891$, and maximum demographic rates resulted in a growth rate of $\lambda = 1.199$. For softshells, populations exhibiting mean demographic rates declined at $\lambda = 0.952$. At minimum demographic rates populations declined further at $\lambda = 0.838$, but at maximum demographic rates population size increased at $\lambda = 1.163$. When we applied our estimated harvest proportions to populations exhibiting mean demographic rates, snapping turtle populations decreased in all instances except when juveniles only were harvested at the minimum harvest rate. For softshells, populations exhibiting mean demographic rates decreased under all harvest scenarios. For populations at mean demographic rates, harvest rates of both adults and juvenile snapping turtles need to be $\leq$ 2.3% to maintain population sustainability ($\lambda = 1$), and for softshells, no level of harvest was sustainable. Conversely, when demographic rates are maximized, harvesting 16.3% of both adults and juveniles was sustainable for softshell populations, and for snapping turtles $\leq$ 18.6% of adults and juveniles may be harvested. In both species, elasticity analyses showed that adults were the most important segment of the population demographically, a finding which coincides with other studies which indicate that even

low levels of harvest may have detrimental local-scale effects on the long-term sustainability of turtle populations.

Commercial harvest of river turtles is restricted to specific rivers in Missouri, though wildlife managers have no way to ensure that turtles are collected from legal waters. To address this issue, we assessed our ability to determine river of capture for individual turtles using microchemistry analysis of turtle nail samples collected from snapping turtles, smooth softshells, and spiny softshells in 2010 through 2012. Sampling occurred in two rivers where turtle harvest is illegal (Gasconade and Osage rivers) and one river where turtle harvest is legal (Missouri River). We used stable isotope analysis (SIA) to determine the composition of stable hydrogen and oxygen isotopes, and inductively coupled plasma mass spectrometry (ICP-MS) to determine the strontium and calcium ratios and concentrations found within turtle nail samples. We used classification and regression tree modeling and *k*-fold cross validation to determine which microchemistry analysis (SIA or ICP-MS) was best at determining the river of capture at the scale of individual rivers and within a classification of legal or illegal waters. Our top-selected CART model, which used results only from the ICP-MS analysis, correctly classified 83.5% of our samples to either a harvested or unharvested river at a rate of based on the ratio of Sr:Ca. Cross-validation indicated that we can expect this model to correctly classify samples at a rate of 76.9%, indicating the level of accuracy we can expect when this model is applied to other data sets. Our methods offer an approach for others interested in confirming the legality of commercial turtle harvest activity, but we caution against application of our model without proper validation.

In order to assist managers in making scientifically-based management decisions regarding commercial harvest of turtles, we provided a list of management recommendations. Recommendations discussed include implementation of slot limits, limiting the harvest season to specific times of the year, rotating harvestable areas annually, requiring thorough harvest reports from harvesters, creating a turtle-specific commercial harvest permit, the use of microchemistry to confirm legal collection, and restricting commercial turtle harvest. These recommendations are discussed in light of sustainable management of harvested turtle populations.

CHAPTER 1

ABUNDANCE AND COMMERCIAL HARVEST PROPORTIONS OF RIVER TURTLES IN MISSOURI

Stephanie A. Zimmer, Jeffrey T. Briggler, Robert A. Gitzen, Joshua J. Millspaugh

ABSTRACT

Turtle populations worldwide are declining, yet managers have little information about the effects of commercial turtle harvests. In Missouri, the common snapping turtle (*Chelydra serpentina*), smooth softshell (*Apalone mutica*), and spiny softshell (*Apalone spinifera*) are harvested commercially in the Missouri River. To help inform future harvest management decisions in Missouri, we completed a mark-recapture study of these species on the Missouri River and two of its tributaries in which harvesting is not legal, the Osage and Gasconade rivers. We completed a pilot study in 2010 to guide future study design and sampling techniques. In 2011 and 2012, we used mark-recapture sampling to compare turtle abundance in harvested versus unharvested rivers. We then conducted mock harvests each year, applying capture methods of the state's primary commercial harvester, to estimate plausible commercial harvest rates. In both years, snapping turtle abundance was lower in the Missouri River than the Osage and Gasconade tributaries. Due to low capture rates, we were unable to compare softshell abundance between harvest and unharvested rivers, but for both softshell species, the same significance test using raw capture data indicated no significant difference in number of unique captures between the Missouri River and the unharvested

tributaries. Mock harvest rates for all turtles averaged a removal of 23% (SE = 5%; 6-79%) of the population, based on our estimates of abundance at each site. Our results suggest that a substantial portion of a population can be harvested on a small scale using the methods we applied. These results will be integrated with other published information as we develop population models for evaluating future harvest management alternatives for river turtles in Missouri.

INTRODUCTION

Turtle populations worldwide are declining as a result of multiple factors, including habitat loss and degradation, mortality from road traffic, and harvesting of wild populations for the food and pet market (Gibbons et al. 2000). Commercial turtle harvest is considered one of the most important influences on population declines (Ceballos and Fitzgerald 2004, Schlaepfer et al. 2005). More than 9.3 million reptiles, 8.9 million of which were turtle and tortoises, were exported from the United States in 1997 alone; a majority of these were shipped to China, Hong Kong, and South Korea (Telecky 2001). Commercial turtle harvest has been closed in many U.S. states, but where permitted, regulations may be loose with few restrictions placed 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 market has been largely under-regulated, which contributes to population declines (Ceballos and Fitzgerald 2004, Cheung and Dudgeon 2006, Gibbons et al. 2000, Schlaepfer et al. 2005).

As long-lived species with delayed reproduction, low fecundity, and no known density-dependent responses to increased mortality rates, turtles are a difficult group to harvest sustainably at a commercial scale (Congdon et al. 1993, Congdon et al. 1994, Crouse et al. 1987, Crouse and Frazer 1995, Galbraith et al. 1997, Heppell 1998, Zhou and Jiang 2008). For common snapping turtles (*Chelydra serpentina*), low rates of commercial harvest can have long-term effects on harvested populations. Natural survival estimates for adult female snapping turtles range from 0.88 to 0.97 (Congdon et al. 1993, Congdon et al. 1994, Galbraith and Brooks 1987) and maintaining this high level of survivorship is considered necessary for long-term population stability (Congdon et al. 1994, Galbraith et al. 1997). 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, model simulations using painted turtle (*Chrysemys picta*) data indicated that the population is susceptible to overharvest when 4-5% of females are removed (Gamble and Simons 2003). Similarly, from a 10 year study of an ornate box turtle (*Terrapene ornata*) population, it was estimated that population declines may occur if total annual adult mortality exceeds 0.05 (Doroff and Keith 1990). Although all turtle size classes have value for 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). Because of low fecundity, 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 harvestable: the snapping turtle (*Chelydra serpentina*), 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 meters of tributary confluences on the Missouri River. 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, federal law prevents sale, holding, and distribution of all turtles less than 4 inches in carapace length. Though no research has assessed abundance of harvested turtle populations in Missouri, a Missouri Department of Conservation (MDC) report showed an increase in total numbers of turtles harvested in Missouri of less than 100 to over 2,000 individual turtles from 1993 to 2007 (approximately 400 individuals were reported in both 2009 and 2012). Despite an overall increase in numbers of turtles removed, the number of commercial turtle harvesters reporting decreased from 17 in 1994 to 6 in 2012, implying that individual harvester activity or effectiveness has increased.

The objective of this study was to estimate abundance and harvest proportions for the three commercially harvestable turtle species (snapping turtles, smooth softshells, and spiny softshells) 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 hypothesized that turtle abundance would be greater in the unharvested Osage and Gasconade rivers than in the Missouri River. We used mark-recapture sampling to estimate abundance and compared abundance among the three rivers. In addition, we carried out mock harvests within our study sites to simulate commercial turtle harvest to determine the proportion of the population that we 'harvested'. Mock harvests were based on methods used by the state's leading commercial harvester. As such, our results indicate the proportion of the population that commercial harvesters might remove on a local scale.

STUDY AREA

Our study was conducted in the Missouri River (9^{th} stream order) and two major tributaries, the Osage River and Gasconade River. These tributaries were chosen as suitable control sites because they are both large-order, and the lower reaches of each maintain similar stream characteristics with the Missouri River, such as high turbidity and presences of sandbars. Additionally, all three of the target species are present in each of these rivers.

We conducted our field work during 2011 and 2012 between river miles (hereafter RM) 154 and 80 of the Missouri River in central Missouri. The confluences of the Osage and Gasconade Rivers occur within this region. The lower reach 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 RM's within our study area contain at least 4 wing dikes, which channelize the river and disrupt the flow along the

banks. 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 balls) also accumulate in these areas, creating appropriate habitat for snapping turtles, as well as 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, the Osage and the Gasconade maintain 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, within the Gasconade River there is wide availability of gravel bars and sandy banks, and relatively little development and recreational use.

River characteristics differed between 2011 and 2012 due to major differences in precipitation. Total rainfall during May through August in central Missouri was 45.85 cm in 2011 vs. 16.28 cm in 2012 (United States Department of Agriculture 2013). On 2 July 2011, the Missouri River at 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 (United States Geological Survey

2013). 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. 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.

FIELD METHODS

PILOT STUDY - 2010

We completed a pilot season in 2010 from 15 June to 8 October on the Missouri, Osage, Gasconade, and Grand Rivers in central Missouri. The purpose of the pilot study was to evaluate different capture methods, assess capture rates of target species, and provide data to guide our future sampling strategy. Sampling took place within a variety of areas in each of the three rivers in order to determine appropriateness of habitat types for trapping and to test effectiveness of various sampling methods (i.e., types of traps, placement of traps within water, type of bait, appropriate water current for setting traps safely). Prior to sampling, we selected trapping locations based on whether turtles were present or likely to be present in the area based on availability of suitable habitat components such as sand bars, sloping banks, woody debris, or submerged root balls. Areas containing no appropriate habitat components for the three target species, as well as areas containing housing and development along the banks, were not sampled.

We used 3 types of traps to capture turtles (round-frame 3-hoop nets, round-frame 7-hoop nets, and mini-fyke nets) because we found that trap types may differ in their effectiveness by habitat type. Additionally, the habitat preferences of snapping

turtles and softshells, as well as 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. We placed approximately 20-30 total nets per night within sections of approximately 5 km of river, predominantly using round-frame 3-hoop nets. We placed these nets in rocky, sandy, gravelly, muddy, or debris-filled areas along banks (Figure 1). Round-frame 7-hoop nets were less versatile, but could be set along stretches banks and sand bars where the current was minimal. We occasionally 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 (Figure 2). All nets were set in contact with the ground and partially submerged, allowing access to the surface of the water for captured animals. Because the purpose of the pilot study was to determine methods to maximize our trapping effectiveness, as well as to locate the three target species and habitat types commonly used by them, traps generally were shifted within a site and to new sites every few days, but if turtles were present trapping continued within one area for up to around 3 weeks in order to assess our ability to recapture marked turtles. GPS coordinates (UTM) were recorded at each trap location.

Minimizing turtle mortality and bycatch was a significant concern when setting traps, necessitating the use of relatively shallow, slow-current areas of the river. We placed all nets to avoid their spinning, collapsing, or becoming completely inundated. We baited all traps using fresh or frozen-thawed fish, typically either invasive carp species or gizzard shad, attached inside the trap. When fish were not available, we used an approximate 1:4 mixture of canned sardines and cracked corn packed into a perforated plastic bottle to allow the scent to disperse throughout the water. We did not allow bait to

remain in a trap longer than two trap nights, as decomposed bait was found to be less effective than fresh bait. We checked traps daily allowing approximately 24 hours per trap night. Traps catching no turtles after 3-4 consecutive days were moved to a new area to minimize time spent at sites where turtles were not present.

We checked all captured turtles for previous marks and tags and recorded all instances of recaptures. All new snapping turtles were given a daily cohort mark by filing marginal scutes according to an alphabetical system that assigns a unique letter code per day. Because softshell turtles do not have defined scutes, this method could not be used with either of the softshell species. New individuals of all three target species were injected with an AVID (American Veterinary Identification Devices; Norco, California) passive integrated transponder (PIT) tags (12 mm, 125 kHz), each encrypted with a unique 9-digit code for individual identification. Initially we injected PIT tags directly underneath the posterior side of either the left or right bridge, but due to difficulty of injecting tags in this bony area, we decided to inject tags subcutaneously in the left inguinal region (Figure 3). Softshell turtles less than approximately 90 mm in carapace length and hatchling snapping turtles were not injected with PIT tags because of issues with size and fragile skin; in these cases, turtles were given unique clips using scissors along the back margin of their carapace (Figure 4). We sexed all individuals and determined stage (hatchling, juvenile, or adult) according to stage-specific size limits, measured with straight carapace length, described by Johnson (2000). Straight carapace length and straight plastron length were measured using calipers. All non-target turtle species were also given a daily cohort mark, and were sexed, staged, and measured as described above. Once processed, all turtles were released at the capture location. These

methods were approved by the University of Missouri Animal Care and Use Committee Protocol #6744.

ABUNDANCE ESTIMATES AND MOCK HARVEST - 2011 AND 2012

Site Selection

Based power and precision analyses using the 2010 pilot data, we randomly selected 6 1-km sites on the Missouri River and 3 1-km sites on both the Osage and Gasconade rivers to be trapped for the 2011 and 2012 field seasons. We selected Missouri River sites by first stratifying a 75 RM stretch of the river into three 25 RM units: RM's 80-104, 105-129, and 130-154. Because the Osage-Missouri confluence (at approximately RM 130) and Gasconade-Missouri confluence (at approximately RM 105) are within this 75-mile 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 8 RM from each of the 3 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 balls, submerged debris). Finally, using aerial imagery with 0.61 m resolution, we randomly selected 2 RM from the remaining sites at each of the 3 units. We defined 1 km trap sites as the downstream-most 1000 m of each selected RM (Figure 5).

We limited selection of trapping sites in the Osage and Gasconade Rivers to within the first 11 RM of the confluence due to the placement of a dam structure on the

Osage River at approximately 11.5 miles 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 decreases rapidly as one moves further upstream. Using 0.61 m resolution aerial imagery in ArcGIS, 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 3 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 (Figure 5).

Field Methods – Abundance Estimates

In 2011 and 2012, we conducted a mark-recapture study within 10 of the 12 randomly selected RM's (Figure 6). We were able to sample 6 of these 10 sites in both 2011 and 2012; two of the Missouri River sites could only be sampled in 2011 due to continuous human disturbance to our traps in 2012, and the two additional Missouri sites selected to replace these were only sampled in 2012. In both years we were unable to carry out sampling within one of the sites at both the Osage and Gasconade rivers due to time constraints and weather-related issues. Trapping took place from 6 May to 8 September in 2011 and from 19 April to 18 August in 2012. We used 3 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. The round-frame 7-hoop nets used during the pilot study were not sufficiently effective and were excluded from the study. We placed approximately 20 total nets at each site, predominantly using round-frame 3-hoop nets. For areas of high current where round-frame nets were prone to rolling, we used D-frame

3-hoop nets (Figure 7) which are less-prone to shifting in the current. We occasionally used mini-fyke nets where appropriate, as described for the pilot study methods. Traps were baited using fresh or frozen-thawed fish (typically either invasive carp species or gizzard shad) attached inside the trap. When 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 a plastic bottle which had been perforated to allow the scent to disperse throughout the water.

Each trap was set for 8 trap nights and checked daily. We checked all captured turtles for previous marks and tags. All new turtles were marked with a PIT tag and daily cohort mark, sexed, staged, and measured following the pilot study methods. All turtles were released at the location of capture.

Field Methods - Mock Harvest

At each of the 10 sampling sites we conducted a mock harvest within 6 days (environmental conditions permitting) of completing the mark-recapture, using D-frame hoop nets manufactured to the exact specifications of the traps used by one of Missouri's leading commercial turtle harvesters (Figure 7). We set 20-25 traps within each 1-km trap site and we trapped 2 sites simultaneously for 4 consecutive trap nights. Within each site, we placed 4 to 5 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. All captured turtles were processed using the same methods

used during the mark-recapture. 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 meters from other active nets. Adult snapping turtles were never held in the same net with either of the softshell species, to avoid risk of aggression, injury, or depredation. Similarly, no more than 2 snapping turtles were held together within the same net. In most situations we kept no more than 3 or 4 softshells together in one net. We checked and provided bait fish daily to all nets containing captive turtles. After completion of the mock harvest, all turtles were released at their capture locations.

ANALYTICAL METHODS

PILOT STUDY - 2010

Using pilot study data, we completed power and precision analyses to design our mark-recapture experiments for 2011 and 2012. To estimate capture probabilities for the power analysis, we used mark-recapture data from a 2010 pilot Missouri River trap site where we spent 18 consecutive days. This 18-day stretch was selected because sample sizes were sufficient and because the methods used during this time most closely represented how sampling would be carried out during the 2011 and 2012 field seasons. We pooled captures across species, sex, and stage class. Although systematic differences in detectability within and among these groups might be expected, we did not examine complex heterogeneity models because of sparse data and the low percentage of animals captured more than once. A preliminary examination of patterns in the data did not indicate that any species, sex, or stage subgroup had dramatically different capture patterns than others.

We analyzed data in Program CAPTURE (White et al. 1982) and Program MARK (White and Burnham 1999) to estimate capture probability. We examined evidence for three sources of heterogeneity in detectability: temporal (the potential for capture probability to vary across trap nights), behavioral (altered probability of capture after first capture of an individual), and individual (additional animal- or group-specific variation). Because using more flexible models did not provide feasible estimates for this data set, we focused on the following three models to estimate capture probability: Model M_t in Program CAPTURE (assumes temporal heterogeneity; favored by Program CAPTURES model discrimination routine), Model M_b (assumes trap response heterogeneity), and Model M_{th} (assumes both trap response and individual heterogeneity).

To evaluate precision of closed population multi-period mark-recapture estimates and our statistical power to detect differences in abundance, we looked at various combinations of average nightly detectability, average abundance per site, trap nights per site, number of sites per site type (harvested or unharvested), and the minimum difference we wanted to detect between harvested and unharvested sites. Daily capture probabilities of 0.05 and 0.10 were used based on estimates by Plummer (1977) and estimates from this study. We considered 500 turtles per km as the upper abundance limit given work by Plummer (1977). For each combination of the two capture probabilities of 0.05 and 0.10 and population densities of 100 and 500 turtles per km of river, we examined 12 different scenarios, combining various number of trap nights (4, 8, 12, or 16) spent at varying numbers of sites (3, 6, or 9). Expected average precision of site-level abundance estimates were based on Darroch's constant probability model (Model M_0), which

assumes no temporal, behavioral or trap-response heterogeneity. The associated estimation variance is (Skalski and Robson 1992:68):

$$\mathrm{Var}(\widehat{N} \mid N) = N\left[\left(1 - p\right)^{-k} - k\left(1 - p\right)^{-1} + k - 1\right]^{-1},$$

where $\widehat{N}$ = estimated abundance; N = true abundance; p = daily probability of capture for each individual; k = number of survey days. Though the model assuming temporal heterogeneity (Model M_t) was favored in analysis of 2010 data, Model M_0 was selected for its simplicity (i.e., no heterogeneity) and because of the limited amount of data. By appropriately selecting a model to be used for analysis of the real data set (i.e., data collected during the 2011 and 2012 field seasons), we assumed that the estimated precision from the pilot data analysis would be similar to that of the analysis of the data collected in the 2011 and 2012 field seasons.

Using the same scenarios examined for the precision analysis (i.e., 4, 8, 12, or 16 trap nights spent at 3, 6, or 9 sites), we assessed our power to detect a 25% difference between the harvested and unharvested populations. We assumed both populations shared a common, constant daily capture probability (p) of either 0.10 or 0.05 and had a true population size of either 100 or 500. To estimate power, the following calculation was used (Skalski and Robson 1992:105, 4.21):

$$\text{Power} = (1 - \alpha) - P\left(Z_{\alpha/2} \leq Z \leq Z_{1-(\alpha/2)} - \frac{\left|\ln K_0 - \ln K'\right|}{\sqrt{\mathrm{Var}(\ln \widehat{K} \mid K)}}\right),$$

where

$\widehat{K}$ = the proportional estimated abundance $\left(\frac{\widehat{N}_2}{\widehat{N}_1}\right)$ for each population, $\widehat{N}_1$ and $\widehat{N}_2$,

K_0 = true proportional abundance value under the null hypothesis,

K' = the alternative real proportional real abundance.

The 95% confidence limits of *K* were determined using the following equation from Skalski and Robson (1992:101, 4.15):

$$Z_{1-(\alpha/2)} = \frac{\frac{K}{\widehat{N}_2} - \frac{1}{\widehat{N}_1}}{\sqrt{\frac{K^2 \widehat{\mathrm{Var}}(\widehat{\mathrm{N}}_2|\mathrm{N}_2)}{\widehat{N}_2^4} + \frac{Var(\widehat{\mathrm{N}}_1|\mathrm{N}_1)}{\widehat{N}_1^4}}},$$

where $\widehat{N}_1$ and $\widehat{N}_2$ = abundance estimates for the two populations (harvested and unharvested) and N_1 and N_2 = real abundance for the two populations, respectively.

ABUNDANCE ESTIMATES – 2011 AND 2012

We paired the 1 km sites based on location due to low sample sizes, resulting in the analysis of 4 harvested (Missouri River) 2 km units and 4 unharvested (Gasconade and Osage rivers) 2 km units. Abundance was estimated within each unit using mark-recapture data from the first 8 trap nights and the capture data from the following 4-night mock harvests. Because we 'harvested' turtles during mock harvests, these individuals were indicated as no longer available for capture during subsequent trap nights when estimating abundance. We used Program MARK to determine estimate abundance within each of these 2-km units, using two closed capture models, Model M_0 and Model M_t. As sample sizes were low in some cases (i.e., 4 total smooth softshell captures on the Gasconade River in 2011), sex and stage were lumped within each species for each of the

three Missouri River trapping units and for each tributary. For groups of turtles that contained no recaptures (i.e., both species of softshells on the Osage River in both 2011 and 2012), data were not sufficient for obtaining reasonable estimates and no additional analysis was carried out.

A comparison of the abundance estimates between the harvested (treatment, *T*) and unharvested (control, *C*) populations was carried out using the following statistic (Skalski and Robson 1992:121, 5.3):

$$d = \frac{\bar{X}_{C\cdot} - \bar{X}_{T\cdot}}{\sqrt{\frac{s^2_{X_C}}{l_C} + \frac{s^2_{X_T}}{l_T}}},$$

where

$$X_{ij} = \ln \widehat{N}_{ij}$$

$$\bar{X}_{i\cdot} = \sum_{j=1}^{l} \frac{\ln \widehat{N}_{ij}}{l}$$

$$S^2_{X_i} = \frac{\sum_{j=1}^{l} (\ln \widehat{N}_{ij})^2 - \frac{\left(\sum_{j=1}^{l} \ln \widehat{N}_{ij}\right)^2}{l}}{l-1}$$

and *d* is approximately distributed as a t-statistic with $(l_C + l_T - 2 = 2l - 2)$ degrees of freedom. To compare harvested and unharvested rivers, $\widehat{N}_{ij}$, the estimated abundance at the *j*th replicate plot ($j = 1, \ldots, l_i$) of the *i*th treatment ($i = C, T$), was modeled as (Skalski and Robson 1992:120, 5.2):

$$\widehat{N}_{ij} = \mu\tau_i\epsilon_{ij} ,$$

where

μ = overall mean

τ_i = effect of the *i*th treatment (*i* = *C*, *T*)

ϵ_{ij} = multiplicative error associated with the *j*th plot (*j* = l, …, l_i) and *i*th treatment (*i* = *C*, *T*)

$$\ln \widehat{N}_{ij} = \ln \mu + \ln \tau_i + \ln \epsilon_{ij}$$

MOCK HARVEST – 2011 AND 2012

To determine the proportion of the population that was removed during the mock harvest, we used the overall abundance estimates and daily capture rates for all trap nights of the mock harvest estimated with Model M_t in Program MARK. 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 nightly capture rate for each night (*i*) of the mock harvest.

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

$$\text{var}\,(H) = \text{var}[f(p_1, p_2, p_3, p_4)]$$

$$= \sum_{i=1}^{4} \mathrm{var}(p_i) \left[\frac{\partial f}{\partial p_i}\right]^2 + 2 \sum_{i=1}^{n4} \sum_{j=1}^{4} \mathrm{cov}(p_i, p_j) \left[\frac{\partial f}{\partial p_i}\right] \left[\frac{\partial f}{\partial X p_j}\right],$$

where H = the estimated 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; $\frac{\partial f}{\partial p_i}$ and $\frac{\partial f}{\partial p_j}$ are the partial derivatives with respect to each nightly capture probability. All variance and covariance estimates were obtained from MARK output for Model M_t.

When determining our percentage of recaptures (Table 1), turtles whose true initial capture occurred outside of the usable data set (i.e., unusable data included capture data from the pilot season, failed trapping attempts, etc.) were considered "new" upon first recapture within the usable data set at each site. This ensured that recapture estimates were not affected by considering an individual "recaptured" when in reality its true initial capture occurred outside of the usable data set. This situation occurred for 29 of the 741 total captures from the usable data set.

RESULTS

PILOT STUDY – 2010

Our estimated nightly capture probabilities (p) using Model M_t (the most supported model) were low, ranging from 0.02 to 0.05 (mean p = 0.024, SE = 0.003). Results from the other two models provided similar, though lower, estimates: Model M_b (p = 0.018), and Model M_{th} (mean p = 0.016, SE = 0.002), and provided comparable results. The data used for this analysis included the capture of 110 turtles of all three target species (66 smooth softshells, 35 spiny softshells, and 9 common snapping turtles).

Of these turtles, 93 were captured once, 13 were captured twice, 3 were captured three times, and 1 was captured 4 times.

Using the different scenarios discussed previously, we assessed relationship between power and effort at $\alpha = 0.05$. We concluded that 8 trap nights at each of 6 randomly selected 1 km sites on the Missouri River and at 3 randomly selected 1 km sites on both the Osage and the Gasconade rivers optimized effort and minimized bias, and would be sufficient to meet our objective to be able to detect at least a 25% difference between unharvested and harvested populations (Appendix A and B). The assumption of homogenous capture probabilities across populations is optimistic, so our power values were an optimistic upper bound.

ABUNDANCE ESTIMATES – 2011 AND 2012

For snapping turtles, we calculated abundance per 2 km at each of the 4 harvested units, and at each of the 4 unharvested units. Abundance was lower at Missouri (harvested) units (Table 1; $\bar{X}$ = 14.750; SE = 7.075) than at unharvested units ($\bar{X}$ = 90.000; SE = 40.330; test of equal log-scale average abundance: two-sample t(6) = -2.961, p-value = 0.025; Skalski and Robson 1992:121, 5.3). For smooth softshells, the greatest abundance estimates occurred at the harvested units (Table 1). No recaptures at 1 of the harvested units (MOJ12) and at 3 of the unharvested units (OS11, OS12, and GA11) prevented us from estimating abundance in each of these cases (Table 1). A test of significance based on estimates of abundance was not possible for harvested versus unharvested populations since a feasible abundance estimate could only be made within one of the unharvested sites. Alternatively, using the raw capture data, we ran the same

significance test as with snapping turtles, but based on the number of unique captures at each site. This test indicated that the number of smooth softshell captures was not significantly different between Missouri River sites ($\bar{X}$ = 58.750; SE = 7.879) and unharvested sites ($\bar{X}$ = 13.500; SE = 28.078; test of equal log-scale average captures: two-sample t(6) = 2.119, p-value = 0.078). Estimating abundance for the remaining three unharvested sites one harvested site was not possible as with smooth softshells. Likewise, a test of the number of unique captures on the Missouri River sites ($\bar{X}$ = 17.500; SE = 4.291) versus captures at unharvested sites ($\bar{X}$ = 17.250; SE = 9.691) indicated no significant difference (test of equal log-scale average captures: two-sample t(6) = 0.7675, p-value = 0.4719).

MOCK HARVEST – 2011 AND 2012

During our mock harvests, we removed from 6.7% to 56.8% of the snapping turtle population (Table 2). In most cases, harvest proportions were lower at unharvested units than at harvested units. For smooth softshells, we removed from 8.8% to 33.6% of the marked population and harvest proportion was greatest at the unharvested unit. Proportions could not be calculated for 3 unharvested units and for 1 harvested unit due to lack of recaptures and inability to estimate abundance. For spiny softshells, we removed from 6.2% to 79.2% of the population and harvest proportions were greater at harvested units than at unharvested units. Similar to the smooth softshell results, spiny softshell harvest proportions could not be calculated for 2 of the harvested units and 2 of the unharvested units (Table 2).

DISCUSSION

Harvest proportions obtained in this study indicate that commercial turtle harvesters have considerable potential for removing a sizeable proportion of harvestable turtle populations, at least on a small scale within the Missouri River. All of our harvest proportions exceeded 6%, and half exceeded 20%. These proportions represent a plausible estimate of removals in trapped regions under the state's current regulations with methods used by the state's leading commercial turtle harvester. Additionally, the lowest of these proportions exceed total mortality rates of approximately 5%, which has been reported to be detrimental to the long-term to the sustainability of other turtle populations including box turtle (Doroff and Keith 1990) and painted turtle populations (Gamble and Simons 2003). Natural mortality rates for adult turtles are generally low, which is important to maintain population stability (Doroff and Keith 1990, Galbraith et al. 1997). Because turtles are not known to respond to decreases in population density via increased reproduction (Brooks et al. 1991), additional mortality resulting from commercial harvest activity may not be sustainable (Ceballos and Fitzgerald 2004, Congdon et al. 1994), particularly when few restrictions are placed on commercial harvesters.

This research is among the few studies to estimate abundance of turtle species in large river systems. Estimates of abundance have been made for snapping turtles in non-riverine systems (e.g., 60.5 individuals per ha; Decker Major 1975), but comparisons with these studies can be difficult to make because of the linearity of riverine habitats when compared to lakes or ponds. For long-lived species such as turtles, feasible abundance estimates are necessary when formulating management decisions. Our

estimates indicated that within our study area, snapping turtle abundance was lower at our Missouri River sites than the unharvested tributaries. Smooth softshell abundance estimates were considerably higher on the Missouri River compared to both spiny softshells and snapping turtles, but is not necessarily an indication that the population can sustain added mortality from harvest pressure. Because our significance tests for both softshell species are based on raw capture data (i.e., unique captures), these calculations may be capture-biased. Where estimating abundance was feasible for smooth softshells, high abundance estimates on the Missouri River may indicate that this species is not being harvested heavily, despite being available for harvest. It has been suggested that commercial harvesters do not target this species as much as the spiny softshell or snapping turtles because of high instances of mortality during shipment (live shipments are typically preferred). Additionally, smooth softshells are typically smaller-bodied at maximum size compared to spiny softshells and snapping turtles, thus making an individual smooth softshell less valuable on the market when sold by weight.

Our trapping sites were randomly selected from approximately 121 consecutive kilometers (75 miles) of river that is open to commercial turtle harvest, and it is unknown if commercial harvest took place within any of our randomly selected sites at any point in time. 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) can also create difficulty in observing large-scale trends within the population. Additionally,

many of these species have not been subjected to long-term research, which creates difficulties in detecting shifts in demographic rates (Gibbons et al. 2000). Because collection of solid 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 harvest proportions we observed, the effects of commercial harvest occur at a local scale. This observation is confirmed 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 3 to 4 years.

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, collection of turtles for commercial purposes has been banned in multiple states (e.g., Illinois, Indiana, Michigan, Nebraska, Kansas, Florida, Alabama, South Dakota). Additionally, states that continue to issue commercial turtle harvest permits have recently moved forward with decisions 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 rates, commercial turtle harvesters have the potential to remove a considerable proportion of

turtle populations at a local scale, and our results have indicated that snapping turtle abundance in the harvested Missouri River is significantly less than in the unharvested tributaries. While the long-term impacts of increased mortality due to commercial harvest of Missouri River turtle populations is unknown, precautionary management of these species is likely warranted.

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TABLE 1: ABUNDANCE ESTIMATES ($\widehat{N}$) PER 2 KM OF RIVER. Unit = 2 km trapping units. Trap Nights = total 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 1 time following initial capture. Mean Capture Probability = the mean nightly probability that an individual will be captured during a given trap night. Capture Proportion = proportion of the population that was captured at least once during the span of each trap run.

Species	River Status	Unit*	Trap Nights	*n*	Proportion Recaptures	Mean Capture Probability	$\widehat{N}$	SE	LCI	UCI	Capture Proportion
Common Snapping Turtle	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
Smooth Softshell	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
Spiny Softshell	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

*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

TABLE 2: HARVEST PROPORTIONS FOR SNAPPING TURTLES, SMOOTH SOFTSHELLS, AND SPINY SOFTSHELLS AT HARVESTED AND UNHARVESTED SITES. Harvest proportion represents the proportion of each population that was captured ('harvested') during each mock harvest, based on nightly capture probabilities and the overall abundance estimates ($\widehat{N}$) at each unit (see Table 1). Unit = 2 km trapping unit. Trap Night = 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 1 time following initial capture. Variance was estimated using the Delta Method (Powell 2007).

Species	River Status	Unit*	Trap Nights	*n*	Proportion Recaptures	Harvest Proportion	SE
Common Snapping Turtle	Harvested	MOH11	164	3	0.333	0.568	0.3
		MOM11	163	1	1.000	0.249	0.2
		MOH12	176	3	0.667	0.086	0.1
		MOJ12	160	2	1.000	0.139	0.2
	Unharvested	OS11	144	14	0.214	0.199	0.1
		GA11	147	7	0.571	0.128	0.1
		OS12	172	14	0.071	0.067	0
		GA12	160	7	0.143	0.260	0.2
Smooth Softshell	Harvested	MOH11	164	35	0.229	0.117	0
		MOM11	163	13	0.231	0.088	0
		MOH12	176	12	0.167	0.088	0
		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	0.1
Spiny Softshell	Harvested	MOH11	164	8	0.500	0.792	0.2
		MOM11	163	4	0.250	0.219	0.1
		MOH12	144	0	0.000	-	-
		MOJ12	147	6	0.000	-	-
	Unharvested	OS11	176	3	0.667	0.062	0
		GA11	160	5	0.000	-	-
		OS12	172	1	0.000	-	-
		GA12	160	17	0.529	0.236	0.1

*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.

Figure 1: A typical set used with the 3-hoop and D-hoop nets.

Figure 2: A typical mini-fyke net set.

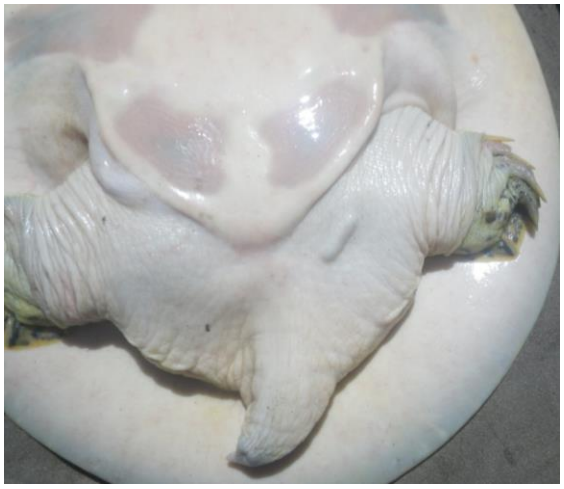


Figure 3: PIT tag injected subcutaneously in the inguinal region of an adult female spiny softshell turtle (Apalone spinifera).

Figure 4: A hatchling smooth softshell turtle (Apalone mutica) exhibiting unique clip marks along the posterior margin of the carapace.

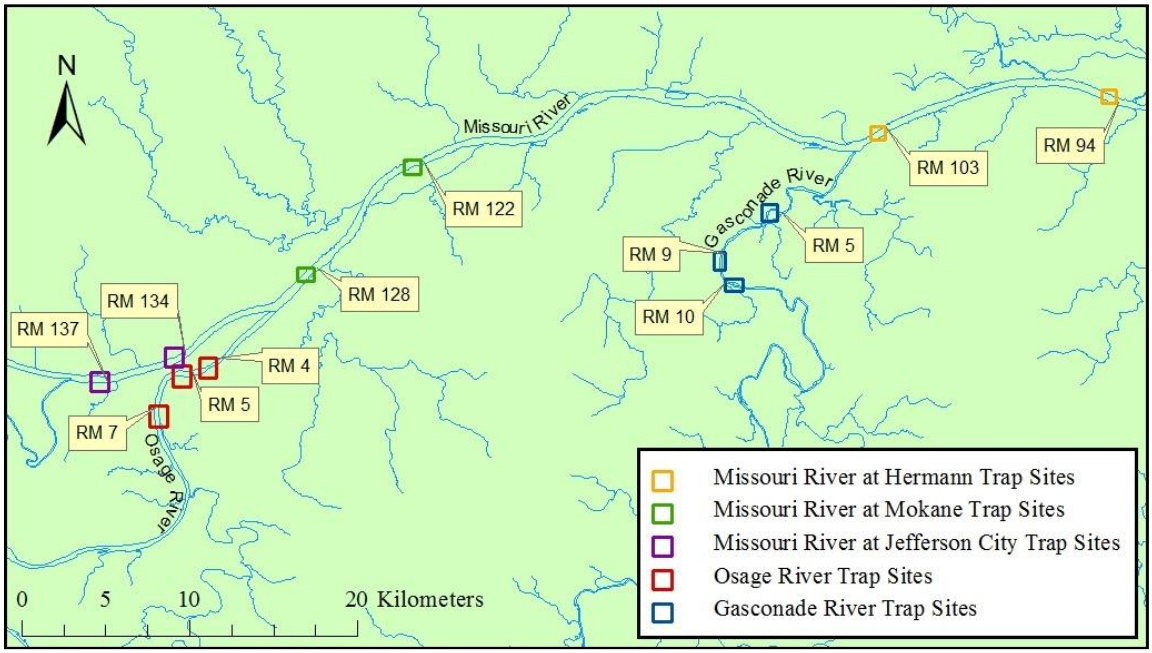


Figure 5: Map of the 12 randomly selected sites to be trapped in the 2011 and 2012 field seasons. RM indicates river mile.

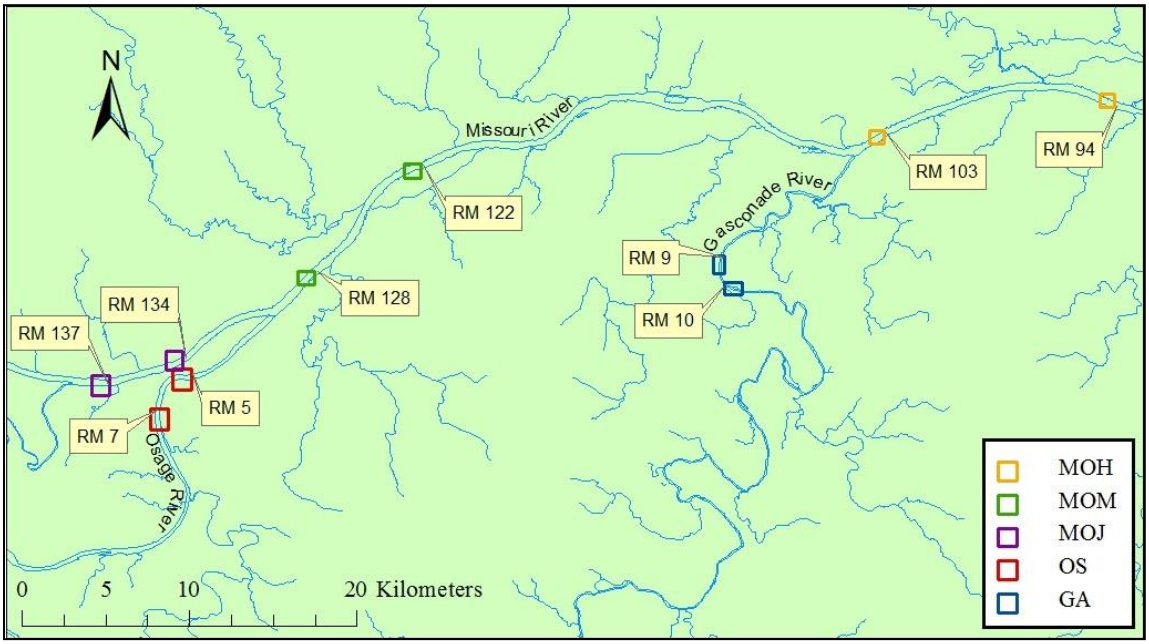
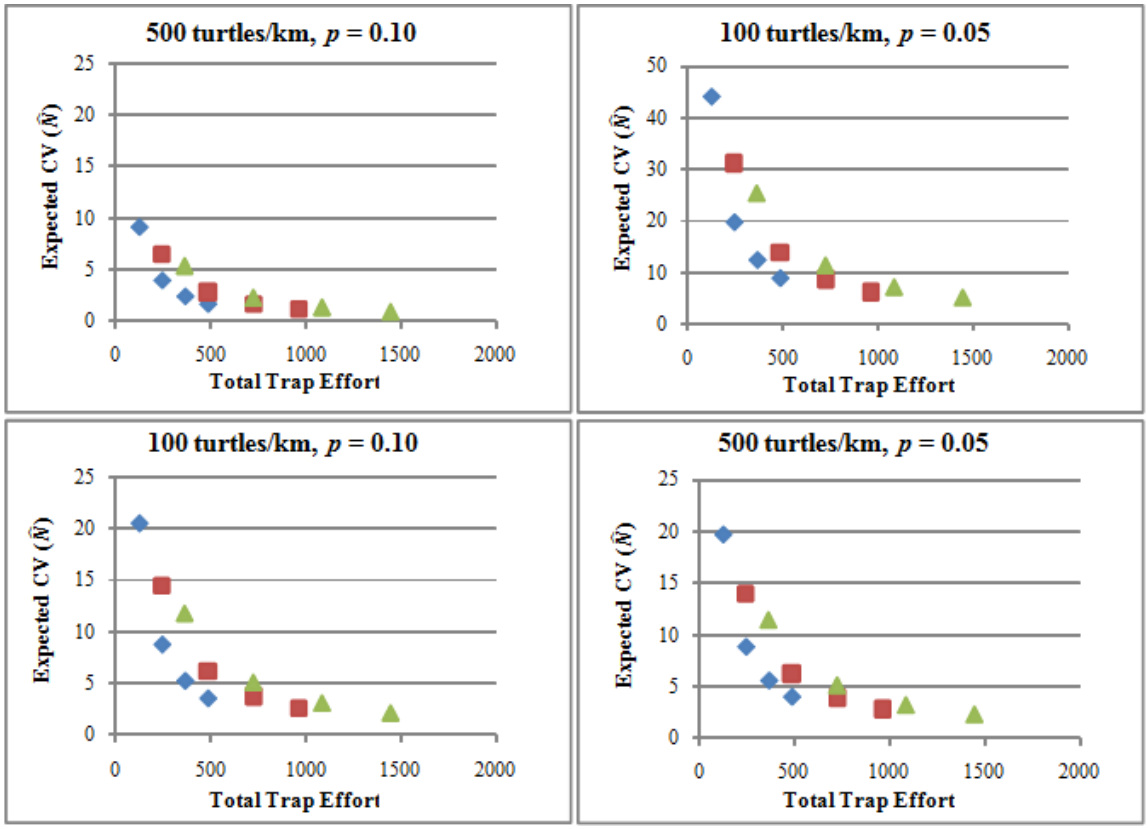


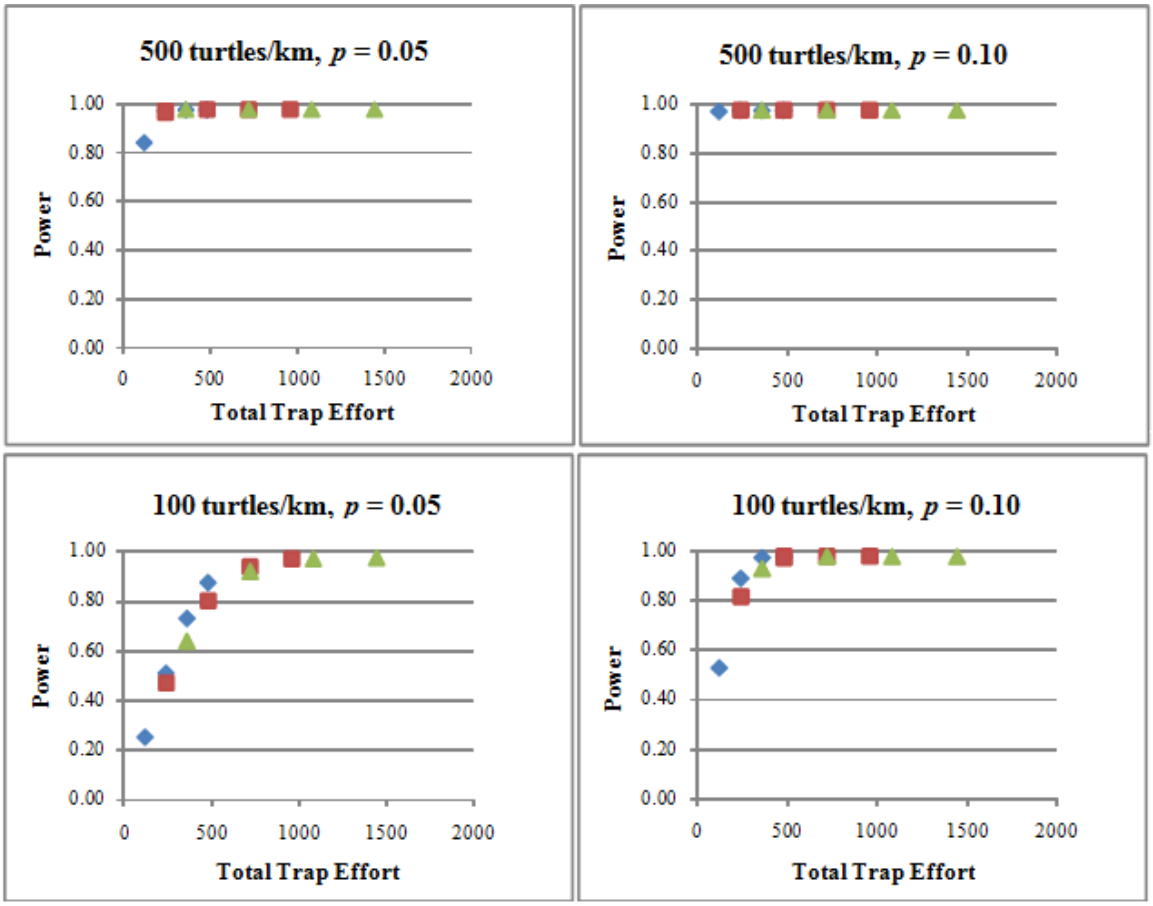
Figure 6: Map of the 10 sites trapped for mark-recapture and mock harvest during the 2011 and 2012 field seasons. RM indicates river mile. MOH = Missouri River at Hermann (river miles 94 and 103, trapped in 2011 and 2012); MOM = Missouri River at Mokane (river miles 122 and 128, trapped in 2011); MOJ = Missouri River at Jefferson City (river miles 134 and 137, trapped in 2012); GA = Gasconade River (river miles 9 and 10, trapped in 2011 and 2012); OS = Osage River (river miles 5 and 7, trapped in 2011 and 2012).

Figure 7: Custom-made traps built to mimic traps used by Missouri's leading commercial turtle harvester. For use during the mock harvest portion of the study, traps built to these exact specifications were purchased.

Appendix A: Our expected precision of mark-recapture abundance estimates for a single population versus total trap effort for the population for a range of sampling scenarios. Two nightly capture probabilities (p = 0.05 and p = 0.10), and two average densities (100 and 500 turtles/km) were assessed at 4 to 16 nights of trapping (periods) per site (periods increment from 4 to 16 moving from left to right across each plot). Finally, these scenarios were assessed at 3, 6, or 9 1-km sites per population, denoted by different symbols (◇ for 3, □ for 6, △ for 9). Total effort per population is calculated as (number of trap periods) x (number of sites) x (10 traps per site); changing the number of traps per site does not affect the shape of the curve.



Appendix B: Our power to detect a 0.25 difference in abundance between two populations (assuming the null hypothesis is that $N_1/N_2 = 1$ and $\alpha = 0.05$) versus total trap effort per population for a range of sampling scenarios. Two nightly capture probabilities ($p = 0.05$ and $p = 0.10$), and two average densities (100 and 500 turtles/km) were assessed at 4 to 16 nights of trapping (periods) per site (periods increment from 4 to 16 moving from left to right across each plot). Finally, these scenarios were assessed at 3, 6, or 9 1-km sites per population, denoted by different symbols (◇ for 3, □ for 6, △ for 9). Total effort per population is calculated as (number of trap periods) x (number of sites) x (10 traps per site); changing the number of traps per site does not affect the shape of the curve.



CHAPTER 2

MODELING THE EFFECTS OF COMMERCIAL HARVEST ON POPULATION GROWTH OF RIVER TURTLES

Stephanie A. Zimmer, Jeffrey T. Briggler, Joshua J. Millspaugh

ABSTRACT

Commercial turtle harvest is considered one of the major contributing factors to declines in turtle populations. Few long-term studies have evaluated turtle population response to harvest and little is known about demographic rates for many turtle species. We gathered demographic rates from the literature for snapping turtles (*Chelydra serpentina*), smooth softshells (*Apalone mutica*), and spiny softshells (*Apalone spinifera*), which are harvested in Missouri, and developed deterministic, density independent, stage-based matrix models to assess turtle population response to plausible harvest rates we estimated from field sampling. We developed one model for snapping turtles and another for both softshell species combined due to the lack of available species-specific demographic data for either softshell species. Using mean demographic rates for survival and fecundity, snapping turtle populations had a growth rate of $\lambda = 1.030$, at minimum demographic rates had a growth rate of $\lambda = 0.891$, and at maximum demographic rates a growth rate of $\lambda = 1.199$. For softshells, population growth at mean demographic rates was $\lambda = 0.952$, at minimum demographic rates was $\lambda = 0.838$, and at maximum demographic rates was $\lambda = 1.163$. When we applied plausible harvest rates to snapping turtle populations exhibiting mean demographic rates, populations decreased in all instances except when

juveniles only were harvested at the minimum harvest rate. Likewise, for softshells exhibiting mean demographic rates, populations decreased under all harvest scenarios. For snapping turtles, harvest rates of both adults and juveniles need to be ≤ 2.3% to maintain population sustainability ($\lambda = 1$) at mean demographic rates. For softshells, no level of harvest is sustainable for populations exhibiting mean demographic rates. Conversely, for both snapping turtles and softshells, harvest is sustainable when demographic rates are at the maximum values examined: for softshells, harvest 16.3% of both adults and juveniles is sustainable for populations under maximum demographic rates; similarly, for snapping turtles, ≤ 18.6% of adults and juveniles may be harvested to maintain population sustainability. In both species, elasticity analyses showed that adults, which are the most vulnerable to commercial harvest, are the most important segment of the population demographically. These results corroborate the findings other studies, which indicate that even low levels of harvest may have detrimental effects on the long-term sustainability of turtle populations at localized scales.

INTRODUCTION

Commercial turtle harvest is a major cause of turtle population declines (Ceballos and Fitzgerald 2004, Schlaepfer et al. 2005), though little is known about the long-term demographic effects (Congdon et al. 1994). Because of their life history characteristics and demographic rates, such as high adult survivorship, low nest and hatchling survivorship, and late age at first reproduction, turtles are not highly amenable to sustainable commercial harvest (Congdon et al. 1993, Congdon et al. 1994, Crouse et al. 1987, Crouse and Frazer 1995, Galbraith et al. 1997, Heppell 1998, Zhou and Jiang 2008). For the common snapping turtle (*Chelydra serpentina*), annual survivorships of

0.88 to 0.97 have been reported (Congdon et al. 1993, Congdon et al. 1994, Galbraith and Brooks 1987) and maintaining this high annual adult survivorship is among the most important factors contributing to long-term population sustainability (Congdon et al. 1994). However, adults are also the most desirable from a harvest standpoint because they are often sold by weight on the food market (Brown et al. 2011). Because harvesters may target adult turtles for this reason, there may be a potential for population declines due to harvest pressure placed on the adult stage class.

In North America, for the few turtle populations with available long-term life history and demographic data, both field data and population modeling suggest that small increases in annual mortality can be detrimental to population sustainability (e.g., Brooks et al. 1991, Congdon et al. 1994). Painted turtle (*Chrysemys picta*) populations in Minnesota are susceptible to overharvest when 4% to 5% of females are removed (Gamble and Simons 2003). Similarly, a 10-year study of an ornate box turtle (*Terrapene ornata*) population in Wisconsin indicated that population declines may occur if total annual adult mortality exceeds 5% (Doroff and Keith 1990). Further, there is no evidence that turtle populations exhibit density-dependent reproductive responses when removals occur (Brooks et al. 1991). Thus, these turtle populations are unable to adequately compensate for losses owed to commercial harvest through increased reproduction (Congdon et al. 1994).

In Missouri, the common snapping turtle, the smooth softshell (*Apalone mutica*), and the spiny softshell (*Apalone spinifera*) are the three turtle species open to commercial harvest. Commercial turtle harvest may take place year round with no size or bag limit;

the only restrictions are the type of net used and the waterways in which turtles may be captured (e.g., the Missouri, Mississippi, and St. Francis rivers). Currently in Missouri, there are no data available on population size or structure for these species, and no indication of the effects of harvest on population sustainability. Given the potential sensitivity of river turtle populations to harvest, it is important to address how plausible harvest rates in Missouri could affect population growth rates for these species.

The objective of this research was to assess the effects of commercial turtle harvest on populations of common snapping turtles, smooth softshells, and spiny softshells using plausible harvest rates (Chapter 1). Using demographic rates found in the literature for the three target species, as well as harvest rates estimated during our 2011 and 2012 field seasons (Chapter 1), we modeled population growth and the effects of commercial harvest on turtle populations under mean, minimum, and maximum demographic rates using female-only stage-structured matrix models (Lefkovitch 1965). We also conducted sensitivity and elasticity analyses to determine which demographic parameters are most important to population growth (λ) and examined the implications of these analyses for conservation of harvested turtle populations.

METHODS

LITERATURE REVIEW

We conducted a literature review to obtain demographic rates for snapping turtles, spiny softshells, and smooth softshells for use in matrix models. We collected values for the following parameters: nest survival, hatchling survival, juvenile survival, adult survival, duration (years) of the juvenile stage class, clutch size (number of eggs in a

single nest), breeding frequency (the proportion of females reproducing annually), and number of clutches produced annually. We used several filters to select data for this analysis. We used data from the literature if when sample sizes were greater than 10 turtles or nests in the study. Additionally, we excluded demographic rates that were estimated under unusual circumstances, such as decreased adult survivorship resulting from an abnormal increase in predation (e.g., Brooks et al. 1991). Because the models we constructed were female-only, we only included adult survivorship rates that were either female-specific (e.g. Congdon et al. 1994) or reported as equal among both sexes (e.g., Paisley et al. 2009). Where authors reported a mean value for a demographic rate, we used the mean value rather than a range (e.g., Congdon et al. 1994 reports nest survivorship over 17 years to range from 0-64%, mean 23%). Because the rates of nest survivorship were sparse in the literature, we also included the reported proportions of known nests not destroyed by predators, a commonly cited source of mortality for nests (e.g., Plummer 1976, Robinson and Bider 1988).

DATA SUMMARIZATION

We divided snapping turtle data (Table 1) from the softshell data (Table 2), but combined softshell .species due to the paucity of species-specific softshell turtle demographic data. In two instances, we used rates reported for the common snapping turtle where softshell data were unavailable (i.e., hatchling survivorship and breeding frequency). We included our estimates of abundance and harvest proportions (Chapter 1) in our data summary.

From the range of variables for each parameter collected from the literature, we calculated mean, minimum, and maximum values for both snapping turtles and for the softshell turtles combined (Table 3) to represent demographic rates under mean, minimum, and maximum demographic conditions. Using these values, we calculated mean, minimum, and maximum fecundity (*F*) for each species based on the mean, minimum, and maximum rates for the following variables: nest survival, clutch size, breeding frequency, adult survival, and number of clutches produced annually:

$$F = \binom{number}{of\ clutches} \times \binom{clutch}{size} \times \binom{breeding}{frequency} \times \binom{adult}{survival} \times \hat{S}_N \times 0.5$$

where

number of clutches = number of clutches laid annually,

clutch size = number of eggs laid in a single nest,

breeding frequency = proportion of adult females reproducing annually,

adult survival = annual survival of the adult female stage,

$\hat{S}_N$ = survival of nests (i.e., the proportion of eggs surviving and transitioning to the hatchling stage)

The value 0.5 assumes a 1:1 sex ratio at birth for all three species (e.g., Graham and Graham 1997).

In this stage-structured model with annual increments, the model treats animals within a stage as having some probability of surviving and transitioning to the nest stage each year, and some probability of surviving but remaining at the current stage. To calculate the probability that a juvenile survives and remains in the current stage, we used the following equation (Crouse et al. 1987):

$$P_i = \left(\frac{1-p_i^{d_i-1}}{1-p_i^{d_i}}\right)p_i,$$

where

P_i = the proportion of individuals surviving and remaining within stage class *i*,

p_i = the survival of stage class *i*,

d_i = the duration stage class *i*; i.e., the number of years spent in that stage class.

Similarly, including the above variables p_i and d_i, to calculate the juvenile survive and transition value, we used the following equation (Crouse et al. 1987):

$$G_i = \frac{p_i^{d_i}(1-p_i)}{1-p_i^{d_i}},$$

where

G_i = the proportion of individuals surviving stage class *i* and transitioning to the next stage class.

For snapping turtles, the duration of the juvenile stage was estimated to be $\bar{x}$ = 8.5 years, based on averaging juvenile duration values from the literature (Christiansen and Burken 1979, Congdon et al. 1987). For softshells juvenile duration based on averaging was $\bar{x}$ = 6.5 years (Ernst and Lovich 2009, Johnson 2000).

MATRIX MODELING

To examine population growth of softshells and snapping turtles in the absence of harvest, we developed female-only, density independent, deterministic 3x3 stage-based matrix models (Lefkovitch 1965, Skalski et al. 2005) using Microsoft Excel (Microsoft Office 2010 for Windows), with stages defined as hatchling (age 0), juvenile (age 1 to adulthood; Tables 1 and 2 indicate specific values for each species), and adult (reproductive). The general model used had the following form (Crouse et al. 1987):

$$\begin{bmatrix} 0 & 0 & F_3 \\ G_1 & P_2 & 0 \\ 0 & G_2 & P_3 \end{bmatrix},$$

where F_i is the fecundity of the stage class (calculation described above) i, G_i is the proportion of individuals surviving stage class i and transitioning to the next stage (calculation described below), and P_i is the proportion of individuals surviving and remaining in the current stage class (calculation described above). Stage classes 1, 2, and 3 represent the hatchling, juvenile, and adult stage classes, respectively. Because the hatchling stage is only 1 year and hatchling survival is accounted for in the transition to the juvenile stage, P_1 is set to 0. We developed 6 separate stage matrix models for estimating population growth without harvest, 3 for each of snapping turtles and

softshells using the mean, minimum, or maximum demographic values (Table 3; Figures 1 and 2).

We determined the stable stage distribution (i.e., the proportion of hatchlings, juveniles, and adults in the population when population growth is stabilized) for each population and applied it to the mean value of our abundance estimates per 2 km for unharvested populations of snapping turtles and softshells (Chapter 1) to generate initial vectors of abundance. For snapping turtles, mean abundance was 90 turtles per 2 km. For softshells, mean abundance was 62 turtles per 2 km. These abundance values were used with the proportion of turtles in each stage at the stable age distribution to calculate the initial abundance vector (Figures 1 and 2). Thus, we assume our models are applicable to the 2 km scale.

HARVEST MATRICES

We applied harvest matrices using harvest rates estimated from mock harvests conducted in the 2011 and 2012 field seasons (Tables 1 and 2). These harvest rates were based on our estimates of abundance (per 2 km) and capture data from mark-recapture studies conducted in the same years, and indicated plausible proportions of the population that we were able to 'remove' during mock harvests at a 2 km scale (Chapter 1). We calculated a mean, minimum, and maximum harvest rate for each species (Table 3). We applied each of these rates to each of the 6 stage matrices described above to examine the effects of varying levels of harvest (hereafter referred to as λ_{Hmean}, λ_{Hmin}, or $\lambda_{Hmax)}$ when applied to populations exhibiting mean, minimum, or maximum demographic rates. Harvest matrices were constructed in the following form:

$$\begin{bmatrix} 1 & 0 & 0 \\ 0 & h_1 & 0 \\ 0 & 0 & h_2 \end{bmatrix},$$

where *h* is the rate of escapement or harvest survival for each stage, i. We examined the effects of mean, minimum, and maximum levels of harvest for three harvest scenarios: (1) harvest of adults only, (2) harvest of juveniles only, and (3) harvest of both adults and juveniles, and applied these to populations exhibiting mean, minimum, or maximum demographic rates.

Ultimately, we examined 30 population growth situations for both snapping turtles (Table 4) and softshells (Table 5): unharvested population growth at [mean/minimum/maximum] demographic rates, then population growth under [mean/minimum/maximum] demographic rates for populations harvested at [mean/minimum/maximum] harvest rates for each of the three harvest scenarios [adult-only/juvenile-only/adult-and-juvenile]. Further, we determined the level of harvest that could be sustained for each of these scenarios in order to maintain $\lambda = 1$ (i.e., sustainable harvest rate).

SENSITIVITY AND ELASTICITY ANALYSIS

We carried out sensitivity and elasticity analyses to determine which demographic parameter is most important to population growth. We calculated sensitivity (*s*) following methods described by Caswell (2001):

$$s_{ij} = \frac{v_i w_j}{<w,v>},$$

where v_i is the i^{th} element of the reproductive value vector (v), or the reproductive value specific to each class (the left eigenvector of the matrix), and w_j is the j^{th} element of the stable stage vector (w), or the proportion of individuals in a given stage at stable stage distribution (the right eigenvector of the matrix).

Similarly, we calculated elasticity, e, or the proportional sensitivity of λ to a change in a specific demographic parameter following methods described by Crouse et al. (1987):

$$e_{ij} = \frac{a_{ij}s_{ij}}{\lambda},$$

where $\boldsymbol{a_{ij}}$ is the matrix element for which we are examining how λ is affected upon changing this value, and $\boldsymbol{s_{ij}}$ is the sensitivity of λ to a change in that value (calculated above).

RESULTS

MATRIX MODELING – SNAPPING TURTLES

Using mean demographic rates, snapping turtle populations exhibited increasing baseline population growth (λ = 1.030; Figure 3). Harvest applied to both juveniles and adults was not sustainable (Table 4). Similarly, limiting harvest to only the adult segment of the population resulted in population declines, though at a lesser rate. When these harvest rates were applied to only the juvenile segment of the population, declines occurred at the mean and the maximum harvest rate, but populations increased slightly under minimum harvest rates (λ_{Hmin} = 1.009). Population sustainability (λ = 1) was achieved for snapping turtles exhibiting mean demographic rates when both adults and

juveniles were each harvested at a rate of 2.3%, indicating that low levels of harvest may be sustainable by these populations. Similarly, when examining the effects of adult-only harvest, harvest was sustainable at a rate of 3.1%. A greater rate of harvest was sustainable when only the juvenile stage was harvested, but population declines occurred when harvest of juveniles exceeded 12% (Table 4). At minimum demographic rates, populations declined without harvest, and no level of harvest was sustained by the population.

Populations grew rapidly at maximum demographic rates without harvest (λ = 1.199; Figure 3). At this level, when applied to both adults and juveniles, harvest resulted in population declines except at the minimum harvest rate. When we applied harvest to only the juvenile segment of the population, population increases still occurred at all three levels of harvest. When harvest was maximized, harvest of the adult segment resulted in population declines, but under mean and minimum harvest rates, the population increased (Table 4).

MATRIX MODELING – SOFTSHELL TURTLES

The baseline population growth for softshells decreased slightly under mean demographic rates (λ = 0.952; Figure 4) and continued to decrease when all harvest rates were applied to both adults and juveniles. When harvest rates were applied to either adults or juveniles separately, populations still declined (Table 5). Similarly, populations declined even more rapidly under minimum demographic rates (λ = 0.838), and continued to decline under all harvest scenarios. These models indicate that softshell turtle

populations are likely unable to sustain harvest when populations are at mean demographic rates.

Using maximum demographic rates, the baseline population increased at λ = 1.163 (Figure 4). For harvest of both adults and juveniles, populations decreased when the mean harvest rate was applied, but increased under the minimum harvest rate. Increasing population growth still occurred when adults only were harvested at mean and minimum rates, and when juveniles only were harvested at the same rates. Maximum harvest rate consistently resulted in declining populations when applied to any of the three segments of the population. Under maximum demographic rates, a harvest rate of 16.3% can be sustained when both adults and juveniles are harvested (Table 5).

SENSITIVITY AND ELASTICITY ANALYSIS

Sensitivity and elasticity analysis indicated that survival of the adult stage has the greatest influence on population growth. For snapping turtles a 1% increase in adult survival will result in a 0.63% increase in population growth (Figure 5), and for softshells, a 1% increase in adult survival would result in a population growth increase of 0.51% (Figure 6).

DISCUSSION

Our results indicate that under mean demographic rates even modest levels of harvest would not be sustainable at a local scale. These results mirror those of other studies that have suggested even modest harvest of common snapping turtles can be detrimental to the long-term viability of turtle populations. For example, in Michigan, it was estimated that continued harvest of 10% of adults annually would reduce the number

of adults by 50% within 20 years (Congdon et al. 1994). The effects of harvest were even more evident with softshell populations where populations were not sustainable at any combination of harvest parameters. However, these results need to be placed in an appropriate context including scale of harvests and the use of mean, minimum, and maximum demographic values. For example, for both softshells and snapping turtles some harvest scenarios were sustained by the populations (i.e., harvest of juveniles only, harvest of either adults or juveniles; Tables 4 and 5) and did not result in population declines. Though it is unlikely that demographic rates would be maintained for long periods (i.e., 25 years represented in our models), these results do illustrate that harvest may be sustained when population growth is maximized.

As our sensitivity and elasticity results indicated, survival of the adult stage has the greatest influence on population growth, and this finding is consistent with the results of other studies (e.g., Congdon et al. 1994, Crouse et al. 1987). This effect is also illustrated when examining the effects of adult-only harvest versus juvenile-only harvest, where growth rates were consistently lower when all harvesting was of the adult stage. Minimizing harvest of this stage would aid in reducing the potential for additional harvest pressure on these populations, and measures may be taken to prevent overharvest of the adult segment of turtle populations such as placement of size limits. Additionally, softshell turtles exhibit sexual dimorphism, with adult females reaching a far greater body size than males. Female smooth softshells may reach up to 35.6 cm in carapace length, and female spiny softshells up to 54 cm, twice the length or more of an adult male (Ernst and Lovich 2009, Johnson 2000). Because turtles are often sold by weight on the food market (Brown et al. 2011), female softshells are likely targeted because of their greater

weight. Placing size limits on softshell turtles could reduce the harvest pressure that may currently be placed on reproductive females and would reduce impacts on turtle populations. Such restrictions have been suggested in order to reduce harvest pressure on adult female painted turtles in Minnesota (Gamble and Simons 2004). Further, in Texas, the enforcement of bag- and size-limits for adult female turtles has been suggested (Brown et al. 2011) for the same reasons. Though reducing the harvest pressure placed on the adult stage could increase the pressure placed on juveniles, the juvenile stage is much less important to the overall demographics of the population.

In Missouri, commercial harvesters may collect turtles year round. Limiting harvest to specific times of year could also reduce harvest pressure placed on adults. For example, softshells often use sand bars and banks to lay nests (Johnson 2000). Limiting turtle harvest to areas away from sandbars and banks, which are used during breeding and nesting season (i.e., May through August; Barko and Briggler 2006), may reduce the harvest mortality of egg-laying females. This would reduce localized effects of harvest on female turtles, which may be more vulnerable to harvest when searching for nest sites if harvesters are trapping within areas containing sand bars. Brown et al. (2011) have suggested preventing harvest during breeding and nesting season for turtle populations in Texas.

There is no evidence to suggest that harvest mortality will be compensated by density dependent reproductive responses (Brooks et al. 1991, Congdon et al. 1994, Galbraith et al. 1997). For example, a population of snapping turtles that has been the subject of long-term research (approximately 16 years) in Ontario, Canada, experienced a

marked and sudden increase in predation by otters (*Lutra canadensis*) from 1986 to 1987. Following this increase in mortality, no density-dependent responses were detected within the snapping turtle population and reproductive rates of females remained the same (Brooks et al. 1991).

Our results illustrate the inability of both softshells and snapping turtles to sustain even minimum harvest pressure at a local scale when populations exhibit mean demographic rates. Assuming such consistency over a long period (i.e., 25 years) is not plausible, but there was insufficient information to adequately parameterize a stochastic model. Further, deterministic models result in overall higher population growth rates than stochastic models, and therefore our population growth models may be slightly optimistic considering the limitations of the models we used. Despite these shortcomings, we believe our results offer important insight into the potential consequences of commercial harvest in Missouri. Further, the variability in demographic rates of turtles as evidenced in our literature review indicates that there may be variability in the demographic rates of populations over time. For example, reproductive rates for turtles can fluctuate greatly from year to year (Plummer 1976, Wilbur 1975), and while turtles may exhibit poor years where mortality rates are high and fecundity is low, these poor demographic years could be buffered by subsequent years when conditions are more favorable.

We conducted these simulations at a local scale using literature-derived values, but it is unlikely that commercial harvesters in Missouri are removing turtles at the harvest rates we have reported throughout all harvestable areas. Though we are not

suggesting river-wide declines in river turtles owed to commercial harvest at the current levels of commercial harvest, the potential for local-scale effects does remain, particularly when commercial harvest regulations do not restrict the number of turtles that may be removed. Thus, high amounts of harvest activity may occur at a local scale, and local populations could be reduced if the same areas were trapped year after year. It follows that harvesters would then be likely to move to new trapping locations (i.e., the law of diminishing returns) in order to increase their catch. Still, because harvesters are not required to report specific locations where turtles were collected (aside from river of capture) it can be difficult to assess the scale of harvest activity. Local-scale effects of harvest on turtle populations have been observed for other turtle populations: harvesters have reported declining numbers of turtles in harvested areas for common snapping turtles on the upper Mississippi River (Paisley et al. 2009) and for alligator snapping turtles (*Macrochelys temminckii*) in Louisiana (Boundy and Kennedy 2006). Further, harvesters have indicated that for the Florida softshell (*Apalone ferox*), reduced population size resulting from harvest activity may last for periods up to 3 or 4 years (Breckenridge 1955). If trapping were limited to specific regions of the river and rotated to new areas annually (i.e., depending on where harvesters reported collected turtles in previous years), this, in combination with the management recommendations described above, may alleviate the potential for localized effects of over-harvesting on turtle populations.

In conclusion, our models suggest that river turtles have a modest capacity to withstand harvest, but the overall impact depends on the scale of harvest and the repeatability of harvest in the same locales. Further, the high variability of turtle

demographics indicates that low levels of harvest may be sustainable by populations in years when populations exhibit high demographic rates, but in average or poor years even low levels of harvest cannot be sustained. To reduce the risk of localized effects of harvest activity on turtle populations, harvest regulations may be modified to restrict harvest to specific regions of the river. Additionally, placement of size and bag limits, with an emphasis on juvenile take, can aid in decreasing the harvest pressure placed on the important adult segment of the population.

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Table 1: Demographic rates from studies of snapping turtle (*Chelydra serpentina*) populations used for construction of common snapping turtle Lefkovitch matrices. Each parameter used listed in the left column. A mean, minimum, and maximum value were calculated for each parameter and used to model mean, minimum, and maximum survival conditions (Table 3). All abundance estimates (per 2 km) and harvest proportions estimated by the authors (Chapter 1). Clutch Size = number of eggs per clutch; Breeding Frequency = proportion of the adult female population that reproduces annually; Number of Clutches = number of clutches laid annually; Juvenile Duration = number of years spent in the juvenile stage (i.e., 2nd year to adulthood as defined in the literature); *n* = sample size reported by source; Location = location of study. Dashes indicate where information is not applicable or unreported (i.e., *n*, sex).

Parameter	**Value**	***n***	**Sex**	**Location**	**Source**
Nest Survival	0.23	-	-	S.E. Michigan, United States	Congdon et al. 1994
	0.157	134	-	Calumet, Quebec, Canada	Robinson and Bider 1988
	0.22	114	-	S.E. Michigan, United States	Congdon et al. 1987
	0.056	18	-	Northern New York, United States	Petokas and Alexander 1980
	0.245	-	-	South Dakota, United States	Hammer 1969
Hatchling Survival	0.17[a]	-	-	S.E. Michigan, United States	Congdon et al. 1994
	0.47[b]	-	-	S.E. Michigan, United States	Congdon et al. 1994
Juvenile Survival	0.77	-	-	S.E. Michigan, United States	Congdon et al. 1994
Adult Survival	0.88	-	M, F	S.E. Michigan, United States	Congdon et al. 1994
	0.93	-	F	S.E. Michigan, United States	Congdon et al. 1994
	0.963	-	M, F	Goose Island, Wisconsin, United States	Paisley et al. 2009
	0.939	-	M, F	Lawrence Lake, Minnesota, United States	Paisley et al. 2009
	0.97	91	M, F	Canaan Valley, West Virginia	Flaherty et al. 2008
	0.966	-	F	Algonquin Provincial Park, Ontario, Canada	Galbraith and Brooks 1987
	0.929	-	F	Algonquin Provincial Park, Ontario, Canada	Galbraith and Brooks 1987
Clutch Size	28	-	-	S.E. Michigan, United States	Congdon et al. 1994
	46.8	-	-	Nebraska, United States	Iverson et al. 1997
	35.2	252	-	-	Ernst and Lovich 2009
	33	18	-	Algonquin Park, Ontario, Canada	Brown et al. 1994
	41.5	18	-	Cootes Paradise, Ontario, Canada	Brown et al. 1994
	5-49	3	-	N.W. Florida, United States	Aresco and Gunzburger 2007[c]
Breeding Frequency	0.85	-	-	S.E. Michigan, United States	Congdon et al. 1994
Number of Clutches	1	-	-	-	Iverson et al. 1997 Ernst and Lovich 2009
Juvenile Duration	11	-	-	S.E. Michigan, United States	Congdon et al. 1987
	6	-	-	Iowa, United States	Christiansen and Burken 1979
	6	-	-	N.W. Florida, United States	Aresco and Gunzburger 2007[d]
Abundance	55	-	-	Gasconade River, Missouri, United States	2011, Chapter 1
	70	-	-	Osage River, Missouri, United States	2011, Chapter 1
	27	-	-	Gasconade River, Missouri, United States	2012, Chapter 1
	208	-	-	Osage River, Missouri, United States	2012, Chapter 1
Harvest Proportion	0.57	-	-	Missouri River, Missouri, United States	2011, Chapter 1
	0.25	-	-	Missouri River, Missouri, United States	2011, Chapter 1
	0.09	-	-	Missouri River, Missouri, United States	2012, Chapter 1
	0.14	-	-	Missouri River, Missouri, United States	2012, Chapter 1
	0.13	-	-	Gasconade River, Missouri, United States	2011, Chapter 1
	0.2	-	-	Osage River, Missouri, United States	2011, Chapter 1
	0.26	-	-	Gasconade River, Missouri, United States	2012, Chapter 1
	0.07	-	-	Osage River, Missouri, United States	2012, Chapter 1

[a]Value based on capture rates
[b]Value obtained through modeling
[c]Not included in our study due to low sample size ($n = 3$)
[d]Mean juvenile duration from study (juvenile duration ranges 5-7 years)

Table 2: Demographic rates from studies of smooth softshell (SMSS; *Apalone mutica*) and spiny softshell (SPSS; *Apalone spinifera*) populations used for construction of softshell turtle Lefkovitch matrices. Each parameter used listed in the left column. A mean, minimum, and maximum value were calculated for each parameter and used to model mean, minimum, and maximum survival conditions (Table 3). Snapping turtle (CSNT) rates used and indicated where data for either softshell species were unavailable. All abundance estimates (per 2 km) and harvest proportions estimated by the authors (Chapter 1). Clutch Size = number of eggs per clutch; Breeding Frequency = proportion of the adult female population that reproduces annually; Number of Clutches = number of clutches laid annually; Juvenile Duration = number of years spent in the juvenile stage (i.e., 2nd year to adulthood as defined in the literature); *n* = sample size reported by source; Location = location of study. Dashes indicate where information is not applicable or unreported (i.e., *n*).

Parameter	**Value**	***n***	**Species**	**Location**	**Source**
Nest Survival	0.43	28	SMSS	Kansas, United States	Fitch and Plummer 1975
	0.02	-	SMSS	Kansas, United States	Plummer 1976
	0.49	-	SMSS	Kansas, United States	Plummer 1976
Hatchling Survival	0.17[a]	-	CSNT	S.E. Michigan, United States	Congdon et al. 1994
	0.47[b]	-	CSNT	S.E. Michigan, United States	Congdon et al. 1994
Juvenile Survival	0.717	-	SPSS	Arkansas, United States	Plummer et al. 2008
Adult Survival	0.836	-	SPSS	Arkansas, United States	Plummer et al. 2008
Clutch Size	16	14	SPSS	Vermont, United States	Graham and Graham 1997
	10.4	102	SMSS	Kansas, United States	Plummer 1977
	12.6	199	SMSS	Kansas, United States	Fitch and Plummer 1975
	14.1	87	SMSS	-	Ernst and Lovich 2009
	18	-	SMSS	Missouri, United States	Johnson 2000
	18	-	SPSS	Missouri, United States	Johnson 2000
	17.9	82	SPSS	-	Ernst and Lovich 2009
Breeding Frequency	0.85	-	CSNT	S.E. Michigan, United States	Congdon et al. 1994
Number of Clutches	1	-	SMSS	Kansas, United States	Plummer 1977
	2	-	SMSS	Kansas, United States	Plummer 1977
	2	-	SPSS	Tennessee, United States	Robinson and Murphy 1978
Duration of Juvenile Stage	5	-		Missouri, United States	Johnson 2000
	8	-		-	Ernst and Lovich 2009
Abundance	51	-	SMSS	Gasconade River, Missouri, United States	2012, Chapter 1
	72	-	SPSS	Gasconade River, Missouri, United States	2012, Chapter 1
Harvest Proportion	0.12	-	SMSS	Missouri River, Missouri, United States	2011, Chapter 1
	0.09	-	SMSS	Missouri River, Missouri, United States	2011, Chapter 1
	0.09	-	SMSS	Missouri River, Missouri, United States	2012, Chapter 1
	0.79	-	SPSS	Missouri River, Missouri, United States	2011, Chapter 1
	0.22	-	SPSS	Missouri River, Missouri, United States	2011, Chapter 1
	0.06	-	SPSS	Missouri River, Missouri, United States	2012, Chapter 1
	0.34	-	SMSS	Gasconade River, Missouri, United States	2012, Chapter 1
	0.24	-	SPSS	Gasconade River, Missouri, United States	2012, Chapter 1

[a]Value based on capture rates
[b]Value obtained through modeling

Table 3: Mean ($\bar{x}$), minimum (min), and maximum (max) demographic rates for snapping turtles (*Chelydra serpentina*) and softshell turtles (*Apalone mutica*, *A. spinifera*)used to model population growth. These values were calculated based on the demographic parameters collected from the literature in Table 1 (snapping turtles) and Table 2 (softshell turtles). Juvenile Duration = number of years spent in the juvenile stage; Clutch Size = number of eggs per clutch annually; Number of Clutches = number of clutches laid annually; Breeding Frequency = proportion of the adult female population that reproduces annually. Dashes indicate where only one value was available in the literature, and in these cases, this value was used for the mean, minimum, and maximum demographic models.

	Snapping Turtles			**Softshell Turtles**		
Parameter	$\bar{x}$	**min**	**max**	$\bar{x}$	**min**	**max**
Nest Survival	0.182	0.056	0.245	0.313	0.020	0.490
Hatchling Survival	0.320	0.170	0.470	0.320	0.170	0.470
Juvenile Survival	0.770	-	-	0.717	-	-
Juvenile Duration [a]	8.500	11.000	6.000	6.500	8.000	5.000
P_i [b]	0.742	0.756	0.709	0.680	0.696	0.651
G_i [c]	0.028	0.014	0.061	0.037	0.021	0.066
Adult Survival	0.940	0.880	0.970	0.836	0.836	0.836
Annual Fecundity[d]	2.676	0.586	4.727	2.553	0.074	6.267
Clutch size	36.900	28.000	46.800	15.286	10.400	18.000
Breeding Frequency	0.850	-	-	0.850	-	-
Number of Clutches	1.000	-	-	1.500	1.000	2.000
Harvest Proportion[e]	0.214	0.070	0.570	0.244	0.060	0.790

[a]The duration of the juvenile stage is maximized when reproduction begins at an earlier age and minimized at a later age (i.e., mean, minimum, or maximum fecundity with respect to age at first reproduction).
[b]The proportion of juveniles surviving and transitioning to the adult stage. Calculated based on the value for juvenile survival and the juvenile duration following methods described by Crouse et al. 1987 (see Analytical Methods).
[c]The proportion of juveniles surviving and remaining in the juvenile stage. Calculated based on the value for juvenile survival and the juvenile duration following methods described by Crouse et al. 1987 (see Analytical Methods).
[d]Calculated using the values for nest survival, clutch size, number of clutches, and breeding frequency (see Analytical Methods).
[e]Plausible harvest rates (proportion of population per 2 km removed by harvest) calculated by the authors (Chapter1).

Table 4: Snapping turtle (*Chelydra serpentina*) population growth rates (λ) for populations with mean, minimum, and maximum levels of demographic rates, harvested at mean, minimum, and maximum harvest rates. Harvest rates calculated by the authors (Chapter 1) based on matrix modeling results. λ = unharvested population growth rate; Harvest Segment = the portion of the population that is removed during harvest (adult, juvenile); λ_{Hmean} = growth rate under mean harvest rate (21%); λ_{Hmin} = growth rate under minimum harvest rate (7%), λ_{Hmax} = growth rate under maximum harvest rate (43%); Sustainable Harvest = the rate of harvest required for population sustainability (λ = 1; negative rates indicate populations where no level of harvest is sustainable).

Demographic Rates	λ	**Harvest Segment**	λ_{Hmean}	λ_{Hmin}	λ_{Hmax}	**Sustainable Harvest**
Mean	1.027	Adult and Juvenile	0.820	0.956	0.468	2.3%
		Juvenile	0.987	1.009	0.956	12.0%
		Adult	0.888	0.973	0.777	3.1%
Min	0.892	Adult and Juvenile	0.706	0.830	0.576	-12.4%
		Juvenile	0.884	0.888	0.881	-31.5%
		Adult	0.774	0.838	0.758	-13.0%
Max	1.203	Adult and Juvenile	0.974	1.125	0.576	18.6%
		Juvenile	1.134	1.176	1.045	80.7%
		Adult	1.056	1.149	0.861	30.2%

Table 5: Softshell turtle (*Apalone mutica*, *A. spinifera*) population growth rates (λ) for populations with mean, minimum, and maximum levels of demographic rates, harvested at mean, minimum, and maximum harvest rates. Harvest rates calculated by the authors (Chapter 1) based on matrix modeling results. λ = unharvested population growth rate; Harvest Segment = the portion of the population that is removed during harvest (adult, juvenile); λ_{Hmean} = mean harvest rate (24%); λ_{Hmin} = minimum harvest rate (6%), λ_{Hmax} = maximum harvest rate (79%); Sustainable Harvest = the rate of harvest required for population sustainability (λ = 1; negative rates indicate populations where harvest is unsustainable).

Demographic Rate	λ	**Harvested Segment**	λ_{Hmean}	λ_{Hmin}	λ_{Hmax}	**Sustainable Harvest**
Mean	0.966	Adult and Juvenile	0.740	0.899	0.236	-5.5%
		Juvenile	0.902	0.937	0.847	-15.8%
		Adult	0.826	0.916	0.698	-7.6%
Min	0.839	Adult and Juvenile	0.638	0.788	0.178	-19.6%
		Juvenile	0.837	0.838	0.836	-50.0%
		Adult	0.689	0.789	0.696	-19.5%
Max	1.195	Adult and Juvenile	0.922	1.103	0.321	16.3%
		Juvenile	1.074	1.140	0.896	45.0%
		Adult	1.024	1.127	0.747	28.3%

$$(1)\ \begin{bmatrix}36\\41\\14\end{bmatrix} = \begin{bmatrix}0 & 0 & 2.676\\0.320 & 0.742 & 0\\0 & 0.028 & 0.940\end{bmatrix} \times \begin{bmatrix}36\\40\\14\end{bmatrix}$$

$$(2)\ \begin{bmatrix}12\\15\\18\end{bmatrix} = \begin{bmatrix}0 & 0 & 0.586\\0.170 & 0.756 & 0\\0 & 0.014 & 0.880\end{bmatrix} \times \begin{bmatrix}14\\17\\21\end{bmatrix}$$

$$(3)\ \begin{bmatrix}49\\47\\12\end{bmatrix} = \begin{bmatrix}0 & 0 & 4.727\\0.470 & 0.709 & 0\\0 & 0.061 & 0.970\end{bmatrix} \times \begin{bmatrix}41\\39\\10\end{bmatrix}$$

Figure 1: Population growth matrices including initial population vectors and stable stage distribution for snapping turtle (*Chelydra serpentina*) populations exhibiting (1) mean, (2) minimum, and (3) maximum demographic rates.

$$(1)\ \begin{bmatrix}23\\27\\9\end{bmatrix} = \begin{bmatrix}0 & 0 & 2.553\\0.320 & 0.680 & 0\\0 & 0.037 & 0.836\end{bmatrix} \times \begin{bmatrix}24\\28\\9\end{bmatrix}$$

$$(2)\ \begin{bmatrix}2\\3\\25\end{bmatrix} = \begin{bmatrix}0 & 0 & 0.074\\0.170 & 0.696 & 0\\0 & 0.021 & 0.836\end{bmatrix} \times \begin{bmatrix}3\\4\\30\end{bmatrix}$$

$$(3)\ \begin{bmatrix}34\\31\\6\end{bmatrix} = \begin{bmatrix}0 & 0 & 6.267\\0.470 & 0.651 & 0\\0 & 0.066 & 0.836\end{bmatrix} \times \begin{bmatrix}29\\27\\5\end{bmatrix}$$

Figure 2: Population growth matrices including initial population vectors and stable stage distribution for softshell turtle (*Apalone mutica*, *A. spinifera*) populations exhibiting (1) mean, (2) minimum, and (3) maximum demographic rates.

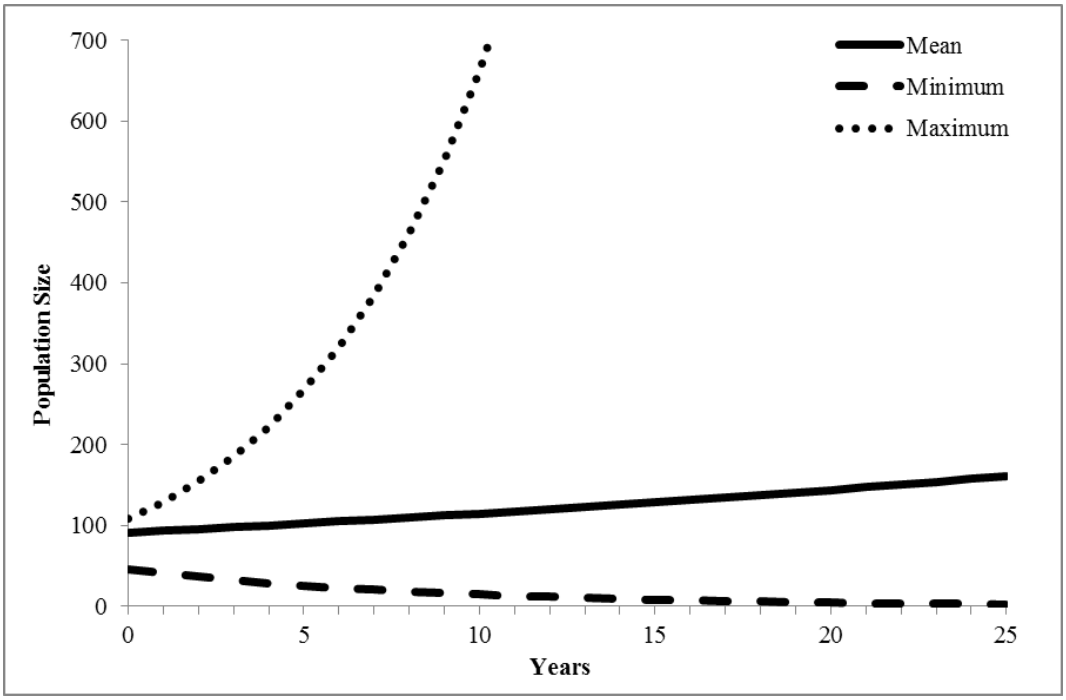

Figure 3: Baseline population growth for snapping turtles (Chelydra serpentina) at stable stage distribution under mean, minimum, and maximum demographic rates.

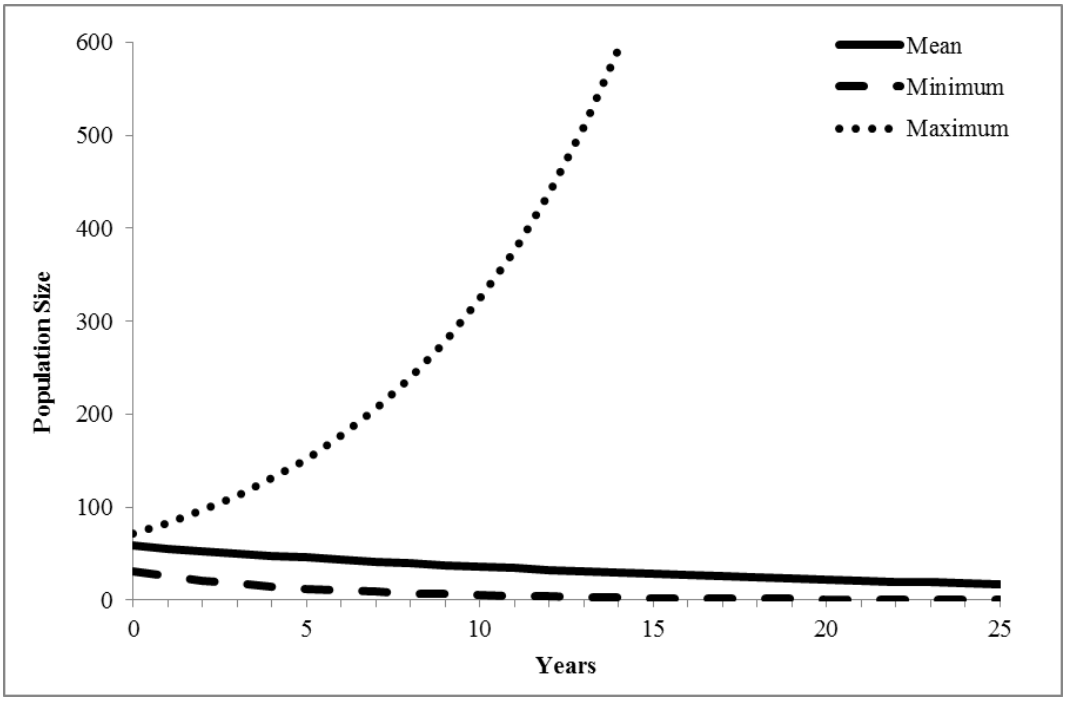

Figure 4: Baseline population growth for softshell turtles (*Apalone mutica*, *A. spinifera*) at stable stage distribution under mean, minimum, and maximum demographic rates.

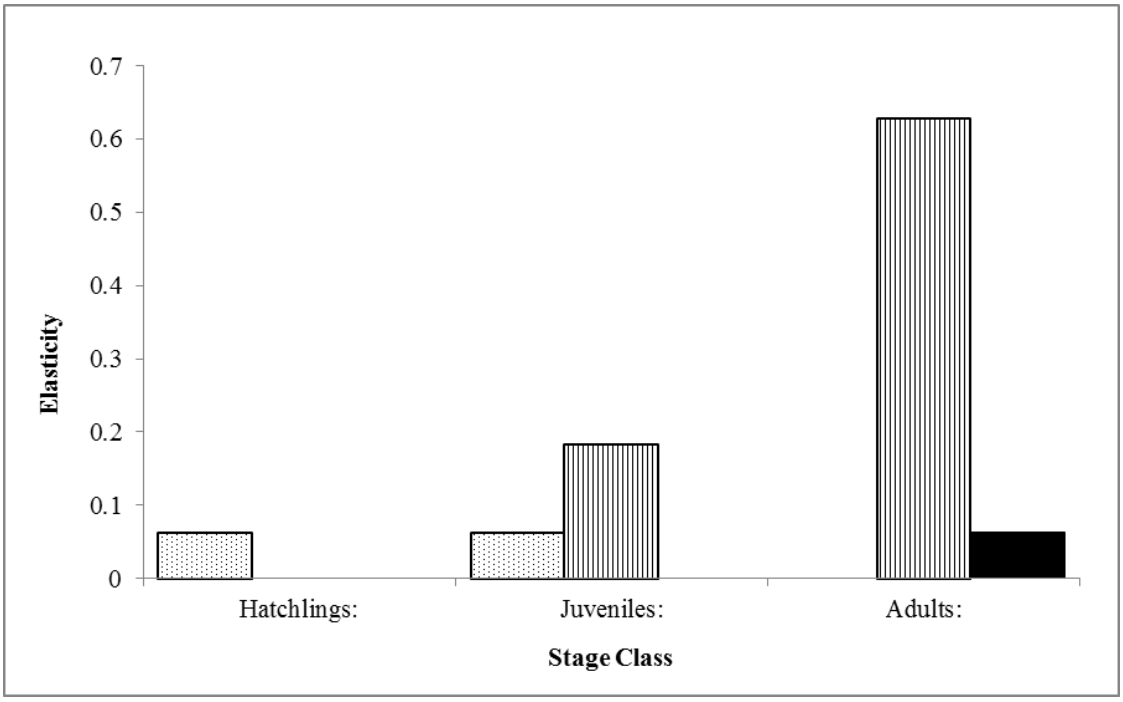

Figure 5: Snapping turtle (*Chelydra serpentina*) elasticity values under mean survival conditions at stable stage distribution. Bars represent the elasticity of transitioning to the next stage class (stippled bars), the elasticity of remaining in a class (striped bars), and the elasticity of fecundity (solid bar).

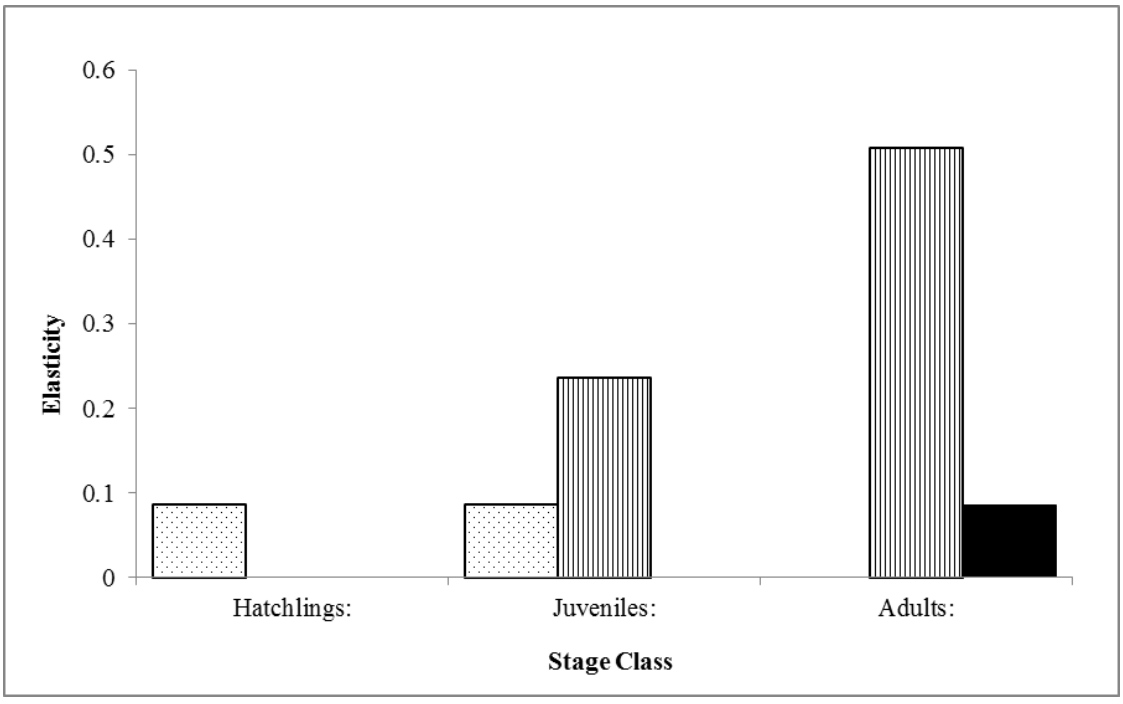

Figure 6: Softshell turtle (*Apalone mutica*, *A. spinifera*) elasticity values under mean survival conditions at stable stage distribution. Bars represent the elasticity of transitioning to the next stage class (stippled bars), the elasticity of remaining in a class (striped bars), and the elasticity of fecundity (solid bar).

CHAPTER 3

USE OF MICROCHEMISTRY ANALYSIS TO DETERMINE RIVER OF CAPTURE FOR COMMERCIALLY HARVESTED RIVER TURTLES

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ABSTRACT

Commercial harvest of river turtles is often restricted to only certain water bodies. However, wildlife managers have no way of ensuring harvested river turtles are collected from legal waters. We used microchemistry analysis on turtle nail samples collected from turtles in Missouri to assess our ability to determine river of capture for individual turtles. From 2010 through 2012, we collected nail samples from turtles open to commercial harvest in Missouri: common snapping turtle (*Chelydra serpentina*), smooth softshell (*Apalone mutica*), and spiny softshell (*Apalone spinifera*). Our sampling occurred in two rivers where turtle harvest is illegal (Gasconade and Osage rivers) and one river where turtle harvest is legal (Missouri River). We used stable isotope analysis (SIA) to determine the composition of stable hydrogen and oxygen isotopes with nail samples, and inductively coupled plasma mass spectrometry (ICP-MS) to determine the strontium and calcium ratios and concentrations. We used classification and regression tree modeling and *k*-fold cross validation to determine which microchemistry analysis (SIA or ICP-MS) was best at determining the river of capture at the scale of individual rivers and within a classification of legal or illegal waters. Our top-selected CART

model, which used results only from the ICP-MS analysis, correctly classified 83.5% of our samples to either a harvested or unharvested river at a rate of based on the ratio of Sr:Ca. Cross-validation indicated that we can expect this model to correctly classify samples at a rate of 76.9%, indicating the level of accuracy we can expect when this model is applied to other data sets. Our methods offer an approach for others interested in confirming the legality of commercial turtle harvest activity, but we caution against application of our model without proper validation.

INTRODUCTION

Commercial turtle harvest in many regions is poorly monitored with few resources available for regulating harvest (Ceballos and Fitzgerald 2004, Cheung and Dudgeon 2006, Congdon et al. 1994). Further, in some states, turtle harvest is restricted to only certain bodies of water, yet there is no way for state and federal agencies to confirm where the turtle was captured. For example, in Missouri, three turtle species can be harvested commercially: the common snapping turtle (*Chelydra serpentina*), the smooth softshell turtle (*Apalone mutica*), and the spiny softshell turtle (*Apalone spinifera*). However, commercial harvest of these species is limited to the Missouri River, the Mississippi River, and the St. Francis River, and commercial turtle harvest is not allowed in the tributaries of these rivers, or within 300 meters of tributary confluences. The extent of any illegal activity is unknown, but even low levels of harvest can negatively impact turtle populations (Congdon et al. 1994, Ceballos and Fitzgerald 2004) so it is important that tools be available to determine the legality of turtle harvests. Such a tool could encourage sustainable harvest of these populations and aid law enforcement.

One option to determine the river of capture of turtles might involve the use of microchemistry analysis of turtle nail tissue. This technique relies on a chemical signature of stable isotopic compositions or concentrations of trace elements found in tissues of animals which reflect the local food web and water bodies in which they reside (Hobson 1999, Whitledge et al. 2006). Chemical signatures can vary between rivers and lakes, even among waters within the same watershed or river basin (Wells et al. 2003), and among animals inhabiting different areas (Hobson 1999, Zimmerman and Reeves 2002). The chemical signature of water bodies are influenced by the anthropogenic or biogeochemical factors of the surrounding region (Brazner et al. 2004, Hobson et al. 1999) and these unique signatures can be used to effectively distinguish the location from which an individual was captured (Zeigler and Whitledge 2011). The use of turtle nail tissue for this analysis is supported by studies of wildlife populations which have successfully tracked an individual's movements or geographic history (i.e., the locations where an individual has resided within its lifetime) based on the microchemistry of keratinous structures such as feathers (Fraser et al. 2008) or claws (Ethier et al. 2013). Such tissues can be sampled without causing mortality to the animal (Ethier et al. 2010), remain metabolically inert (Caumette et al. 2007, Ethier et al. 2010), and are representative of the location of the animal at the time of growth which can indicate an individual's geographic history (Hobson 1999, Mizutani et al. 1990).

Using the microchemistry analyses, researchers can examine geographic history of an animal over time. For migratory fish species, otolith material is commonly used to assess life history characteristics because the stable isotopic composition of specific sections of the otolith can be analyzed to track the general location of a fish over time.

More specifically, the natal location of a fish is reflected in the core of the otolith, and the most recent history is reflected in the outermost layers (Campana and Nielson 1985, Zimmerman and Reeves 2002). In a study of westslope cutthroat trout (*O. clarki lewisi*) inhabiting 3 streams within one watershed, individuals were reclassified with 100% accuracy to their stream of capture based on the microchemistry of the otolith core, and with 82% accuracy based on fish scale microchemistry (Wells et al. 2003). For reptiles, a majority of microchemistry studies have examined trophic ecology using stable isotopes of carbon and nitrogen (e.g., Seminoff et al. 2007, Wallace et al. 2006). For example, dietary stable nitrogen isotope ratios from various tissue samples of loggerhead (*Caretta caretta*), green (*Chelonia mydas*), and leatherback (*Dermochelys coriacea*) sea turtles were significantly different between the loggerhead and green sea turtles, indicating they occupy separate trophic levels; the leatherback sea turtle occupies a generalist trophic level and isotope levels were less distinguishable from the other two species (Godley et al. 1998).

To our knowledge, no microchemistry research has been used with freshwater turtle species to determine an individual's river of capture. To address this question, we analyzed the microchemistry characteristics of nail samples taken from snapping, smooth softshell, and spiny softshell turtles in Missouri and used classification and regression tree (CART) models to determine whether we could determine the river of capture. We assessed the utility of this approach for determining legality of river-turtle harvest.

STUDY AREA

We captured turtles from three rivers in central Missouri, the Missouri River (legally open to commercial turtle harvest) and two of its major tributaries, the Osage and Gasconade rivers (both closed to commercial turtle harvest). The Missouri River is one of the largest rivers in North America, and the lower reach of the river is characterized by a high number of modifications, mainly wing dikes for channelization, along both sides of the bank (Galat and Lipkin 2000, Pegg et al. 2003). Along and within the banks of the Missouri River, private development (housing, docks) and recreation is limited and much of the river within this area is bordered by agricultural fields. The Osage and the Gasconade Rivers maintain similar habitat to the Missouri River within our study area, but recreational use within and along the banks of the Osage River is common, as is private development.

On the Missouri River, trapping took place between river miles (RM) 154 and 80; the confluences of the Osage and Gasconade rivers occur within this region. We limited selection of trapping sites in the Osage and Gasconade rivers to within the first 11 RM of the confluence due to the placement of a dam structure on the Osage River at approximately 11.5 miles upstream, which may not only restrict the movement of turtles, but is also impassable by boat.

METHODS

TURTLE SAMPLING

Field work took place during the summer months of 2010, 2011, and 2012. We conducted a pilot season in 2010 to determine the availability of turtle habitat and our

ability to capture turtles for a broader study assessing the demographic consequences of commercial harvest on river turtle populations (see Chapter 1). We trapped in areas containing turtle habitat, such as sand bars, sand banks, gravel bars, and shallow areas of slow current (Barko and Briggler 2006, Ernst and Lovich 2009). We trapped turtles following methods described by Cagle and Chaney (1950) using 3-hoop nets, 7-hoop nets, and mini-fyke nets baited with shad, carp, canned sardines, chicken gizzards, or chicken hearts. No set amount of days was spent per trap location, since the aim of the pilot field work was to locate turtles and appropriate habitat for future field seasons.

In 2011 and 2012, we trapped within 6 randomly selected sites on the Missouri River and within 2 randomly selected sites on both the Osage and the Gasconade rivers. All sites were 1 km in length, and were randomly selected from within areas of appropriate turtle habitat using aerial imagery. We captured turtles using 3-hoop nets, 7-hoop nets, custom D-hoop nets, and mini-fyke nets baited as with the 2010 pilot study. We set 20 traps per 1 km site; traps were checked daily for 8 days. We injected all captured target species with AVID (American Veterinary Identification Devices; Norco, California) passive integrated transponder (PIT) tags (12 mm, 125 khz), each encrypted with a unique 9-digit code for individual identification to ensure that no individual was double-sampled. We collected two nail samples from each newly captured turtle using dog toe nail clippers from the tip of the first and second nail of the posterior left foot. We placed each nail into individual 1.5 ml microcentrifuge vials with either a screw-top lid or a snap-top lid; all samples were refrigerated until preparation for analysis. Species, sex, stage (hatchling, juvenile, adult; based on straight carapace length measurements described by Johnson 2000), river and location of capture (UTM coordinates), and date

were recorded for each sample. Following collection of the nail sample, each turtle was released at its point of capture. These methods were approved by the University of Missouri Animal Care and Use Committee Protocol #6744.

MICROCHEMISTRY ANALYSIS

We obtained 658 individual turtle nail samples, and from these, we randomly selected nails for microchemistry analysis. We considered the following criteria when choosing nail samples from those available. First, we included at least 20 samples from each of the three turtle species per river (Tables 1, 2) in order to maintain a sufficient sample size (Whitledge et al. 2006 reported collection of 5-23 otolith samples per location). We selected an approximate 1:1 ratio of male to female samples, but in some instances we were unable to achieve this balance due to lack of captures. We selected only adult and large juvenile samples (i.e.,turtles with nails greater than approximately 2 mm in length) because hatchling and small juvenile (e.g., turtles in their second year) nail samples were too small to analyze or too thin and flexible to clip successfully. We excluded samples collected from any turtles at a river confluence, which might confound our ability to determine river of capture for those individuals.

We used two separate microchemistry analyses on each turtle nail sample. We used stable isotope analysis (SIA), a commonly used method (Whitledge et al. 2006), to determine the compositions of stable isotopes of hydrogen ($\delta^{2}H$) and oxygen ($\delta^{18}O$) in turtle nail samples. We also determined the concentrations of trace elemental strontium (Sr) and calcium (Ca), and the ratio of these two elements (Sr:Ca), for each nail sample

by means of inductively coupled plasma mass spectrometry (ICP-MS; Bickford and Hannigan 2005, Rodushkin and Axelsson 2000).

For the SIA, we analyzed two batches of nail samples at separate times, employing a slightly different method of sample preparation for each. For the preparation of Batch 1, we ultrasonically cleaned (Mechanical Ultrasonic Cleaner 0.5 L, 120 V 50/60Hz; Fisher Scientific, Pittsburgh, Pennsylvania, USA) all samples in ultra-pure trace elemental analysis grade water (Fisher Scientific) for approximately 2 minutes to remove dirt or excess organic material. We allowed samples to air dry, then chipped them into pieces by hand using a razorblade.

We found that the particle size of some of the samples was too large for successful mass spectrometry. This prompted us to adjust our preparation methods to achieve a finer particle size and analyze a second batch of nails. For Batch 2, all were prepared for analysis according to the following methods: we ultrasonically cleaned each sample as for Batch 1 and placed in a Thermo Scientific Precision (Waltham, Massachusetts) drying oven at 55 degrees Celsius for 60 hours. Once dry, we pulverized all samples individually in liquid nitrogen using a ceramic mortar and pestle to achieve a finely ground sample. Following preparation, all samples for the SIA were weighed individually using a Mettler-Toledo XS3DU microbalance (Columbus, Ohio) and analyzed for stable hydrogen and oxygen isotopes using a high temperature conversion elemental analyzer (TC/EA) interfaced with a Thermo Finnigan Delta V isotope ratio mass spectrometer (Thermo Electron Corporation, Waltham, Massachusetts; Whitledge et al. 2006) at the Mass Spectrometry Facility at Southern Illinois University - Carbondale.

Isotopes were reported in δ notation in parts per thousand (δ^2H ‰ and δ^{18}O ‰) as the deviation of the sample isotope ratio relative to the standard (Krabbenhoft et al. 1994).

In preparation for the ICP-MS analysis, all nails were ultrasonically cleaned in ultra-pure trace elemental analysis grade water (Fisher Scientific) for approximately 2 minutes to remove any dirt or excess organic material. Nails and sample vials for storage were bathed in 1 molar trace metal grade hydrochloric acid (Fisher Scientific) diluted in ultra-pure trace elemental analysis grade water (Fisher Scientific). After air drying, nail samples were weighed to the nearest 0.0001 grams (Ohaus Analytical Plus Electronic Balance model AP110S; Florham Park, New Jersey). Sample digestion and analysis proceeded similarly to the methods described by Rodushkin and Axelsson (2000). Samples were digested at overnight at room temperature by adding 250 µL of concentrated ultra-pure nitric acid (Seastar Baseline) plus 250 µL of 30% H_2O_2 (reagent grade) to each sample. Subsequently, the digest was diluted 10-fold in 0.016 M ultra-pure nitric acid containing 2 ppb of In as an internal standard. Diluted samples were analyzed using a ThermoFisher Element 2 sector field-inductively coupled plasma–mass spectrometer (Thermo Fisher Scientific; Bremen, Germany) at the Center for Trace Analysis, University of Southern Mississippi. Concentrations of strontium (Sr) and calcium (Ca) were determined using medium resolution mode of the instrument and measuring ^{44}Ca and ^{88}Sr with calibration by external standardization.

STATISTICAL ANALYSIS

To determine how well we could predict the river of capture of our samples, we developed CART models using the microchemistry SIA and ICP-MS data. CART

models are non-parametric procedures that result in a binary decision tree, a kind of automated taxonomic key that permits the classification of new cases (Breiman et al. 1984, Vayssières et al. 2000). A tree is constructed by repeatedly splitting the data, defined by a simple rule based on a single explanatory variable. At each split, data are partitioned into two mutually exclusive groups, each of which is as homogeneous as possible (De'ath and Fabricius 2000). In our case, we used CART modeling to determine the probability of correctly classifying samples based on river of capture using the microchemistry results.

We used recursive partitioning (RPART) routines in program R (Therneau and Atkinson 2013) and constructed 18 CART models (Table 2) incorporating various permutations of the 5 microchemistry variables that resulted from the microchemistry analysis: compositions of δ^2H and $\delta^{18}O$, concentrations of Sr and Ca, and the ratio of Sr:Ca. To be included in any of the CART models, each sample needed to have been successfully analyzed for at least one of the variables. We assessed our ability to classify samples to a specific river (Missouri, Osage, or Gasconade) and at a broader level of harvested (Missouri River) or unharvested (Osage or Gasconade rivers). This resulted in an overall rate of correct classification (i.e., the total proportion of samples that could be correctly classified using this model). In order to test the applicability of these models to other sets of data, we used *k*-fold cross-validation, which is a component of the RPART routine. To cross-validate models, the data are split into *k* subsets and each of the *k* sets is used to validate the model fit on the rest of the data. This gives a cross-validation correct classification rate (hereafter X-$Val_{correct}$, which is an indication of how well the model should perform when applied to other datasets (Therneau and Atkinson 2013).

RESULTS

Stable isotope analysis was successfully completed for 137 turtle nail samples for δ^2H both and $\delta^{18}O$ (out of 215 total samples); δ^2H only was obtained for an additional 8 samples (Table 1). ICP-MS analysis was successful for 121 samples for both Sr and Ca (out of 128 total samples; Table 1). A value for one or more of the microchemistry variables was obtained for 154 samples, and 108 of the samples were successfully analyzed for all variables (Table 1). When developing CART models with these results, individual samples used to develop the model did not necessarily contain a value for each of the microchemistry variables involved in the model.

The greatest rates of cross-validation correct classification ($X\text{-}Val_{correct}$) occurred when classifying turtles to the Missouri River vs. the Osage and Gasconade rivers (Table 2), using either the ICP-MS or SIA results. We determined that the Sr:Ca parameter is the single most important variable in distinguishing between the Missouri River vs. the two tributaries for these species in central Missouri (Figure 1), with which we obtained a correct classification rate of 83.5%, and $X\text{-}Val_{correct}$ = 76.9%. Likewise, we obtained a high $X\text{-}Val_{correct}$ values with the model incorporating δ^2H, Sr, and the Sr:Ca (77.9%). Though these two models obtained similarly high rates of cross-validation correct classification, the addition of δ^2H from the SIA only improved cross-validation performance by 1%. This level of improvement does not justify both analyses when considering cost; therefore, we selected the Sr:Ca model as our top-performing model. Using only the SIA results, the highest $X\text{-}Val_{correct}$ value (63.4%) was obtained using both δ^2H and $\delta^{18}O$. $\delta^{18}O$ alone, which has been used to successfully classify fish species

(Zeigler and Whitledge 2011), resulted in some of our lowest rates of correct classification.

We achieved lower rates of correct classification when classifying turtles among the three rivers (Table 2). Using the model incorporating only Sr:Ca, we achieved a much lower X-$Val_{correct}$ value (54.5%) when classifying among the three rivers than we did when classifying to the Missouri River vs. the two tributaries. Further, of the 9 total models classifying turtles to a specific river, models incorporating a single microchemistry variable (i.e., only Sr, Ca, Sr:Ca, δ^2H, or $\delta^{18}O$) resulted in both the 5 lowest rates of correct classification ($\leq$ 68.6%) and X-$Val_{correct}$ values ($\leq$ 56.2%; Table 2). This indicates that when classifying turtles to a specific river, models constructed using more than one variable are needed in order to maximize rates of correct classification. For example, our highest X-$Val_{correct}$ value was 60.4%, based on both SIA and ICP-MS microchemistry variables (δ^2H, $\delta^{18}O$, Sr, and Sr:Ca). The rate of correct classification for this model was 75.3%, only slightly greater than the lowest rate of correct classification that we achieved when classifying turtles to being collected from a harvested vs. unharvested river (i.e., 73.7%, based on the $\delta^{18}O$ value alone).

DISCUSSION

Our results indicate that microchemistry analyses can be useful tools for determining whether turtles were captured in either the Missouri or one of the tributaries (i.e., the Osage River or Gasconade River) with fairly high rates of correct classification. Our result that Sr:Ca classifies turtles with high rates of correct classification is supported by other studies which have found the Sr:Ca ratio to be among the more useful ratios of

trace elements for predicting location of capture (Wells et al. 2003), and also in distinguishing the type of water body (e.g., tributary, floodplain lake) where an individual was captured (Zeigler and Whitledge 2011). We recommend the model constructed using the ratio of Sr:Ca from the ICP-MS analysis (Figure 1) as a useful tool to assist managers with legal decisions regarding turtle harvester activity. Samples may be taken from commercially harvested turtles and tested in order to confirm legal collection by classifying turtles, though several factors should be considered when conducting microchemistry work with river turtles in order to ensure the appropriate application of the Sr:Ca model. In contrast, $\delta^{18}O$ has been used to successfully determine location of capture for fish species (Zeigler and Whitledge 2011), but when we classified turtles based on this isotope alone, it resulted in some of the lowest rates of correct classification for this study.

We were unable to classify turtles to one of the three rivers at the same level of accuracy as when classifying at a broader level to the Missouri River vs. the two tributaries. The microchemistry characteristics of rivers within the Missouri River basin can vary based on water sources and inputs, agricultural runoff, and geochemistry (Winston and Criss 2003). Though rivers within the Missouri River basin may be distinct and variable from one another, both of the tributaries examined here flow from the Ozark region of Missouri, are heavily fed by groundwater, and can be distinct from the Missouri River (Winston and Criss 2003). As such, our inability to obtain high levels of accuracy when classifying turtles at the river-specific level may be a result of these water chemistry variations (i.e., streams flowing from the Ozark region vs. the Missouri River).

One area of concern is the lack of available information about the rate of nail growth in reptile species, which may vary by species (Ethier et al. 2010), age of the turtle, diet, or habitat substrate (i.e., muddy versus rocky habitat). Additionally, reptile claw structures can contain both old and new material at the tip (Ethier et al. 2010) and therefore, we do not know the time range being sampled in this analysis. Still, keratinous structures represent continuous growth over a given period of time, and can be representative of a geographic location (Ethier et al. 2010). For more commonly studied species where information about growth rates of keratinous structures (i.e., claws, hooves) is available, stable isotope analysis has been used to determine the geographic history of individuals (Fraser et al. 2008, Ethier et al. 2013). For lesser-studied species where few studies have been carried out on keratinous tissues, detailed species-specific knowledge of nail growth rates would greatly improve the potential for microchemistry studies (Ethier et al. 2010) because such information would aid researchers in assessing microchemistry turnover and composition throughout the nail. Turnover rates of stable isotopes have been examined for non-keratinous tissues (i.e., muscle tissue, blood; a turnover rate of at least 146 days depending on the tissue) of pond sliders (*Trachemys scripta*; Seminoff et al. 2007), but little is known about the rates of turnover for nail material.

The regularity of movement of turtles between rivers is another concern which may confound results of the microchemistry analysis. Turtles may increase activity during the breeding and nesting seasons (Brown and Brooks 1993) and have the potential to move between rivers. Considering that commercial turtle harvesters in Missouri can collect turtles year-round, individuals making long-distance movements during periods of

high activity may be collected on occasion. Precaution should be taken if microchemistry analysis is to be used to confirm legal collection of turtles commercially collected during these periods of high activity because analysis of samples taken from turtles making long-distance movements from a river closed to harvest to a legally harvested river may incorrectly suggest illegal collection of these individuals. This issue reiterates the need for information detailing turtle nail growth rates and the varying locations which may be represented in a sample. For example, for migratory warblers, microchemistry of the migratory destination may not be reflected in the nail tip until after 4-7 weeks following arrival of an individual, but analysis of the individual deposited keratin layers (e.g., as with fish otolith layers; Wells et al. 2003) may present researchers with a means to examine migratory movements on a finer scale (Fraser et al. 2008). Analysis of the individual layers of nail keratin from turtle species, along with information on scale of individual turtle movement during periods of high activity, may aid managers in narrowing down potential rivers of capture as well as an individual's history of movement over time.

Since the microchemistry of rivers can be distinct and may vary among rivers within the same watershed (Wells et al. 2003, Zeigler and Whitledge 2011), we do not recommend the use of these models outside the region we sampled. For those interested in assessing their ability to determine river of capture of turtles from other regions, while we do recommend the use of ICP-MS to obtain a ratio of Sr to Ca concentrations as a sufficient classifying variable, we also encourage the additionally formulation of region-specific models based on regional microchemistry data. The microchemistry of samples taken from turtles of other regions may not be well represented by our Sr:Ca model (e.g.,

Figure 1). Further, considering the known variation of water chemistries among watersheds and of the turtles within those waters, we encourage researchers to assess the usefulness of multiple trace elements and stable isotopes as indicators of geographic location specific to their region or watershed. Our field and analytical methods are by no means site-specific and can easily be applied to other areas in order to confirm the legal collection of harvested turtle species.

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TABLE 1: NUMBER OF TURTLE NAIL SAMPLES SUCCESSFULLY ANALYZED FOR MICROCHEMISTRY VARIABLES. Data are organized by river of capture, species, life stage (A = adult, J = juvenile; Johnson 2000), and sex (F = female, M = male, U = unknown); Selected for SIA = number of randomly selected samples for SIA from each group (215 total). $\delta^{18}O$ = number of samples for which we obtained only the $\delta^{18}O$ composition value from the SIA. $\delta^{2}H$ = number of samples for which we obtained the$\delta^{2}H$ composition from the SIA. All samples successfully analyzed for $\delta^{18}O$ were also successfully analyzed for $\delta^{2}H$; 8 total samples were only successfully analyzed for $\delta^{2}H$. Selected for ICP-MS = number of randomly selected samples for ICP-MS from each group (128 total). Sr and Ca = number of samples from the total for which we obtained values for both Sr and Ca concentrations from the ICP-MS analysis; we obtained both Sr and Ca values for all successfully analyzed samples. All Variables = number of samples that were successfully analyzed for all microchemistry variables.

River	Species	Age	Sex	Selected for SIA	$\delta^{18}O$	$\delta^{2}H$	Selected for ICP-MS	Sr, Ca	All Variables
Missouri	Common Snapping Turtle	A	F	5	4	4	4	4	4
			M	7	7	7	7	7	7
			U	1	1	1	1	1	1
		J	M	1	1	1	1	1	1
			U	7	7	7	5	5	5
	Smooth Softshell	A	F	13	11	13	9	8	8
			M	9	8	8	3	3	3
		J	F	3					
	Spiny Softshell	A	F	9	9	9	8	8	8
			M	9	9	9	5	5	5
		J	U	2					
Osage	Common Snapping Turtle	A	F	9	3	3	6	6	3
			M	14	4	8	9	9	4
		J	U	3	2	2	2	2	2
	Smooth Softshell	A	F	6	1	1	1	1	1
			M	14	2	2	5	5	2
	Spiny Softshell	A	F	12	6	6	7	7	6
			M	12					
		J	F	1			1	1	
Gasconade	Common Snapping Turtle	A	F	14	12	14	10	9	9
			M	16	10	10	9	9	9
		J	M	1					
			U	6	3	3	2	1	1
	Smooth Softshell	A	F	16	15	15	16	14	14
			M	4	4	4	2	1	1
			U	1	1	1	1	1	1
	Spiny Softshell	A	F	9	9	9	7	7	7
			M	10	8	8	7	6	6
		J	U	1					

TABLE 2: ERROR AND CROSS-VALIDATION (X-VAL) ERROR FOR EACH CART MODEL. Classify To: River = models assessing our ability to classify samples to either the Missouri, Osage, or Gasconade rivers; Status = models assessing our ability to classify samples as being from either a harvested river (the Missouri) or an unharvested river (the Osage or Gasconade). H = composition of δ^2H (‰); O = composition of δ^{18}O (‰); Sr = concentration of Sr; Ca = concentration of Ca; Sr:Ca = ratio of Sr to Ca; *n* = samples size (number of turtle nails included in analysis; samples included need to have been successfully analyzed for at least one of the microchemistry variables to be included in the model); Root Error = baseline classification error of the model prior to construction of the CART model; Splits = number of times the CART model splits the data into two mutually exclusive groups based on a single explanatory variable; Error = the rate of classification error of all data for the constructed CART model; Relative % Correct = the proportion of samples that were correctly classified; X-Val Error = the cross-validation error rate; $\text{X-Val}_{\text{Correct}}$ = the cross-validation correct classification rate; X-Val SD = the cross-validation standard deviation.

Classify To:	Model	*n*	Root Error	Splits	Error	% Correct	X-Val Error	$\text{X-Val}_{\text{Correct}}$	X-Val SD
River	[3]H, O, Sr, Ca, Sr:Ca*	154	0.584	7	0.247	0.753	0.396	0.604	0.039
	[1]Sr, Ca, Sr:Ca	121	0.603	8	0.190	0.810	0.405	0.595	0.045
	[3]H, Sr, Ca, Sr:Ca**	154	0.584	4	0.266	0.734	0.416	0.584	0.040
	[2]H, O	145	0.559	8	0.283	0.717	0.428	0.572	0.041
	[1]Sr	121	0.603	6	0.314	0.686	0.438	0.562	0.045
	[2]H	145	0.559	3	0.352	0.648	0.441	0.559	0.041
	[1]Sr:Ca	121	0.603	7	0.347	0.653	0.455	0.545	0.045
	[2]O	137	0.547	6	0.358	0.642	0.482	0.518	0.043
	[1]Ca	121	0.603	7	0.397	0.603	0.636	0.364	0.044
Status	[3]H, Sr, Ca, Sr:Ca*	154	0.383	6	0.182	0.818	0.221	0.779	0.033
	[1]Sr:Ca	121	0.347	3	0.165	0.835	0.231	0.769	0.038
	[3]H, O, Sr, Ca, Sr:Ca*	154	0.383	7	0.175	0.825	0.299	0.701	0.037
	[1]Sr	121	0.347	6	0.215	0.785	0.322	0.678	0.042
	[2]H, O	145	0.407	6	0.234	0.766	0.366	0.634	0.040
	[2]H	145	0.407	8	0.255	0.745	0.372	0.628	0.040
	[2]O	137	0.416	4	0.263	0.737	0.394	0.606	0.042
	[1]Sr, Ca, Sr:Ca	121	0.603	3	0.215	0.785	0.405	0.595	0.065
	[1]Ca	121	0.347	7	0.256	0.744	0.413	0.587	0.045

[1]Models incorporating various permutations of results from the ICP-MS analysis.
[2]Models incorporating various permutations of results from the SIA.
[3]Models incorporating various permutations of the combined ICP-MS and SIA results.
*The Ca concentration was included but disregarded by the model.
**The Ca and Sr concentrations were included but disregarded by the model.

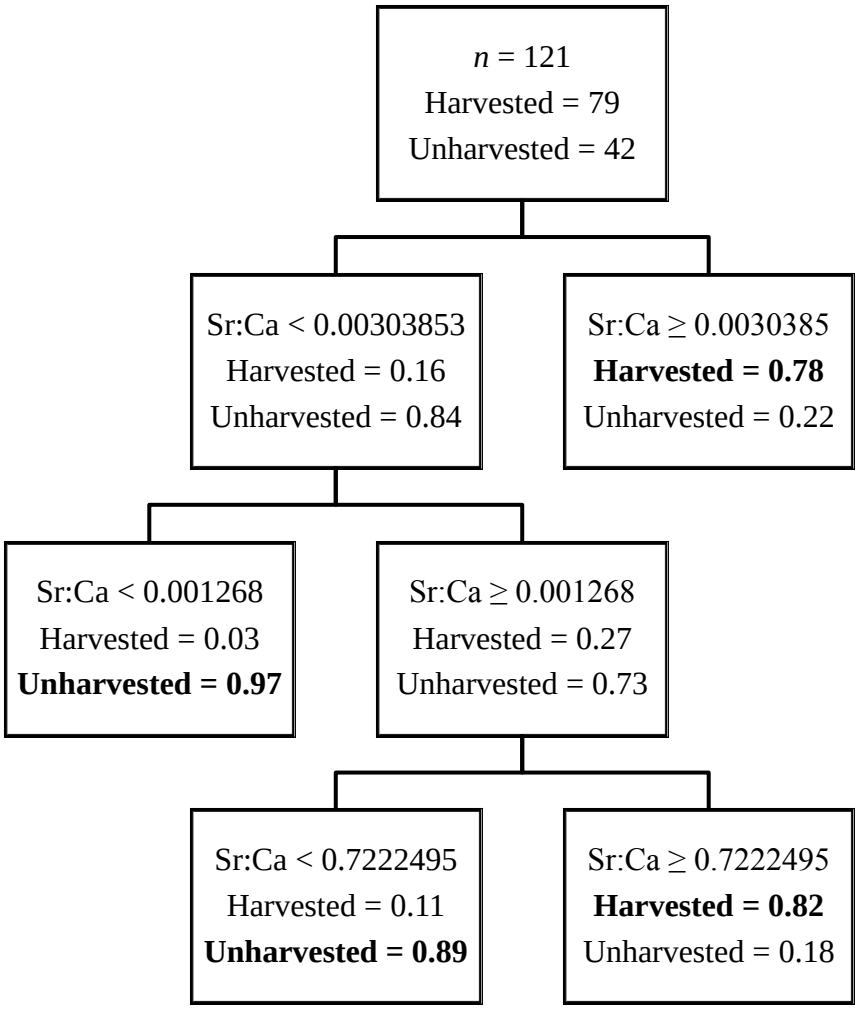

Figure 1: Classification and regression tree for the top-selected model classifying turtle nail samples (*n* = 121) by legal river status (harvested vs. unharvested) based on the Sr:Ca ratio from the ICP-MS analysis. Following the initial node, all nodes represent splitting of the data into two mutually exclusive groups. This model resulted in one of the lowest overall error and cross-validation error rates. Each node represents the rate of correct classification for our samples based on the value in the given and preceding nodes. Rates following "Harvested" or "Unharvested" represents the proportion of correctly classified samples into either harvested or unharvested rivers based on the given value of Sr:Ca. The terminal nodes indicate the proportion of correctly classified samples to either harvested or unharvested rivers based on the given rate (greatest rates bolded).

CHAPTER 4

COMMERCIAL TURTLE HARVEST MANAGEMENT RECOMMENDATIONS

Based on the results and data from this research and the findings of other studies, we provide the following list of management recommendations. While not all of these recommendations are intended to be implemented simultaneously, they can promote sustainable river turtle populations in Missouri.

1) USE OF SLOT LIMITS

The commercial turtle harvest regulations in Missouri do not limit harvesters to the size of common snapping turtles (*Chelydra serpentina*), smooth softshells (*Apalone mutica*), or spiny softshells (*Apalone spinifera*) that may be harvested. Turtles are often sold by weight on the food market (Brown et al. 2011), and as such, harvesters have an incentive to collect larger (i.e., adult) individuals. For the softshell species which exhibit marked sexual dimorphism, this may result in a female-biased harvest.

Survival of the adult stage is most important to population sustainability of many turtle populations (Congdon et al. 1994, Crouse et al. 1987; Chapter 2). Considering the known negative effects that increases in mortality of the adult stage can have on turtle populations (e.g., Brooks et al. 1991, Congdon et al. 1994, Doroff and Keith 1990, Gamble and Simons 2003; Chapter 2) limiting the removal of these individuals by means of slot- or size-limits may reduce the impacts that harvest activity has on population sustainability. The placement of such limits has been suggested for adult female painted

turtles (*Chrysemys picta*) in Minnesota (Gamble and Simons 2004), and also in Texas (Brown et al. 2011) for multiple harvested turtle species, specifically in the interest of reducing pressure on reproductive females. Though this action could increase the harvest of juvenile turtles, the juvenile survival has been shown to be of lesser importance than survival of the adult stage (Chapter 2).

2) IMPLEMENTATION OF A HARVEST SEASON

In Missouri, commercial turtle harvesters can collect turtles year-round. Due to the life histories of these species, turtles may be particularly vulnerable to harvest at certain times of the year. For example, softshells make use of sand bars and banks for nesting and breeding (Barko and Briggler 2006). Commercial harvesters trapping in these areas during the nesting or breeding seasons could prevent nesting females from laying eggs, reduce the number of nest laid annually, and reduce the number of turtles available for mating. Given these potential implications, one option would involve limiting harvest during these times of year which has been suggested for harvested turtle populations in Texas (Brown et al. 2011). Restricting commercial turtle harvest during these months can reduce the mortality of reproductive individuals (i.e., gravid females) and would allow turtles to carry out breeding and nesting without additional pressure of harvest mortality.

3) ANNUAL ROTATION OF HARVESTABLE AREAS

Depending on the location and extent of commercial turtle harvest, it holds the potential for population declines at a local scale (e.g., Boundy and Kennedy 2006, Paisley et al. 2009; Chapters 1, 2). Further, turtles are not known to exhibit density-dependent

reproductive responses to increases in mortality (Brooks et al. 1991, Congdon et al. 1994, Galbraith et al. 1997) and reduced population numbers may persist (Breckenridge 1955, Congdon et al. 1994). Commercial turtle harvesters may return to a 'favorite' area of the river year after year in order to find turtles, continuously placing pressure on the local turtle population, which could result in local population declines. Personal communication with a leading commercial turtle harvester in Missouri indicated that trapping occurs in an area until the turtles are removed. In the state of Missouri, within waters where commercial harvest is allowed, harvesters are not limited to a specific area of the river (aside from within 300 meters on all sides of a tributary confluence with the harvestable river). In order to address the potential issue of local-scale overharvest, harvest may be restricted to specific areas of the river (e.g., within specific river miles, rotated annually in a systematic way) and would allow local turtle populations to rebound via reproduction or annual emigration or immigration following harvest activity. This approach might help alleviate the local effects of harvest and would reduce the potential for over-harvest of turtle populations.

4) REQUIRE DETAILED REPORTS FROM TURTLE HARVESTERS

To investigate the usefulness of the previously discussed management actions, managers would be greatly benefitted by the collection of information specific about the extent and location of harvest activity, as well as information on turtles collected. Annual commercial turtle harvest reports returned by harvesters do not require a report of location of harvest, date of harvest, or size or sex of harvested turtles, and this limits the ability of managers to assess the extent of harvest activity in Missouri. In order to examine the usefulness of restricting the location or season of harvest activity as

discussed previously, commercial turtle harvesters may be required to report the location (e.g., GPS or river mile) of harvested turtles and the date which turtles were collected. This information would not only provide managers with information about where harvesters are focusing their efforts when collecting turtles, but would also indicate the time of year at which harvesters are most active and successful. Further, harvesters could be required to report a sex and size for each individual turtle that is collected. This requirement would give insight into harvester preferences and would provide an indication of any size- or sex-based bias for collected turtles. The ability to collect such information does not require extensive knowledge of turtles in order to be accurate, and would be simple for harvesters to gather and report. This information would provide managers with useful data on targeted turtle populations and commercial turtle harvest activity in this state.

5) IMPLEMENT A TURTLE-SPECIFIC COMMERCIAL HARVEST PERMIT

In Missouri, commercial harvest of turtles is covered by the commercial fishing permit and there is no turtle-specific commercial harvest permit. Such a permit could be implemented in order to address the previously discussed management action of requiring harvesters to report specific information on harvest activity and collected turtles. Currently, commercial fishermen may collect turtles as bycatch though turtles may not be their targeted species, and individuals are then able to harvest and sell these turtles. This activity is difficult to regulate because these turtles may be captured, sold, and go either under-reported (e.g., Gamble and Simons 2004) or completely unreported since there is no way to track this activity and turtles may be bought or sold among harvesters. A turtle-specific commercial harvest permit may reduce instances of fishermen from selling

incidentally captured turtles (and in turn, possibly failing to report these captures), and may also be used to require harvesters who have obtained this permit to provide explicit information about turtle harvest activity in annual harvest reports.

6) USE OF MICROCHEMISTRY TO ENSURE LEGAL COLLECTION

In order to confirm the legal collection of turtles (i.e., collection of turtles only from legal waters), the implementation of microchemistry methods discussed in Chapter 3 may be used to regulate harvest activity. However, additional work is needed to develop this tool beyond those central Missouri rivers we sampled. Currently, harvesters are not required to report specific locations from which turtles were harvested. The use of microchemistry to test commercially harvested turtles, even if not used for legal purposes, can be used in order to provide an idea of the extent of illegal activity at the scale discussed in Chapter 3 (i.e., within central Missouri).

7) RESTRICT COMMERCIAL TURTLE HARVEST

One last possibility is to restrict or eliminate commercial-scale harvest of turtle species which has been suggested for other states (e.g., Congdon et al. 1993, Congdon et al. 1994, Crouse et al. 1987, Crouse and Frazer 1995, Galbraith et al. 1997, Heppell 1998, Zhou and Jiang 2008). Further, research has indicated that commercial turtle harvest is an important influence on turtle population declines worldwide (Ceballos and Fitzgerald 2004, Schlaepfer et al. 2005) and that the life-history traits common to turtle species make commercial-scale harvest an unfeasible option (Congdon et al. 1994). The plausible harvest rates estimated in this research demonstrated that on average, 23% of local turtle populations can be removed, and harvest rates ranged from 6-79%. All of

these rates exceed those reported in the literature as being the threshold for turtle population sustainability. For example, for painted turtles (*Chrysemys picta*) annual removal of 4-5% of adult females results in population declines (Gamble and Simons 2003). For ornate box turtles (*Terrapene ornata*) annual adult mortality rates exceeding 0.05 may result in population declines (Doroff and Keith 1990). Additionally, matrix modeling carried out in this study indicated that harvest could not be sustained when ≥ 2.3% of both adult and juvenile snapping turtles were harvested from populations exhibiting mean demographic rates. Softshells could sustain no harvest at this level. In 20 of the 27 total harvest scenarios modeled for snapping turtles, and in 22 of the 27 total harvest scenarios modeled for softshell turtles, harvest could not be sustained (Chapter 2). For snapping turtles, a minimum harvest (7%) of only juveniles could be sustained for populations exhibiting mean demographic rates. Other than this instance, harvest could only be sustained by snapping turtle and softshell populations exhibiting maximum demographic rates. All scenarios indicated that populations have a consistently reduced ability to sustain harvest of adults only or harvest of both juveniles and adults, and this coincides with the findings of other studies which suggest that adult survivorship is the most important contributor to population sustainability (Congdon et al. 1994, Crouse et al. 1987). Considering the paucity of demographic data that is currently available in the literature for harvested turtle populations, loose commercial harvest regulations lack foresight since there is no way to quantify the effects of harvest on targeted populations. Researchers have warned against taking no action at all when it comes to regulation of turtle harvest activity (Congdon et al. 1994, Gamble and Simons 2004, Gibbons et al.

2000). Management actions that are formulated with a primary goal of maintaining population sustainability are in the best interest of these vulnerable populations.

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