Potential recovery of a declined turtle population diminished by a community shift towards more generalist species

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Abstract. Models suggest that a declined turtle population may rebound if the cause of decline is remedied and adult mortality is reduced, but recovery time will likely be slow. In 2005-2007, we reexamined a river turtle community which included a population of Northern Map Turtles (Graptemys geographica) that had been reduced by approximately 50% between 1969 and 1980 likely as a result of harvesting, and had failed to rebound by 2004 despite no evidence of continued harvesting. Comparisons of population estimates for G. geographica showed no significant differences between 2005 and 2006 (z = 1.79, P = 0.073) or between 2006 and 2007 (z = 1.07, P = 0.284). However, the population estimate for 2007 was not significantly different from the population estimate for 1969 (z = 0.48, P = 0.629) but was significantly higher than the population estimate for 1980 (z = 2.96, P = 0.003), suggesting the population had returned to its pre-decline (1969) size. While the recovery of the G. geographica population demonstrates that a previously harvested river turtle population may rebound if no further harvesting occurs, the recovery period will be extensive, thus confirming model predictions. Furthermore, the turtle community composition was shifting towards a higher relative abundance of generalist species and a lower relative abundance of specialist species – a pattern that can be expected with habitat degradation, another threat which may present new challenges to G. geographica, a dietary specialist.

Keywords: community composition, Graptemys geographica, habitat degradation, harvested turtle population, Sternotherus odoratus, Trachemys scripta elegans.

Introduction

Over-exploitation of wildlife is a well-documented cause of population declines and extinctions, yet subsistence-level, recreational, and commercial harvesting of wildlife continues to threaten a wide variety of species (Klemens and Thorbjarnarson, 1995; Noss, 1998; Post et al., 2002; Stuart et al., 2004; Butchart, Stattersfield and Collar, 2006). Harvesting affects species disproportionately and long-lived species are particularly susceptible to exploitation as their life history traits limit their ability to respond to increases in mortality (Congdon, Dunham and Van Loben Sels, 1993). While, perhaps deservedly, habitat loss and climate change have gained the spotlight of much of the conservation community, over-exploitation continues to be a primary driver of rapid decline for many vulnerable, long-lived taxa, including many turtle species – one of the most threatened taxonomic groups worldwide (Buhlmann et al., 2009) – and therefore harvesting should not be overlooked when considering major threats to biodiversity.

Harvesting of turtles for the food, pet, and traditional Chinese medicine trades is a well-documented, ongoing threat affecting turtle populations worldwide (Roman and Bowen, 2000; Moll and Moll, 2004; Schlaepfer, Hoover and Dodd, 2005). Accounts of harvested populations declining exist for a large variety of turtle species (Kuchling, 1997; Roman and Bowen, 2000; Moll and Moll, 2004; Schlaepfer, Hoover and Dodd, 2005) and population model analysis suggests that even low levels of turtle harvesting are unsustainable (Congdon, Dunham and Van Loben Sels, 1993). Harvesting may also alter the structure of populations as selective harvesting of large turtles for the food trade or as breeding stock has corresponded with smaller...
mean body sizes of turtles in exploited populations compared to unexploited populations (Close and Seigel, 1997). While conservation efforts and protective legislation have helped to curtail the exploitation of many marine turtle populations (at least in the United States), freshwater turtle populations have not garnered such legal or public support for conservation, and harvesting has likely contributed to and/or resulted in the irreversible decline of a variety of turtle populations and species (Gibbons et al., 2000; Roman and Bowen, 2000; Moll and Moll, 2004). Despite the extent and potentially dire consequences of turtle exploitation, there is a dearth of long-term studies that followed the fate of harvested freshwater turtle populations and many of the data-derived conclusions drawn about the impacts of exploitation on turtle populations were based on analyses of population models (e.g., Congdon, Dunham and Van Loben Sels, 1993; Heppell, 1998), comparisons of spatially distinct populations subjected to various harvest levels (e.g., Close and Seigel, 1997), and/or short-term experiments (e.g., Fordham, Georges and Brook, 2009). Furthermore, the impact of exploitation may extend beyond the harvested population as population declines of a single species may substantially alter turtle community composition as turtle communities are typified by low species richness and evenness (Moll and Moll, 2004; Smith, Iverson and Rettig, 2006).

An opportunity to evaluate the long-term trends of a turtle population that was subjected to harvesting became available due to periodic assessment beginning in 1969 of a turtle community located within a section of the North Fork of White River (NFWR), Ozark County, Missouri (Nickerson and Pitt, 2012; Pitt and Nickerson, 2012). A previous study revealed a population decline of approximately 50% of the numerically dominant species in the community, the Northern Map Turtle (Graptemys geographica), between 1969 and 1980 (Nickerson and Pitt, 2012). The population decline was typified by the loss of the larger size classes of females (i.e., the larger sex of this highly sexually dimorphic species) – a pattern consistent with and attributed to harvest for the food trade (Nickerson and Pitt, 2012). A follow-up study conducted in 2004 revealed the G. geographica population had not rebounded from the reduced population size observed in 1980 despite no evidence of continued harvest after 1980, suggesting the population was naturally slow to rebound due to life history constraints and/or that interspecific or habitat factors limited population growth (Pitt and Nickerson, 2012). Comparison of the population structure observed in 1969, 1980, and 2004 revealed that the larger size classes that were diminished in 1980 had recovered by 2004, but there were few turtles in the smallest size class, suggesting low recruitment (Pitt and Nickerson, 2012). The decline of G. geographica between 1969 and 1980 corresponded with the addition of the Red-eared Slider (Trachemys scripta elegans) to the community within the research section suggesting the reduced population of G. geographica may have opened a niche that a small population of T. s. elegans was able to exploit (Nickerson and Pitt, 2012). Between 1980 and 2004, notable changes in the research section occurred that may have impacted or had the potential to impact the turtle community, including the reestablishment of North American River Otters (Lontra canadensis), an increase in recreational use of the river, water quality degradation, filamentous algae blooms, substrate distribution changes, and loss of large boulders (Pitt and Nickerson, 2012). The habitat changes and reestablishment of predators which had been absent from the area since the 1800’s posed additional challenges to the G. geographica population and had the potential to further alter the turtle community (Pitt and Nickerson, 2012). We sought to (1) determine if the increase in the relative proportion of large female G. geographica observed in 2004 foreshadowed increased recruitment into the smallest size class and overall G. geographica population growth in subsequent years and (2) evaluate whether further
changes to the turtle community occurred since 2004, including an increase in the relative abundance of generalist species – a trend that may be expected in light of habitat degradation (Moll, 1977).

Materials and methods

In 2005, 2006, and 2007, we surveyed the turtle community in the same 4.6 km-long section of the NFWR previously examined by Nickerson and Pitt (2012) in 1969 and 1980 and Pitt and Nickerson (2012) in 2004. As we sought to compare the data collected in 2005-2007 with the data collected in previous years and reported in prior studies, we followed the same standardized protocols employed by Nickerson and Pitt (2012) and Pitt and Nickerson (2012). Nickerson (who led the field surveys in 1969 and 1980) participated in the initial surveys of the NFWR in 2004 to train Pitt (who led the field surveys in 2004-2007) and thus ensure that the standardized protocols were followed and the resulting data were comparable through time. While it is likely impossible to remove all sampling bias when multiple investigators collect data, the use of standardized protocols and in-field training served to minimize sampling bias among years. The 4.6-km research section was surveyed every other day throughout the summer (15 June-20 August) between 09:00 and 18:00 h, weather permitting, for a total of 415 person hours. Surveys were conducted by hand-capturing turtles while snorkeling and all captured turtles were weighed, measured, marked, and released at their capture sites following the protocol of Pitt and Nickerson (2012). We used nail polish to create unique numerical identification marks on each turtle. We applied a clear topcoat (AM Cosmetics, Inc., North Arlington, NJ) over the colored mark to ensure that marks lasted throughout the field season. The marks used were smaller than those employed by Gordon and MacCulloch (1980) which were not found to increase mortality. Turtles with plastron lengths \( \geq 8.6 \) cm were additionally tagged with a passive integrated transponder (PIT) tag (Destron-Fearing Corporation, So. St. Paul, MN) which we injected into the anterior inguinal region parallel to the bridge of the shell as described by Buhlmann and Tuberville (1998). We disinfected injection sites and needles using 70% isopropyl alcohol and antibiotic ointment. We applied New-Skin Liquid Bandage (Medtech Laboratories, Inc., Jackson, WY) to cover the insertion hole. We determined turtles’ sex visually when possible based on morphological diagnostic characteristics including tail length and thickness, relative position of the anal opening, and foreclaw characteristics, depending on the species (Ernst, Lovich and Barbour, 1994).

We calculated population size estimates with 95% confidence intervals for \( G. \) geographica using the Schumacher-Eschmeyer method (Krebs, 1989). We compared the population estimates using the Chapman and Overton method (1966 as described in Seber, 1982) to identify significant differences between sampling years. We calculated standardized density estimates using the Schumacher-Eschmeyer estimated population sizes and the area calculated from the product of the mean stream width (calculated from field measurements of the distance between the banks at each station marker along the 4.6-km research section) and length (4.6 km) of the research section. We used the Chapman and Overton method (1966 as described in Seber, 1982) to assess whether the population size estimate generated for the last sampling year (2007) was significantly different from that generated by Nickerson and Pitt (2012) for 1969 (i.e., the year of the original survey of the NFWR turtle community that occurred prior to the \( G. \) geographica population decline) or Pitt and Nickerson (2012) for 1980 (i.e., the year when the \( G. \) geographica population decline was first detected) to determine if the population had rebounded. We conducted a one-way ANOVA test to determine whether the mean plastron length of the \( G. \) geographica populations, partitioned by sex, varied among sampling years when assumptions of normality and equal variance were met. We tested assumptions of normality and equal variance using the Kolmogorov-Smirnov and Levene analyses, respectively. We used a nonparametric Kruskal-Wallis test when assumptions of normality and equal variance were not met. We used binomial tests to identify if sex ratios of each population differed from 1:1 (male:female) in any sampling year. We used chi-squared \( (\chi^2) \) tests of independence to identify if sex ratios differed among sampling years. We used SPSS version 11.5 (SPSS Inc.) with \( \alpha = 0.05 \) to perform statistical analyses unless otherwise specified.

To assess changes in the NFWR turtle community, we calculated values for heterogeneity, which accounts for both species richness and evenness (Krebs, 1989), based on Hurlbert’s Probability of Interspecific Encounter (PIE; Hurlbert, 1971) using EcoSim version 7.72 (Gotelli and Entsminger, 2011).

Results

No significant differences were detected between \( G. \) geographica population estimates for 2005 and 2006 \( (z = 1.79, P = 0.073) \) and 2006 and 2007 \( (z = 1.07, P = 0.284) \); table 1). The \( G. \) geographica population estimate for 2007 was not significantly different from the population estimate generated by Nickerson and Pitt (2012) for 1969 \( (z = 0.48, P = 0.629) \), but was significantly higher than the population estimate generated by Nickerson and Pitt (2012) for 1980 \( (z = 2.96, P = 0.003) \); table 1). No significant differences were observed within the mean plastron lengths, separated by sex, of the \( G. \) geographica populations in any year (males: \( F_{2,82} = 1.32, P = 0.272 \); females: \( \chi^2 = 2.59, P = 0.270 \); table 2; fig. 1). Sex ratios of \( G. \) geographica for
Table 1. Schumacher-Eschmeyer population size and corresponding density estimates of Northern Map Turtles (Graptemys geographica) in 2005, 2006, and 2007 in the 4.6-km research section in the North Fork of White River, Ozark County, Missouri, USA. N (95% CI) = estimated population size (95% confidence interval). Density estimates were based on area calculated from the mean stream width and total length of the research section.

<table>
<thead>
<tr>
<th>Sampling year</th>
<th>N (95% CI)</th>
<th>Estimated density</th>
<th>Data source</th>
</tr>
</thead>
<tbody>
<tr>
<td>1969</td>
<td>274 (237-324)</td>
<td>1 turtle/698 m²</td>
<td>Nickerson and Pitt, 2012</td>
</tr>
<tr>
<td>1980</td>
<td>139 (94-264)</td>
<td>1 turtle/1197 m²</td>
<td>Nickerson and Pitt, 2012</td>
</tr>
<tr>
<td>2005</td>
<td>114 (80-198)</td>
<td>1 turtle/1751 m²</td>
<td>this study</td>
</tr>
<tr>
<td>2006</td>
<td>246 (163-500)</td>
<td>1 turtle/812 m²</td>
<td>this study</td>
</tr>
<tr>
<td>2007</td>
<td>308 (204-621)</td>
<td>1 turtle/648 m²</td>
<td>this study</td>
</tr>
</tbody>
</table>

Table 2. Mean plastron lengths (PL) of Northern Map Turtles (Graptemys geographica) in 2005, 2006, and 2007 in the 4.6-km research section of the North Fork of White River, Ozark County, Missouri, USA. n represents the sample size. SD represents the standard deviation.

<table>
<thead>
<tr>
<th>Sampling year</th>
<th>Sex</th>
<th>n</th>
<th>Mean PL ± SD (cm)</th>
<th>Range (cm)</th>
</tr>
</thead>
<tbody>
<tr>
<td>2005</td>
<td>male</td>
<td>14</td>
<td>7.8 ± 0.86</td>
<td>6.7-9.4</td>
</tr>
<tr>
<td></td>
<td>female</td>
<td>23</td>
<td>13.0 ± 5.71</td>
<td>6.0-19.6</td>
</tr>
<tr>
<td>2006</td>
<td>male</td>
<td>23</td>
<td>7.3 ± 1.03</td>
<td>5.5-8.8</td>
</tr>
<tr>
<td></td>
<td>female</td>
<td>33</td>
<td>12.5 ± 5.94</td>
<td>5.0-19.6</td>
</tr>
<tr>
<td>2007</td>
<td>male</td>
<td>48</td>
<td>7.5 ± 0.95</td>
<td>5.3-9.6</td>
</tr>
<tr>
<td></td>
<td>female</td>
<td>30</td>
<td>14.3 ± 5.59</td>
<td>5.1-19.5</td>
</tr>
</tbody>
</table>

which sex was distinguishable did not differ significantly from 1:1 (male:female) in any sampling year (male:female_{2005} = 1:1.6, n_{2005} = 37, P_{2005} = 0.188; male:female_{2006} = 1:1.4, n_{2006} = 56, P_{2006} = 0.229; male:female_{2007} = 1:0.6, n_{2007} = 78, P_{2007} = 0.054). Sex ratios of G. geographica for which sex was distinguishable were significantly different among sampling years with a higher proportion of males observed in 2007 ($\chi^2 = 8.12, P = 0.017$).

Graptemys geographica was the most abundant turtle species in all years (fig. 2). Trachemys scripta elegans and Eastern Musk Turtles (Sternotherus odoratus) composed a higher percentage of the turtle community in 2005-2007 (fig. 2) than observed in previous studies of the community in 1969, 1980 (Nickerson and Pitt, 2012), and 2004 (Pitt and Nickerson, 2012). River Cooters (Pseudemys concinna) and Snapping Turtles (Chelydra serpentina) were found in low numbers (fig. 2). Only one Spiny Softshell (Apalone spinifera), a hatchling, was observed in the research section in 2005-2007 (fig. 2). Hurlbert’s PIE values were similar in 2005 (Hurlbert’s PIE = 0.59), 2006 (Hurlbert’s PIE = 0.60), and 2007 (Hurlbert’s PIE = 0.54), 2012).
but higher than the values calculated by Nickerson and Pitt (2012) and Pitt and Nickerson (2012) for the turtle communities observed in 1969 (Hurlbert’s PIE = 0.29), 1980 (Hurlbert’s PIE = 0.47), and 2004 (Hurlbert’s PIE = 0.42).

**Discussion**

Congdon et al. (1993) cautioned that turtle life history traits limit these species’ ability to respond to chronic increases in mortality of any life stage, but especially juveniles and/or adults. Heppell (1998) concluded that the survival of adult freshwater turtles was critical for population persistence and that conservation programs that reduce adult mortality are most effective for stabilizing declining populations. In any case, it should be expected that declined turtle populations would be slow to rebound if the cause of the decline was remedied (Congdon, Dunham and Van Loben Sels, 1993). Based on size distribution data, Pitt and Nickerson (2012) concluded that no further harvesting for the food trade of the *G. geographica* population in the NFWR research section had occurred since 1980 and, without the chronic loss of adults, the *G. geographica* population structure had recovered by 2004. However, the population size had not recovered by 2004 (Pitt and Nickerson, 2012). In the absence of continued harvesting, we found that the *G. geographica* population in the NFWR research section may have finally rebounded to 1969 levels by 2007, which represents a population recovery period of at least 27 years following the population reduction of approximately 50% that occurred prior to the 1980 sampling season (Nickerson and Pitt, 2012). Consistent with Congdon et al.’s (1993) prediction regarding the recovery of declined turtle populations for which the cause of decline had been remedied, the population was slow to rebound. To place the population recovery time within the context of the species’ life history, the life expectancy of *G. geographica* is estimated to be at least 20 years in the wild and the age of sexual maturation for female *G. geographica* is estimated to be more than 10-12 years and potentially as old as 14 years of age (Ernst and Lovich, 2009), suggesting that the recovery time of the *G. geographica* population in the NFWR research section was more than an individual’s life expectancy and approximately twice the amount of time it takes for female *G. geographica* to achieve sexual maturation after hatching. While the comparisons of population estimates for years 2005-2007 did not reveal significant differences, the population distribution indicated increased recruitment during the aforementioned time period (fig. 1). Comparisons of population estimates for 1969 and 2007 revealed similarly sized populations, but the population estimate for 2007 was significantly larger than the population estimate for 1980, suggesting that the population had finally rebounded to its pre-decline (1969) size. The increased recruitment in 2005-2007 likely aided the population recovery and may be a result of the breeding population reaching a critical size threshold that allowed for the observed recruitment trends. It should be noted that the earliest known population estimate for the *G. geographica* population in the NFWR are those reported by Nickerson and Pitt (2012) for 1969, therefore no conclusions can be drawn regarding the status of the population prior to 1969. Additionally, as the assumption of equal catchability is rarely, if ever met in surveys of wild populations (Koper and Brooks, 1998), the population estimates should be viewed as comparable indices of the population size.

Sex ratios of *G. geographica* for which sex could be distinguished visually did not significantly differ from 1:1 (male:female) in any sampling year, but among year comparisons revealed that the population became more male dominated between 2006 and 2007. While determining the cause of the observed shift in sex ratio was beyond the scope of this study, we encourage investigation of factors that may have resulted in the observed pattern. In particular, it is important to determine whether the observed pattern was a temporary fluctuation or indica-
tive of a more permanent trend associated with unequal recruitment or mortality of sexes.

_Graptemys geographica_ remained the numerically dominant species in all sampling periods (fig. 2). This result is consistent with patterns observed for other lotic systems, where river turtle fauna is dominated by _Graptemys_ (Bury, 1979; Moll and Moll, 2004). Six river turtle species were observed in the research section between 2005 and 2007, but no more than five species were observed in the research section in any given year (fig. 2). This discrepancy in the number of species observed in the research section in any given year was associated with the observation of rare species (fig. 2). The failure to observe all rare species in all years may be a result of species being transient and not remaining in an area. Alternatively, rare species may not be observed in a given year due to the low detection probability of numerically rare species.

Heterogeneity, which takes into account both species richness and evenness, was higher in 2005-2007 than in 1969. These results are indicative of the increased species evenness associated with an increase in _S. odoratus_ and _T. s. elegans_ observed in 2005-2007 (fig. 2). The _T. s. elegans_ population has been present in the NFWR research section since 1980 (Nickerson and Pitt, 2012) and has remained a substantial component of the turtle community since it was first observed. While _S. odoratus_ has been observed in all previous sampling years (Nickerson and Pitt, 2012; Pitt and Nickerson, 2012), the number of individuals observed in 2005-2007 was substantially higher than previously recorded for the research section and the species comprised a much larger component of the turtle community (fig. 2). The increase in the number of _S. odoratus_ in the research section appeared to correspond with an increase in the amount and extent of algal mats that were not observed in surveys preceding 2004 (Pitt and Nickerson, 2012). Although data are not available for quantitative comparison with previous sampling years, qualitatively, in 2005-2007, we observed larger amounts of rooted submerged and emergent vegetation which served as a substrate around which filamentous algae (Cladophora spp.) collected, creating extensive algal mats at the water’s surface. These algal mats served as basking habitat for _S. odoratus_ in 2005-2007, suggesting that a niche was created that _S. odoratus_ was able to exploit. These observations also suggest that nutrient-loading was occurring in the NFWR as algal blooms are often associated with nutrient-loading (Groom and Vynne, 2006). Previous studies confirm that nutrient-loading has occurred in NFWR (Solís et al., 2007). The turtle community shift towards a higher relative proportion of _T. s. elegans_ and _S. odoratus_ (i.e., generalist species) observed in the NFWR research section is consistent with what would be expected in a river subjected to habitat degradation. Previous investigation of the turtle community in the Illinois River demonstrated that community composition changes from a community with more specialized species to a community with more generalized species following habitat degradation (Moll, 1977).

The results of this study demonstrate that a river turtle population subjected to an approximately 50% population reduction with the notable loss of large adult females may rebound if the cause of decline is remedied (i.e., harvesting is ceased), but the population recovery time may be substantial and in excess of the species’ estimated lifespan. However, we caution that as promising as the observed population recovery may be, that the turtle community shift observed may be indicative of other factors, primarily habitat degradation, that may substantially alter the turtle community and ultimately lead to the loss of sensitive species such as _G. geographica_ that have specialized dietary and habitat requirements. The results of this study suggest that management and conservation plans for long-lived organisms with delayed sexual maturation must consider (1) the lengthy recovery times of diminished populations, (2) short-term stressors (e.g., one-time harvesting events)
can have multi-generational effects, and (3) pervasive threats (e.g., habitat degradation, climate change) may present additional challenges such as community and ecosystem alterations with which the population of interest must contend.

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References


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