The Alligator Snapping Turtle [*Macrochelys* (*Macroclemys*) *temminckii*]:

A review of ecology, life history, and conservation, with demographic analyses of the sustainability of take from wild populations

a report to:

Division of Scientific Authority
United States Fish and Wildlife Service

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Photos courtesy of David E. Scott, SREL. Layout and design by Laura L. Janecek, SREL.

…Executive Summary…

The alligator snapping turtle (*Macrochelys temminckii*) is the largest freshwater turtle in North America. It is a highly aquatic and somewhat secretive turtle, such that some aspects of its biology remain poorly known. The historical distribution of the species spans 14 states, and includes the Mississippi River and most other rivers draining into the Gulf of Mexico. While only one species is recognized in the genus, there is marked genetic structuring evident among populations from different drainages. A literature review revealed that body size, diet, and reproductive biology of *M. temminckii* have been adequately documented, but data on survivorship, longevity, recruitment, and habitat use remain scarce. Many alligator snapping turtle populations were decimated by increased levels of commercial harvest in the 1960's and 1970's, and the species is now protected from commercial harvest in all states except Louisiana.

We analyzed the demography of this turtle using standard techniques. Results indicate that *Macrochelys* populations are characterized by delayed maturation and high adult survivorship, even among turtles. These factors make this species extremely sensitive to harvest of adults. Annual harvest of less than 2% of adult females is unsustainable and results in population declines. We found no evidence that harvest is sustainable.

…Introduction…

The alligator snapping turtle is the largest freshwater turtle in the United States. The species has a moderately wide distribution in the greater Mississippi drainage and numerous Gulf drainages. Despite this broad distribution, however, the alligator snapper is poorly known ecologically. It is a secretive and almost entirely aquatic turtle, such that individuals are rarely seen by the public. Other than one book-length summary (Pritchard 1989), published ecological studies of *M. temminckii* are few. No long-term studies of the survivorship and demography of any population have been published, and most life history data have come from examination and dissection of individuals harvested for the meat trade. Most populations appear to have undergone severe declines due to habitat degradation and exploitation, and these factors remain as threatening factors in many parts of the range of *M. temminckii*.

The goals of this report are two-fold. First, we summarize available knowledge of the ecology, life history, and status of the alligator snapper, with special reference to the literature published since Pritchard's (1989) book. Second, we use available data to construct a stable life table for this turtle, and estimate sensitivity of a population to changes in life history variables, including the effects of simulated anthropogenic take of adults.

…Taxonomy, Distribution, and Systematics…

The alligator snapping turtle is a member of the family Chelydridae, in the order Testudines, class Reptilia. This North American family contains two species in two monotypic genera; the alligator snapping turtle (*M. temminckii*), and the common snapping turtle (*Chelydra serpentina*). The Chinese big-headed turtle (*Platysternon megacephala*) was formerly considered a member of this family, but is now placed in the monotypic family Platysternidae.

The nomenclatural history of the alligator snapping turtle is complex and apparently still evolving. The species was first described as *Testudo planitia* in 1789, but Gray erected the genus *Macroclemys* in 1855. Some subsequent authors referred to the genus as *Macrochelys*, but this was refuted by Smith (1955). More recently, Webb (1995) showed that *Macrochelys* has precedence over *Macroclemys*, and the Society for the Study of Amphibians and Reptiles has adopted this revision (Crother *et al*. 2000). In this report, therefore, we refer to the alligator snapping turtle as *Macrochelys temminckii*.

Macrochelys temminckii is historically known from Alabama, Arkansas, Florida, Georgia, Illinois, Indiana, Kansas, Kentucky, Louisiana, Mississippi, Missouri, Oklahoma, Tennessee, and Texas. Within this range, populations in Illinois, Indiana, Kansas, Kentucky, Oklahoma, and Tennessee are thought to be generally small or extirpated. These small population sizes may be due to past exploitation or because these states are on the edges of the geographic range of *Macrochelys*. A detailed distribution map and specimen records are given in Pritchard (1989) and Lovich (1993).

The genus *Macrochelys* is considered to be monotypic. However, many populations are distributed allopatrically, raising the question of whether independent evolutionary lineages exist. This topic was explored by Roman *et al*. (1999), who sequenced mitochondrial DNA from 158 individuals from 12 drainages throughout the range of *Macrochelys*. Their results indicate strong phylogeographic structuring, indicating that major genetic divergence has occurred among river drainages. Within this overall structure, three major evolutionarily significant units were found. These roughly correspond to the greater Mississippi drainage, the Gulf drainages to the east of the Mississippi, and the Suwannee River. In contrast to the common snapping turtle, *Chelydra* *serpentina*, which undertakes significant overland movements and has little mtDNA variation over its range, the aquatic habits of *Macrochelys* have resulted in strong divergence among populations. Roman *et al.* (1999) also concluded that population-specific genetic markers should allow geographic identification of individuals in the meat or pet trade, allowing a means of monitoring interstate transport of illegally collected animals.

Range of the alligator snapping turtle, Macrochelys temminckii.

…Ecology and Natural History…

Size and growth rates: Contrary to common perception in the United States, the alligator snapping turtle is not the world's largest freshwater turtle. The Asiatic softshell turtles of the genera *Chitra* and *Pelochelys* may exceed 200 kg, much larger than *Macrochelys* (Pritchard 2001). However, *Macrochelys* is the largest freshwater turtle in the New World and reaches impressive sizes. In a Louisiana population, adult males averaged 49.46 ± 7.04 cm in carapace length (CL; n=11, range 36-57.1), whereas adult females averaged 43.08 ± 4.32 cm CL (n=53, range 35-50.9; Sloan *et al.* 1996). Nesting females along the Apalachicola River in Florida were larger, averaging 45 cm CL (range 41.8-51; Ewert and Jackson 1994). Males attain larger sizes than do females, and the largest known male was 80 cm CL (Lovich 1993). However, Tucker and Sloan (1997) estimated an asymptotic size in Louisiana of 39.9 cm CL for females and 50.3 cm CL for males; the latter estimate is smaller than the maximal size of Lovich (1993) or the 57.6 cm CL given by Dobie (1971). Immature females harvested in Louisiana averaged 33.8 cm CL, whereas males averaged 34.5 cm CL (Tucker and Sloan 1997). Hatchlings are 4.1-4.3 cm CL in Louisiana (Dobie 1971) and 3.4-3.8 cm CL in Florida (Powders 1978).

Because most available data are from harvested individuals, estimates of growth rates in the wild are few. Among 12 recaptured subadults (3 male, 9 female) in a Louisiana bayou, annual CL growth rates were 5.3% among males and 5.2% among females (Harrel *et al.* 1997). Weight gain in these turtles averaged 4.1% among males and 10.6% among females. Dobie (1971) gave growth curves calculated from harvested turtles; these data indicated that growth rates were variable both within and between individuals, especially before attainment of sexual maturity.

Longevity and age at first reproduction: Alligator snapping turtles are long-lived organisms. Using ventral scute annuli as indicators of annual growth, Sloan *et al.* (1996) estimated average ages of 25.24 ± 11.37 years among adult males (n=11, range 11–45) and 22.23 ± 5.93 years among adult females (n=53, range 15–37) in Louisiana. Also in Louisiana, Dobie (1971) stated that the oldest animal that he could reliably age was a 36-year-old male. Tucker and Sloan (1997) stated that immature individuals averaged 16 years (females) and 16.8 years (males), whereas mature individuals averaged 21.4 years (females) and 29.3 years (males). The oldest individuals of known age in the latter study were 39 years (females) and 45 years (males). Alligator snapping turtles have lived longer than 70 years in captivity (Snider and Bowler 1992).

Estimates of the age at first reproduction are important in demographic analyses. Dobie (1971) estimated that sexual maturity is attained at 11–13 years for both males and females (Dobie 1971). Based on laprascopic examination of the reproductive tracts of free-ranging subadults, however, J.B. Harrel (personal communication, 24 January 2002) found no reproductive females under 15 years old, and no reproductive males under 17 years old. Similarly, Tucker and Sloan (1997) found that immature females averaged 16.0 years and immature males 16.8 years for a sample of harvested Louisiana turtles. These more recent data may indicate that Dobie (1971) underestimated minimum age at maturity.

While ventral scute annuli may be reliable indicators of annual growth in some cases, they may be occasionally misleading. For instance, Powders (1978) aged a reproductive female at 28–31 years old using scute annuli, but stated that its size would place it in the 11–14 year old age class using Dobie's (1971) growth curves. Without long-term population data, it is not possible to determine whether this female was an exceptionally slow-growing individual or whether scute annuli are not reliable indicators of growth at older ages.

Reproductive biology: In captivity, mating has been observed from February to October (Allen and Neill 1950, Grimpe 1987), but geographic variation in mating season is poorly understood. Males apparently are capable of sperm production year round (Dobie 1971). Females ovulate in the spring, and most nesting occurs in May through July (Ewert 1976; Powders 1978; Grimpe 1987). Females appear to breed annually, but may skip a year if they have poor foraging success (Tucker and Sloan 1997). Production of multiple clutches in a single year has not been observed in the wild.

Somewhat surprisingly considering their larger size, *M. temminckii* has a lower average reproductive output than *C. serpentina* and has not been observed to lay more than one clutch per year (Dobie 1971). Clutch sizes are 31-40 (n=17) in the Apalachicola River (FL; Ewert 1976), but some adult females (38.5 cm CL) may lay as few as 9 eggs in GA (Powders 1978). In Louisiana, a series of 13 harvested females had clutch sizes averaging 23.8 (range 16–38), and egg sizes were 34.0–51.8 mm at their greatest diameter (Dobie 1971). Reproductive output is positively correlated with female body size, but this relationship is characterized by high variability among females (Tucker and Sloan 1997). Two Louisiana populations (Dobie 1971, Tucker and Sloan 1997) had lower clutch sizes and smaller female sizes than were observed in a Florida population (Ewert and Jackson 1994). However, this observation is likely an artifact of size-specific fecundity and differential exploitation. Long-term exploitation of Louisiana populations may have resulted in fewer large, fecund females relative to the Florida population which has experienced lower levels of exploitation.

Survivorship: The main roadblock to rigorous demographic analyses for *M. temminckii* is an almost

Alligator snapping turtles frequent slow-moving rivers and streams such as the one pictured here.

complete absence of data on survivorship of various age classes. Like most turtles (Congdon *et al.* 1994), it appears that *Macrochelys* has high adult survivorship under natural conditions (i.e., absent anthropogenic mortality). Average age of adults is greater than that of many other turtles, suggesting that adult survivorship of *Macrochelys* is especially important demographically.

Diet: Alligator snapping turtles are very nearly omnivorous and consume a wide variety of plant and animal matter. They possess a unique lingual lure used to catch fish, and fish are a dietary mainstay (Redmond 1979, Harrel and Stringer 1997). However, dietary items other than fish are common in turtle stomachs; these include plant matter (oak acorns, tupelo fruits, wild grapes, roots, palmetto fruits, hickory nuts, persimmons, etc.) and animal matter (salamanders, crayfish, mussels, snakes, alligators, turtles, clams, mammals, snails, etc; Redmond 1979, George 1987, Spindel *et al.* 1987, Shipman *et al.* 1991, Sloan *et al.* 1996).

Habitat use and movement: Alligator snapping turtles are among the most aquatic of freshwater testudines, and overland movements appear to be undertaken only by nesting females and juveniles moving from the nest to water. Females have been observed to nest up to 72 m from the nearest water, although nests averaged 12.2 m from the nearest water (Ewert 1976). Radiotelemetry has been used to study the aquatic movements of subadults (Harrel *et al.*, 1996) and adults (Sloan and Taylor 1987) in Louisiana. These results indicate that adults are capable of moving >1 km/day, and mean daily distances traveled ranged 27.8–115.5 m/day. Home range sizes were variable and ranged 18-247 ha. Both subadults and adults used cypress-lined river channels heavily. In Arkansas, mark-recapture of *Macrochelys* revealed that individuals moved both upstream and downstream, with a maximum distance between capture locations of 1.8 km (Trauth *et al.* 1998). Pritchard (1989) proposed that some individuals may move up river continuously during their lifetimes, thus accounting for large isolated individuals in stream headwaters. This poorly supported hypothesis (based on literature records of long-distance upstream movements of two turtles) was disputed by Ernst et al. (1994).

…Historical Exploitation, Conservation, and Commercialization…

Alligator snapping turtles have long been harvested by humans as a food source in the southeastern United States. However, the size of this industry increased dramatically in the late 1960's through the 1970's. During this period Campbell's Soup Company produced frozen turtle soup, with meat largely obtained from *Chelydra* and *Macrochelys* (Pritchard 1989). Numerous New Orleans seafood restaurants and dealers also purchased large numbers of *Macrochelys* from trappers in southeastern states. The appetite of the consumer was such that the industry seasonally took three to four tons of alligator snapping turtles from Georgia's Flint River every day during the early 1970's to meet demand, until population sizes decreased below commercial viability (Al Redmond, cited in Pritchard 1989). Populations in Louisiana, Florida, and Alabama, were also depleted by commercial harvest (Pritchard 1989).

Large-scale harvesting of reproductive adults caused swift declines in most populations of *Macrochelys*. However, an absence of data on historical population sizes of these turtles meant that declines were usually documented by interviews with turtle trappers and others who exploited the resource. These individuals were unlikely to have kept detailed records, and so their perceptions of massive population declines are fairly subjective. The current inability of the *Macrochelys* fishery to sustain historical numbers of turtle trappers is itself evidence of widespread population decline. Pritchard (1989) gives an excellent overview of the documentation of declines in populations of *Macrochelys*, including multiple corroborative reports from former turtle trappers.

The abovementioned population declines resulted in legal protection of *M. temminckii* in most states where it occurs. However, commercial harvest is still legal in Louisiana. New

Orleans is the center of this trade, especially for turtle soup and Cajun restaurants. As additional examples, the mail-order outdoor retailer Cabela's Inc. offers turtle meat in its catalogs, and mail-order frozen turtle meat is available on-line from a number of New Orleans seafood houses. While much of this meat is undoubtedly from *Chelydra*, *Apalone*, or emydid turtles, it is unknown how many *Macrochelys* are exploited for this trade.

Louisiana has recently instituted a 15 inch (38.1 cm) carapace length minimum size limit for *Macrochelys* taken by commercial operations, but still allows harvest of unlimited numbers of individuals above this size. Although designed as a conservation measure, Louisiana's minimum size limit is very likely ineffectual in stabilizing populations. First, because of the low meat to weight ratio of small turtles, these individuals would rarely be taken by commercial collectors anyway. More importantly, the 15" minimum allows continued harvest of 71% of adult females and 100% of adult males in Louisiana (Tucker and Sloan 1997). Continued harvest of adult females is currently not known to be compatible with long-term population persistence of any turtle species (Congdon *et al.* 1993, 1994; Close and Seigel 1997) and is likely to be especially harmful to a long-lived species like *M. temminckii*.

As the turtle meat trade has waned, the pet trade in alligator snapping turtles has increased tremendously. Based on USFWS export documentation, exports of *Macrochelys* have increased from 290 individuals in 1989 to 23,780 individuals in 2000. Virtually all of these are hatchlings from commercial turtle 'farming' operations, and are bound for overseas pet and food markets (Franke and Telecky 2001). These animals wholesale for less than $20, and may retail for $35. Ironically, most of these hatchlings are not legal for sale in the U.S. due to existing laws prohibiting sale of turtles <4 inches (10.16 cm) carapace length. The geographic origin of the exported turtles is difficult to analyze, as many individuals are exported from states where they do not occur (primarily California). At least 10,000 turtles are exported annually from the state of Arkansas, which apparently has the most extensive network of *Macrochelys* farms (6-8 licensed farmer/dealers operated during 1998-2001; K. Irwin, personal communication 3/26/02).

The impact of turtle farming on wild populations of *Macrochelys* has not been quantified. Breeding stock was almost certainly obtained from natural populations. Using Dobie's (1971) average of 23.8 eggs per female, the export tally of 23,870 hatchlings for the year 2000 would require 1002 adult females on the farms, plus a smaller number of males. A persistent rumor states that Arkansas requires turtle farming operations to release at least 150 captive-hatched *M. temminckii* per year. There is no such requirement according to the Arkansas Game and Fish Commission herpetologist (K. Irwin, pers. comm., Feb. 2002). Those people who have released turtles have largely released commercially undesirable individuals, likely with low fitness (e.g., turtles with 'kinktail' and other defects caused by overly high incubation temperatures; J.B. Harrel, personal communication 24 January 2002). Because turtle farmers are under no obligation to keep records of the origins of breeding stock, released hatchlings may also be of mixed genetic provenance. Given the marked genetic structuring of allopatric populations of *Macrochelys*, (Roman *et al.* 1999), this practice is indefensible from a conservation standpoint.

Widespread commercialization of wild-caught alligator snapping turtles has generally decreased, and the species is largely protected in most states where it occurs. All else being equal, these measures may allow eventual population recovery in the case of populations that have not been extirpated. Unfortunately, however, all else is not equal, as ongoing habitat loss may ultimately be a more destructive influence than past commercialization.

…Current Legal Status…

Macrochelys temminckii is currently unprotected by either the U.S. Endangered Species Act of 1973 or the Convention on International Trade in Endangered Species. *Macrochelys* is subject to the Food and Drug Administration ban on sale of turtles under four inches carapace length, but this applies only to sales in the United States; exported animals currently can be of any size (FDA 21 CFR 1240.62). Despite minimal protection at the federal level, the species is protected by many of the U.S. states encompassing its native geographic range. These protections are discussed below; most of this information was taken from Levell (1997) or SSAR (2002).

Alabama: Legally protected non-game animal; collection, possession, and sale are prohibited. Permits are required for any activity involving this species.

Arkansas: Wild individuals are protected from take, including eggs. Import of *Macrochelys* prohibited. All captive *M. temminckii* over 10" carapace length must be tagged by an agent of the Game and Fish Commission (plans to reduce the minimum size for tagging to five inches are in process; K. Irwin, personal communication 3/26/02).

Florida: Listed as a Species of Special Concern. Possession limit of one specimen. May not be sold.

Georgia: Listed as Threatened, may not be taken without scientific collection permit.

Illinois: Listed as Threatened, may not be possessed without permit.

Indiana: Listed as Endangered, may not be taken without permit. Imports are not restricted.

Kansas: Listed as In Need of Conservation, legally protected from take.

Kentucky: No official list of state threatened or endangered species exists for Kentucky. The Kentucky State Nature Preserves Commission lists *M. temminckii* as Threatened, but this listing has no statutory or legal implications. Harvest of *M. temminckii* for personal use is legal, but commercial harvest is prohibited (commercial harvest is limited to the genera *Chelydra* and *Apalone*; Tim Slone, personal communication 3/26/02).

Louisiana: A fishing license is required to collect *M. temminckii* for non-commercial purposes, and there is a recreational take limit of 4 specimens (no size limit applies to non-commercial use). Commercial take is limited to individuals over 15 inches in carapace length, with no limit on the number of specimens which can be taken.

Mississippi: Classifed as Nongame Species in Need of Management. Non-commercial possession limit of four individuals (valid hunting license required). No reptiles taken from the wild may be purchased or sold, and reptiles may only be imported under the authorization of a nongame importer's permit.

Missouri: Residents may possess five individuals for personal use. Commercialization of native species is prohibited, and commercialization of imported native species from other states requires a Class I Wildlife Breeders Permit. Despite these apparent rules, however, there is at least one commercial alligator snapping turtle farm in Missouri.

Oklahoma: Listed as a Species of Special Concern, with no legal implication. There is a closed season on *Macrochelys*, which may only be taken with a scientific collecting permit.

Tennessee: Listed as In Need of Management. Permits required for all activities involving *M. temminckii*. Commercialization of *Macrochelys* prohibited, but sale of *Chelydra* permitted.

Texas: Listed as Threatened, permits required for all activities involving *M. temminckii*.

Demographic processes (birth, death, and migration) are rarely equal among age classes in a population. For most species, certain life history stages or age classes are characterized by increased risk of mortality, while maximal reproductive output may be achieved by members of entirely different age classes. Life tables are tabulations of patterns of mortality and survivorship in a population and allow construction of graphical representations of survivorship and fecundity (Begon *et al.* 1986). Only after demographic analysis is it possible to understand trends in population sizes, or to predict future population sizes.

Almost invariably, construction of life tables requires long-term study of a population in order to record schedules of births and deaths. Turtles typically display a Type III survivorship curve (Pearl 1928), with high juvenile mortality followed by adult age classes with high annual survival (Congdon and Gibbons 1990). Because the lifespans of adult turtles may exceed those of turtle researchers, few studies of turtle ecology are of suitable temporal duration for rigorous demographic analyses.

Demography of alligator snapping turtles is poorly known. Variables such as clutch size and body size have been examined, but our knowledge of survivorship across age classes is scanty. The most appropriate study for comparison is that of a population of common snapping turtles in Michigan (Congdon *et al.* 1994). This population is characterized by high adult survivorship, and adult females are the most important segment of the population in terms of population persistence. However, this type of rigorous analysis was only possible after 17 years of intensive field research. Similar studies are lacking for any population of *Macrochelys*. We therefore used very conservative values for life history variables in our analyses. Wherever possible, we erred on the side of an assumption of population stability (discussed below). This type of conservatism means that our results probably underestimate the importance of adult survivorship for population stability.

Our methods largely followed Congdon *et al.* (1993, 1994). We performed standard demographic analyses, using the following variables:

Annual fecundity (m_x): Defined as the number of eggs produced annually, divided by two. This adjusts for production of males by making an assumption of an equal primary sex ratio. Annual fecundity was not adjusted for clutch frequency; i.e., we operated under the assumption that all adult females reproduce annually and lay no more than one clutch annually.

Adult survivorship ($S_{x\ Adult}$): Defined as the proportion of adult females surviving every year; assumed to be constant among all adult age classes. This assumption is validated by long-term studies of common snapping turtles in Michigan, among which adult survivorships are high and constant (Congdon *et al.* 1994). It is also characteristic of adult turtles in other long-term studies (Gibbons and Semlitsch 1982, Mitchell 1988, Frazer and Gibbons 1990, Congdon *et al.* 1993).

Juvenile survivorship ($S_{x\ Juvenile}$): Defined as the proportion of juvenile females surviving every year after emergence from the nest, and was also assumed to be constant among all juvenile age classes.

Nest survivorship ($S_{x\ Nest}$): Defined as the proportion of juvenile females that survived the period between oviposition and emergence from nests.

Basic reproductive rate (R_o, also known as the fundamental net per capita rate of increase): The mean number of female offspring produced per original female by the end of the cohort (i.e. death of the oldest female in the cohort). It therefore indicates both average number of female offspring produced by a female over the course of its life, and the population multiplication factor which will indicate the size of the population one generation hence. Thus, population sizes will decrease when $R_o < 1.0$, and vice versa.

Intrinsic rate of natural increase (*r*): Calculated as $\ln(R_o)$, and indicates the change in population size per individual per unit time.

The derivation and calculation of the abovementioned variables are discussed in detail by Begon *et al.* (1986).

We constructed a stable life table using the following population parameters, which were obtained from various sources cited above (see Ecology and Natural History section):

Stable adult $S_x = 0.98$
Stable juvenile $S_x = 0.687$
Stable nest $S_x = 0.201$
Fecundity (m_x) = 16 female eggs/year

The resultant stable life table for *Macrochelys temminckii* resulted in a cohort generation time (T_c) of 49.07 years, and a doubling time of the population of 8507 years. The basic reproductive rate (R_o) was 1.004, and the intrinsic rate of population increase (*r*) was 8.147 x 10^{-5} (Table 1).

After construction of the stable life table, we examined the consequences of changes in survivorships among adults, juveniles, and nests. These are the variables most likely to be important for management and conservation of alligator snapping turtles, as it is unlikely that fecundity or age at maturity can be manipulated via management. Manipulation of survivorship allows an estimate of the future ramifications of anthropogenic harvest of these animals, expressed as predicted changes in population size. Rather than attempting to model these changes by focusing on esoteric variables such as R_o or *r*, we chose population doubling time as a more intuitive measure of population size. Population doubling time (D_{Time}) was calculated as the number of years required to double population size as a consequence of changes in survivorship. Negative values for this variable indicate the time required to halve the population.

Table 1: A summary of values used in construction of a stable life table for Macrochelys temminckii, including stable population parameters resulting from the life table.

Reproduction	
Clutch size	32
Clutch frequency	1.00
Annual fecundity	16
Survivorships (l_x)	
Nest (Age 0)	0.2010
Juvenile (ages 1-12)	0.6870
Adult females	0.9800
Emigration rate	0.00 per year
Age at maturity	13-16 years
Stable population parameters	
Basic reproductive rate (R_0)	1.004004
Intrinsic rate of population increase (*r*)	8.1475 x 10^{-5}
Cohort generation time (T_C)	49.06625
Population doubling time (D_{Time})	8507.45

Results of these analyses were striking. In order to maintain a stable population using biologically realistic values for fecundity, age at maturity, and survival of nests and juveniles, annual adult survivorship of females must be 98%. Reducing adult survivorship by as little as one quarter of one percent (to 97.75%) will result in population size being halved in 410 years (Table 2). Reducing adult survivorship by two percent (to 96%), which would be equivalent to annually removing only two adult females from a total population size of 200 turtles (assuming even sex ratios) will halve the population in only 50 years (Table 2). Reducing survivorship of juvenile females also affects long-term population stability, but at a rate indicating that roughly two juveniles must be removed from the population to equal the removal of a breeding female (Table 3, Figure 1). Finally, we modeled the population consequences of increasing nest survivorship via anthropogenic protection of nests and hatchlings (e.g., headstarting). Increasing nest survivorship by a 5% (to 25%) still requires 145 years to achieve a doubling of the population, and

Table 2. Effects of increased annual mortality of adult female alligator snapping turtles on population stability. See Table 1 and text for definition of variables.

Survivorship (S_X)	R_0	*r*	T_C	D_{Time} (years)
0.980 (STABLE)	**1.004004**	**8.1475×10^{-5}**	**49.066**	**8507.45**
0.9775	0.922356	-1.6875×10^{-3}	47.328	-410.75
0.9750	0.8508517	-3.4522×10^{-3}	45.671	-200.78
0.9725	0.7879845	-5.2125×10^{-3}	44.099	-132.98
0.9700	0.7324935	-6.9680×10^{-3}	42.612	-99.48
0.9675	0.6833208	-8.7186×10^{-3}	41.211	-79.50
0.9650	0.6395776	-1.0464×10^{-2}	39.892	-66.24
0.9625	0.6005147	-1.2204×10^{-2}	38.657	-56.79
0.9600	0.5654996	-1.3938×10^{-2}	37.499	-49.73

40% nest survivorship is required to double the population in less than 50 years (Table 4).

The relationships between reductions in survivorship and population halving time depicted in Figure 1 appear to be asymptotic at about 50 years, such that the observer may be lulled into believing populations are safe for decades even with increased mortality from harvesting. However, this is not the case. Figure 2 shows the same data, plotted on logarithmic scales. Clearly, the *relative* decline of alligator snapping turtle populations continues as smaller population sizes result from sustained harvest. Incremental decreases in adult or juvenile survivorship would result in even shorter times required to halve population sizes.

Comparisons of population doubling times with population halving times offer insight on trade-offs between increases in nest survivorship and either decreased adult or juvenile

Table 3. Effects of increased annual mortality of juvenile alligator snapping turtles on population stability. See Table 1 and text for definition of variables.

Survivorship (S_X)	R_0	*r*	T_C	D_{Time} (years)
0.6870 (STABLE)	**1.004004**	**8.1475×10^{-5}**	**49.066**	**8507.45**
0.6845	0.9575465	-8.7861×10^{-4}	49.066	-788.91
0.6820	0.9130802	-1.8292×10^{-3}	49.065	-378.92
0.6795	0.8705269	-2.7705×10^{-3}	49.065	-250.18
0.6770	0.8298107	-3.7027×10^{-3}	49.064	-187.20
0.6745	0.7908589	-4.6260×10^{-3}	49.063	-149.84
0.6720	0.7356009	-5.5405×10^{-3}	49.062	-125.10
0.6695	0.6513252	-8.2342×10^{-2}	49.061	-84.18
0.6670	0.6838982	-7.3444×10^{-2}	49.061	-94.38

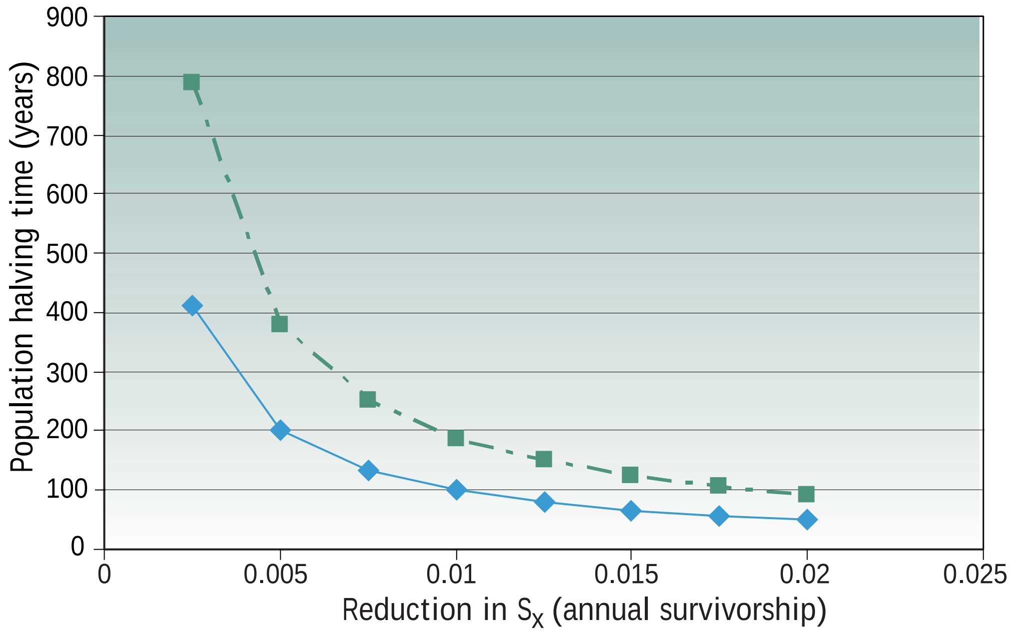

Figure 1. Relationship between reductions in annual survivorship (S_x) and time required to halve population size among alligator snapping turtles (Macrochelys temminckii). Solid line and diamonds indicate results for adult females, dashed line and squares indicate results for juveniles. Stable population survivorships were 0.98 for adult females and 0.687 for juvenile females. Figure thus depicts the population-level effects of reducing survivorship from 0.0025 to 0.02, such that the lowest survivorship depicted is 0.96 for adults and 0.667 for juveniles.

survivorship (Tables 2, 3, 4). For example, the population halving time of 133 years resulting from a .075% decrease in adult survivorship is roughly temporally equal to the population doubling time of 145 years resulting from a 5% increase in nest survivorship, indicating that a large jump in the latter is necessary to counteract the former. A more careful examination of the numbers reveals that, in order to maintain population sizes, a reduction of adult survivorship by 2.0% requires an increase in nest survivorship of 16%. Among juveniles, reduction of survivorship by 2.0% requires an increase in nest survivorship of 8.5%. These results unambiguously point towards the overwhelming importance of adult survivorship for population stability.

Attempts at managing alligator snapping turtle populations for the purposes of maintaining a sustainable commercial harvest would likely hinge on two schemes. The first is controlling the rate of adult harvest, while the second is increasing survivorship of nests (via headstarting or similar programs). Our analyses indicate that controlling the former

Table 4. Effects of increased nest survivorship of age class 0 alligator snapping turtles on population stability. See Table 1 and text for definition of variables.

Survivorship (S_X)	R_0	*r*	T_C	D_{Time} (years)
0.201 (STABLE)	**1.004004**	**8.1475 x 10 -5**	**49.066**	**8507.45**
0.251	1.253757	4.7656 x 10 -3	49.066	145.44
0.301	1.503509	8.8356 x 10 -3	49.066	78.45
0.351	1.753261	1.2461 x 10 -2	49.066	55.63
0.401	2.003013	1.5745 x 10 -2	49.066	44.02

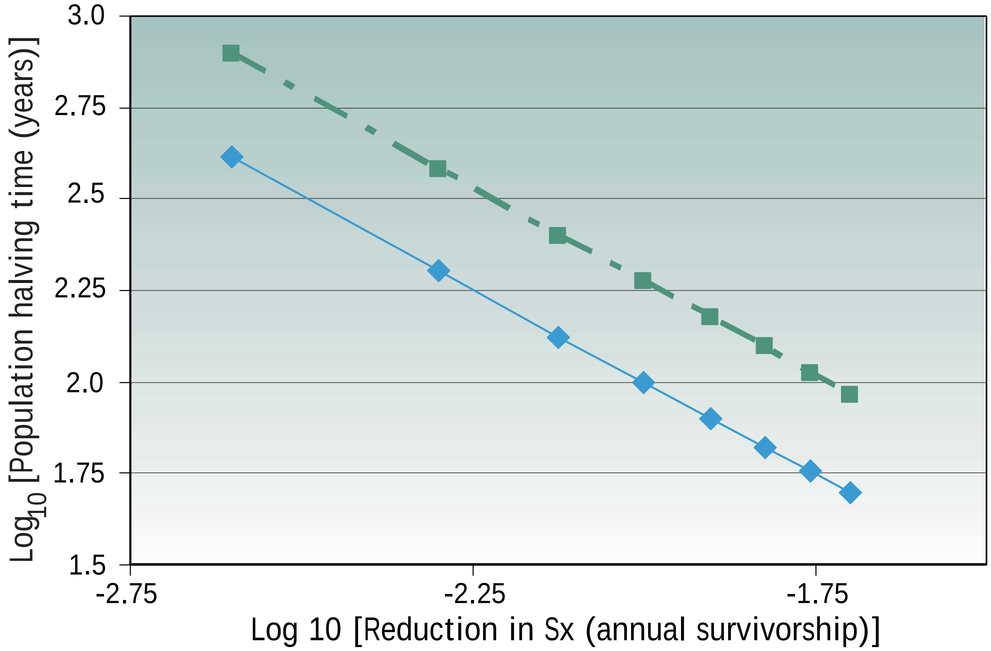

Figure 2. Relationship between reductions in annual survivorship (S_x) and time required to halve population size among alligator snapping turtles (Macrochelys temminckii). However, axes are logarithmically transformed in this graph (log_{10}).

is unlikely to prevent population declines, as increasing mortality of adult females by as little as 1% results in decline. Currently the state of Louisiana is alone in permitting commercial harvest of *Macrochelys*, subject to a 15" minimum carapace length size limit. Unfortunately, this size limit allows legal harvest of virtually all adults, while imposing no statewide quota on the numbers of legal-sized turtles taken from wild populations. To rectify these problems, the state of Louisiana could perhaps impose an annual quota on harvest of adults, or harvest could be limited to adult males only. The former solution, however, does not guarantee a geographically balanced harvest of individuals from metapopulations or demes. In other words, intensive local population exploitation could satisfy statewide quota requirements but result in severe local population crashes requiring decades of recovery time. The option of limiting harvest to adult males may be difficult for commercial trappers to implement because it would require a working knowledge of anatomy and mathematics, as adult males are chiefly distinguished by the ratio of carapace length to precloacal tail length (Ernst *et al.* 1994). Pronounced male-biased sexual size dimorphism within the species means that alligator snappers over a certain body size are almost certainly males, but these animals are also the oldest in a population and will likely be rapidly depleted by sustained harvest without replacement occurring at a rate that could sustain commercial harvest operations.

It is conceivable that continued harvest of adult alligator snapping turtles could be offset by artificially raising nest survivorship. Similar efforts have been undertaken on a massive scale for sea turtles via collection and incubation of eggs from the wild, followed by release of hatchling or juvenile turtles (headstarting; Donnelly 1994). The return on this investment of time and money is hotly debated (Wibbels *et al.* 1989, Frazer 1992, Heppell et al 1996), and headstarting may not offset continued take of adults. A recent review of headstarting concluded that, "…under the most favorable of conditions, headstarting must be judged an interesting experiment, not a conservation technique; it should never be used as an excuse to weaken protection for adult wild turtles or for the nests and juveniles of wild populations. When conditions are less than favorable, headstarting is not even an interesting experiment and may do serious harm…" (Meylan and Ehrenfeld 2000). Thus headstarting may be useful for re-establishing locally extirpated populations or increasing the size of depleted populations, but is unlikely to be an effective countermeasure for harvest of adults. Commercial turtle farmers have shown that production of thousands of *Macrochelys* hatchlings is possible so long as an economic stimulus exists. If headstarting for conservation purposes is attempted, however, the participating agencies must also consider the drainage-specific genetic identities of existing populations in order to avoid loss of overall genetic diversity.

While sustained harvest of adults is clearly precluded by the demographic characters of alligator snapping turtles, in situ measures may help long-term population recovery efforts without invoking expensive headstarting techniques. Reducing levels of nest predation by subsidized predators may allow greater numbers of eggs to survive, boosting the numbers of individuals in early age classes. Subsidized predators are those which occur at unnaturally high levels because of subsidies provided by humans (Mitchell and Klemens 2000). Among subsidized turtle nest predators, the raccoon (*Procyon lotor*) has been identified as the single most important predator of turtles in North America (Stancyk 1982, Mitchell and Klemens 2000), and the reduction of raccoon populations results in increased nest survival among turtles (Christiansen and Gallaway 1984, Smith 1997). Despite the various options for increasing the numbers of juveniles into declining populations, however, the continued removal of adults will ultimately result in extirpation.

As discussed earlier, our analyses were marked by extreme conservatism. This conservatism was mandated by the uncertainty associated with some demographic aspects of alligator snapping turtles. Our wish was to forestall criticism that our analyses were driven by a conservation-minded agenda rather than by objective science. As an example, our estimate of 98% adult survivorship is extremely high, exceeding known survivorship rates of virtually all turtle populations studied thus far (Congdon et al 1993, 1994, Frazer and Gibbons 1990, Gibbons and Semlitsch 1982). If actual survivorship of adults is lower, then these adults become even more important to the population, and harvest of adults will reduce population size at a greater rate than our calculations indicate. Similarly, our estimate of 20% nest survivorship may be higher than that experienced by wild populations. Based on observation of *Macrochelys* nests in Louisiana, J.B. Harrel (pers. comm., Feb. 2002) has estimated nest survivorship of 5% or less. Increased nest mortality may be due to recent collapses in the fur market and elimination of large-bodied predators across the southeastern U.S., which in turn has resulted in booming populations of meso-predators such as raccoons and foxes (Congdon *et al.* 1993). Finally, we utilized a conservative estimate of fecundity by assuming that 100% of females produce clutches annually. The sister taxon of *Macrochelys* is the common snapping turtle (*Chelydra serpentina*), which should be the most appropriate organism for comparisons of reproductive frequency. Among *Chelydra* in Michigan, only 85% of females reproduce annually, thus reducing average fecundity by 15%. A reduction of this magnitude would result in fecundity of 13.6 eggs per year for *M. temminckii* rather than 16 eggs per year. Thus, taken in aggregate, our results depict a demography of alligator snapping turtles that is more stable than can be reasonably expected in wild populations.

…Overall Conclusion…

Our demographic analyses provide no support for the sustainability of harvest of adult alligator snapping turtles. Increasing annual mortality of adult females by less than 1% will result in long-term population declines, although these declines may occur on timescales longer than human lifetimes. Additionally, the life history of *Macrochelys temminckii* is characterized by a suite of demographic traits which imply that exploited populations will take decades to recover even after cessation of exploitation.

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