Abstract.—We examined demographic features of 2 Ontario populations of snapping turtles (Chelydra serpentina) to provide an empirical basis for developing management guidelines. The northern population matured later (18-20 yr) than did the southern populations (<10 yr), and displayed an older age distribution. Long-lived, “bet-hedging” species have low annual reproductive success and are unusually susceptible to exploitation. A preliminary life table is presented for the northern population. Our results indicate that the northern population cannot sustain even minimal levels of exploitation by humans without undergoing a decline in numbers.

In general, turtles have not been a major concern of wildlife managers in North America, and in many jurisdictions they are given little or no protection. They are perceived to have limited ecological, commercial, aesthetic or recreational value, and because they are usually cryptic and slow moving they are uninteresting to most people. Partly for these reasons, there have been remarkably few studies of their life history and ecology. In addition, their great longevity makes them difficult to study, except on a long-term basis. Nevertheless, turtles are, or should be, of interest to wildlife managers for at least three major reasons.

First, they are major components of a variety of both terrestrial and aquatic ecosystems and therefore play significant, though often unrecognized roles as carnivores, herbivores and scavengers. In both aquatic and terrestrial habitats, the standing-crop biomass of turtles is generally much higher than that of any other reptile (Iverson 1982). In aquatic systems, turtle biomass often exceeds that of sympatric endothemers by an order of magnitude and is similar to levels reported for fishes (Iverson 1982). Similarly, annual production of turtles is comparable to that reported in most other vertebrates, although well below levels found in some fishes (Iverson 1982). Many turtles that are especially long-lived may have low annual productivity. This low productivity may be underestimated because of the high standing-crop biomass of turtles. Their life history is markedly different from those of the birds and mammals that typically occupy the attention of wildlife managers. As such, these species represent special problems in conservation and management. Therefore, turtles should be of interest to managers, because they are important components of a variety of ecological communities and because in many cases their longevity and low annual production relative to standing crop, characteristic of a “bet-hedger” (Obbard 1983) is a life-history strategy that may be highly susceptible to exploitation or to other sources of mortality of adult animals such as unsuitable overwintering conditions or heavily polluted waters.

Secondly, managers should have an interest in turtles because many species are harvested for commercial profit, usually as food or for the pet trade (Bergmann 1983, Congdon et al. 1987, Lovisek 1982). There is evidence of marked, recent declines in harvests of most turtle species, but this evidence is difficult to quantify because estimates of total stocks do not exist for any turtle species. For snapping turtles, the annual commercial catch in Minnesota was estimated at 36000-40800 kg or approximately 6000-6800 average-aged adults (Helwig and Hora 1983). In southern Ontario, Lovisek (1982) estimated the annual catch of C. serpentina to be 30000-50000 kg or 5000-8300 adults. There is evidence from trappers (J. Bullard pers. comm.) that numbers of this species are a fraction of former numbers over much of their southern range in Ontario, but again no quantitative estimates exist. At present, therefore, it is necessary to measure the impact of harvesting turtles on a local basis (Hogg 1975).

Thirdly, snapping turtles may be of interest to managers because they are often regarded as pests or as a danger to human swimmers, or as destructive predators of waterfowl and game fish (Hammer 1969, Kiviat 1980, Pell 1941).

In this paper, we review the biology of snapping turtles in relation to these three areas of potential importance for wildlife managers. We present demographic characteristics of 2 populations in Ontario, and in addition, we develop a life table for the more northern population of snap-
ping turtles which will allow us to predict the impact of different levels of harvesting pressure on this population.

Snapping Turtles in Aquatic Ecosystems

Regulation of Population Density

There is at present little understanding of what factors regulate populations of any turtle species, but it is known that turtles may reach very high densities and high biomass densities (Galbraith et al., in press; Iversen 1982). It seems likely that primary productivity would be the best predictor of variation in numbers of turtles in a habitat. In snapping turtles, population density ranges from 1-75 adult turtles per ha (Galbraith et al., in press). Density among populations correlates positively with latitude and primary production levels and negatively with the size of the body of water (Galbraith et al., in press), although data are too sparse to rely heavily on these correlations. Other possible factors influencing density are predation pressure, especially on nests and hatchlings, climatic influences on egg survival and embryo development, and availability of suitable nesting sites. Again, the role of these factors has not been studied.

Annual Energy Budgets

No complete energy budget has been determined for any turtle population, although some efforts have been made to estimate critical components of the energy budget (Congdon et al. 1982). Almost all efforts in this area have concentrated on the energy content and cost of the eggs (Congdon and Gibbons 1985, Congdon and Tinkle 1982, Shine 1980) and on the rates of digestion, especially in relation to temperature (Parmenter 1981).

Food-Web Connections

Snapping turtles are widely regarded as voracious predators, but most studies of their diet indicate that plant material is a major component of their food (Alexander 1943, Hammer 1972, Pell 1941). Hammer (1972) found that plants made up the majority of the diet of snapping turtles in a North Dakota marsh. In Connecticut, fish (mostly nongame species) and aquatic plants were of equal importance and birds made up only a small fraction of the diet (Alexander 1943). In Maine, snapping turtles ate significant numbers of ducklings in local areas where both turtles and waterfowl were common, but widespread control of turtles was not recommended (Coulter 1957). Lagler (1943), working in Michigan, concluded that snapping turtles had minimal impact on waterfowl and pan fish and subsisted primarily on plant material and invertebrates. In general then, snapping turtle predation on waterfowl or game and sport fish poses no serious problem to these valuable species except perhaps in local situations where numbers of turtles may be very high and the turtles have easy access to young waterfowl.

Adult snapping turtles are largely immune to predation other than by humans over most of their range. A wide diversity of predators prey on snapping turtle eggs (foxes, skunks, raccoons) and hatchlings (herons, large fish), and mortality is very high during these stages.

Rationale for the Development of Life Tables

The demography of populations of freshwater turtles under exploitation has not been extensively studied. Some reports have cited large catches being removed from specific locations with apparently little impact on remaining numbers in the short term (e.g. Hogg 1975) but no study has followed an exploited population in detail for any length of time. It is necessary, therefore, to infer the effect of harvesting on populations using demographic parameters of unexploited populations under long-term study. This paper describes 2 snapping turtle populations in Ontario, Canada and presents a life table for one of these populations.

Study Areas

Lake Sasajewun, Algonquin Provincial Park, Ontario

The Ontario Ministry of Natural Resources Wildlife Research Area (W.R.A. 45°35’ N, 78°30’ W, mean annual temperature 4.4°C), is located in the central area of Algonquin Provincial Park, in a region of mixed forest last logged in the 1930s. The snapping turtles inhabiting the lakes and streams running through the W.R.A. have been studied since 1972. Each year, adult female turtles are captured after nesting and both males and females are captured using baited hoop traps. Of the approximately 185 tagged snapping turtles in the watershed of the North Madawaska River, about 100 are recaptured each year. Approximately 70 nests of known females are located each year.

Snapping turtles are the largest aquatic vertebrate in the W.R.A., with the exception of beavers (Castor canadensis) and occasional river otters (Lutra canadensis). The only other species of turtle in this watershed is the midland painted turtle (Chrysemys picta marginata), present in very small numbers (< 10). The density of the W.R.A. snapping turtle population is approximately 1.5 adults/ha in lakes (Galbraith et al., in press). The study area and the snapping turtle population have been described extensively elsewhere (Galbraith and Brooks 1987; Galbraith et al. 1987, in press; Obbard 1983).
Royal Botanical Gardens, Hamilton, Ontario

The Royal Botanical Gardens (R.B.G.) consist of approximately 700 ha of woodlands and waterways within the metropolitan Hamilton area (43°17'N, 79°33'W; mean annual temperature 9.8°C). This study area and the snapping turtle population in the R.B.G. have been described previously (Galbraith et al., in press). We have captured, tagged, and released adult and juvenile snapping turtles in this watershed since 1984. In addition to snapping turtles, map turtles (Malaclemys geographica) and painted turtles are common aquatic chelonians in this system. The painted turtle is at least as common as the snapping turtle.

The turtles inhabit a highly productive, eutrophic waterway which is artificially enriched by effluent from a sewage treatment plant. West Pond (9.8 ha), where our trapping has taken place, also connects with heavily-polluted Hamilton Harbour. Despite the contaminants, this population exhibits one of the highest densities yet reported for this species, approximately 60-70 adults/ha (Galbraith et al., in press).

Methods and Results

Life Tables

Two approaches are commonly taken in preparing life tables. Static or vertical life tables are prepared by deriving mortality rates from the observed population age-structure. Cohort-specific, or horizontal life tables are prepared by following a specific cohort and observing age-specific mortality rates throughout life (Deevy 1947). At present, only static life tables can be prepared for snapping turtle populations, because individual cohorts cannot be followed effectively in these animals which may have a maximum longevity of over a century (Galbraith and Brooks 1987).

Therefore, we will only consider static life tables.

Life-Table Parameters for Algonquin Park (W.R.A.)

Snapping turtles experience large fluctuations in annual reproductive success (Obbard 1983). In the W.R.A. population, for example, most years do not produce any emergent hatchlings (R. J. Brooks, unpubl. data) whereas occasional years may produce large numbers of hatchlings. This highly stochastic survivorship throws some doubt on the utility of static life tables, because age curves could be highly biased by errors due to irregular recruitment. Therefore, we will use an average mark-recapture survivorship rate (Galbraith and Brooks 1987) for all adult females for the construction of the life table.

Several critical pieces of information have never been obtained for any snapping turtle population. For example, no estimate of survivorship of hatchlings or juveniles has ever been published. A crude estimate of this rate can be obtained by assuming that the number of turtles recruited per year into the population is fairly represented by the average recruitment rate, and that the number of eggs being produced per year has not varied greatly between the years when recruits were initially produced (i.e. as eggs) and the present time. In the W.R.A. population, on average, one new nesting female is captured per year on nesting sites used by approximately 85 other females. The mean clutch size of 34 eggs once per year gives an annual egg production of 2890 eggs. Assuming half these eggs produce females, the net survivorship across all age classes (including eggs) until age at first nesting (approximately 19 yr, (Galbraith 1986)) is therefore 1/1445 (0.000692).

In the W.R.A. population, Obbard (1983) observed a mean rate of emergence of hatchlings from eggs of 0.0635, averaged over 142 nests in 5 yr. Taking this into account, in addition to the adult recruitment rate of one mature female per year, the probability of mortality between hatching and maturity for females in this population is 99.17%. Average annual juvenile survivorship from this estimate is therefore 0.7541 from hatching to 19 yr (table 1).

High rates of statistical errors within age estimates of individual turtles (Galbraith 1986) make documentation of horizontal rates of age-specific changes in fecundity unreliable, and therefore we have constructed our life table using mean clutch size for all age classes. Net fecundity, however, is a function of both clutch size and clutch frequency. Obbard (1983) estimated that 72.1% of adult females, on average, lay a clutch each year in this population. Mean annual egg production is therefore 24,514 eggs per female (mean clutch size is 34 eggs). For the purposes of a life table, the female turtles are considered as producing only female offspring. It is also necessary, therefore, to consider the effects of biases in hatchling sex ratios. Snapping turtles experience environmental sex determination, whereby incubation temperature during the middle third of the incubation period determines offspring sex (Yntema 1976). Between 1981 and 1985, the mean hatchling sex ratio of naturally incubated nests in the W.R.A. was 66% female (R. J. Brooks, unpubl. data). Therefore, each female turtle, on average, produces 16.18 female-destined embryos per nesting season. Although snapping turtles are long-lived, the life table for female snapping turtles in the W.R.A. suggests that they do not reproduce enough to sustain the population (table 1).

Life-Table Parameters for the Royal Botanical Gardens (R.B.G.)

Although data are inadequate to construct a meaningful life table for
snapping turtles from the R.B.G., some population parameters are known. For example, females in the very large snapping turtle population in the R.B.G. appear to nest for the first time at 10 yr of age (R.J. Brooks, unpubl. data), and the mean clutch size in the R.B.G. population between 1985 and 1987 was 45 eggs. The rate of mortality in this population is likely higher than in the Algonquin population, because numerous dead turtles are found each year (C.A. Bishop, unpubl. data). Essential but currently unavailable information from the R.B.G. population includes long-term estimates of emergence rates of hatchlings or of adult survivorship, annual nesting frequency, and primary sex ratio.

### Table 1.—Life table for female snapping turtles in Algonquin Park (W.R.A.), Ontario, Canada.

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\( q_x \) = numbers of individuals.
\( I_x \) = probability of survival from year class 0 to year class \( x \).
\( q_x \) = probability of survival from year class \( x \) to year class \( x+1 \).
\( m_x \) = net fecundity at year class \( x \) (female-destined embryos produced).
\( \Sigma m_x I_x \) = sum of all reproduction from year class 0 to year class \( x \), equals \( R_0 \), total lifetime reproduction, when \( x \) is at its maximum.

Life-Table Implications for Management Guidelines

Clearly, exploitation of a population similar to that in Algonquin Park would quickly reduce numbers below any chance of recovery by reproduction within that population. In formulating our life table for the W.R.A., we have had to make several assumptions. The most important concerns our estimate of the rate of survival of hatchlings and juveniles. A comparison between the 2 populations indicates that the advantages in the R.B.G. population of having a larger clutch size than the more northern population and being able to initiate nesting almost 10 yr before the W.R.A. population may be tempered by overestimating adult survivorship in the R.B.G. population. Consequently, lifetime reproduction may not be as high as one might predict. These comparisons must be improved by direct observation of survival in the critical juvenile years, and by following individuals of known age throughout life, in a variety of populations.

Considerable variation in population characteristics exists between these 2 populations located about 280 km apart. Trapping guidelines applicable to the R.B.G. population may not be suitable to the population in the W.R.A. Regardless, neither could likely tolerate harvests of more than 10% of the adult population.

Management Practices to Increase Yields of Snapping Turtles

It is evident that unregulated harvesting of adult snapping turtles will rapidly decrease population sizes, because adult turtles are normally...
subject to very low rates of mortality (Galbraith and Brooks 1987). Two strategies are possible to increase harvestable numbers of turtles.

First, practical experience with sea turtle farming has shown that large numbers of eggs can be incubated under artificial or protected conditions (Mrosovsky and Yntema 1980), although care must be taken to incubate the eggs at a selection of temperatures which will produce a balanced sex ratio. Similar propagation of snapping turtles should result in increased numbers of juveniles in populations where adult numbers are not density-dependent.

Secondly, enrichment of the environment could provide faster growth rates for these poikilotherms. Increases in available protein will probably result in an increase in growth rates of individuals and increases in adult carrying capacities (MacCulloch and Secoy 1983).

Organochloride Contaminants and Human Consumption

Long-lived bottom-dwellers can accumulate high levels of environmental toxins, and snapping turtles have been found to carry very high loads of PCBs of various forms (Bryan et al. 1987a). Several studies have considered the way in which PCBs accumulate and in which tissues, and snapping turtles are now being employed as biomonitors for organochlorides in some studies (C.A. Bishop et al., unpubl. data).

Bryan et al. (1987) demonstrated that local levels of pollutants markedly affected the levels of organochloride toxins in snapping turtle tissues. Tissue-specific accumulation of PCBs is not random in snapping turtles, but is a function of lipoprotein content of the tissue and the high lipoprotein solubility of the toxins. Especially high concentrations (as high as 1600 ppm PCB in turtles from polluted locations) are found in fat bodies, brain, and testes. However, Bryan et al. (1987) indicated that toxic PCB congeners did not remain in the large fat reserves of female turtles, as some had suggested, but were passed on in bulk to the egg yolks. It is necessary, therefore, to test tissue or egg samples to ensure that turtles being harvested for human consumption are not loaded to a dangerous degree with organochloride contaminants.

Management of Snapping Turtles as Predators

Several studies have considered the impact of snapping turtles on waterfowl populations (Alexander 1943, Hammer 1972, Lagler 1943). Highly-productive bodies of water present ideal habitat for waterfowl and for turtles.

Destroying turtle nesting locations may not reduce local populations of snapping turtles, because females may migrate several kilometers between their usual home range and their nesting sites (Obbard 1977). In addition, such habitat interference will remove nesting opportunities for other turtle species.

Reduction in numbers of adult snapping turtles through trapping will rapidly deplete isolated populations and should reduce risks to prey species. However, if turtles can emigrate into the management area, then the expected long-term effect of culling adults will not be realized because the population can increase from these new adult immigrants.

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