

Impact of Agricultural Development on a Population of Wood Turtles (*Clemmys insculpta*) in Southern Québec, Canada

RAYMOND A. SAUMURE^{1,2} AND J. ROGER BIDER^{1,3}

¹Department of Natural Resource Sciences, McGill University,
21111 Lakeshore Road, Ste-Anne-de-Bellevue, Québec, H9X 3V9, Canada;

²Department of Live Collections, Biodôme de Montréal,
4777, avenue Pierre-De-Coubertin, Montréal, Québec, H1V 1B3, Canada;

³Present Address: Saint-Lawrence Valley Natural History Society,
21125 chemin Sainte-Marie, Ste-Anne-de-Bellevue, Québec, H9X 3L2, Canada

ABSTRACT. – The effects of agricultural development on wood turtles (*Clemmys insculpta*) were investigated in Québec during 1994 and 1995. Age structure, growth, and mutilation rates were compared between an agricultural population and a reference site in an undisturbed forest. Turtles in the 0–4 year age class were absent from samples taken at the agricultural site. Overall, 23% fewer juveniles were encountered at the agricultural site. In addition, relatively fewer adults from the 20+ age class were captured. Shell injuries were twice as common at the agricultural site when compared to the forest site, whereas limb amputations were twice as frequent at the forest site. Although shell injuries inflicted by predators occurred with similar frequencies at both sites, there were 2.7 times more fractures resulting from anthropogenic sources at the agricultural site. Multiple limb loss occurred only at the forest site. Tail amputations occurred with similar frequencies at both sites. Casts of costal scute annuli revealed that turtles at the agricultural site had significantly lower growth rates during their second decade of life. Females at the forest site were significantly larger for all measurements recorded, whereas males differed only with respect to carapace and plastron lengths. Agricultural development may have resulted in reduced predation, but also in reduced growth and recruitment, as well as increased adult mortality.

KEY WORDS. – Reptilia; Testudines; Emydidae; *Clemmys insculpta*; turtle; mutilation; predation; growth; age structure; ecology; habitat; agriculture; conservation; Canada

The North American wood turtle, *Clemmys insculpta*, is considered a species in decline and has been placed on CITES Appendix II in order to monitor collecting and international trade (Buhlmann, 1992; 1993). Theories for the apparent declines of certain populations of wood turtles have been formulated and tentative solutions have been proposed (Harding, 1991; Kaufmann, 1992a; Buech et al., 1993; Garber and Burger, 1995; Litzgus and Brooks, 1996). Garber and Burger (1995) suggested that *C. insculpta* would be an ideal experimental organism for comparative studies on the effects of forest fragmentation and human disturbances. Indeed, several studies have documented that wood turtles actively seek out ecotones (Brewster and Brewster, 1991; Ross et al., 1991; Kaufmann, 1992a). Ecotones, or edge habitats, are defined as transition zones of increased vegetative heterogeneity at the junction of two discrete habitat types (Allaby, 1991). Anthropogenic ecotones, such as shelterbelts, farmsteads, and clearcuts (Hasbrouck et al., 1992), have been shown to increase the foraging efficiency of numerous species of animals (Pearson, 1968; Wallmo, 1969; DeByle, 1981; Thompson and Fritzell, 1990). Consequently, it has been suggested that wood turtles might benefit from moderate agricultural or logging activities which produce these edge habitats (Harding, 1991; Kaufmann, 1992a). The use of ecotones as a viable management tool has however, been questioned (Gates and Gysel,

1978; Saunders et al., 1991). Temple (1987) reported that the foraging efficiency of Blanding's turtle (*Emydoidea blandingii*) nest predators increased near ecological edges, whereas Congdon et al. (1983) documented otherwise in another population. Furthermore, Kaufmann (1992a) conceded that crop rotations and farm machinery could pose important risks to wood turtles. Although wood turtles might indeed benefit from moderate agricultural or logging activities within their home ranges, this claim has never been investigated. Bayley and Highfield (1996) documented several negative effects of deforestation and agriculture on *Testudo graeca graeca*. Our objective was to determine whether agricultural development had any negative impacts on *Clemmys insculpta* populations in Québec. We compared degrees of mutilation, age structures, and growth rates between two populations of *C. insculpta* found in agricultural and forest habitats.

MATERIALS AND METHODS

Study Sites. — We studied wood turtles, *Clemmys insculpta*, at two sites in the Great Lakes – St. Lawrence forest region of southern Québec, Canada. In keeping with the conservation recommendations of Litzgus and Brooks (1996), the exact locations of our study sites are not dis-

closed. Both sites were comprised of approximately 6 km of meandering river.

The agricultural site was located in Brome County at an altitude of 140 m above sea level. The average number of frost-free days (FFD) for this site was 110, based upon 30 years of data (1951–80). This population has been subjected to various forms of agricultural disturbances since 1797. Extensive hay fields and cattle pastures covered approximately half the site, with the remaining half being mostly deciduous forest. The dominant tree species were Manitoba maple (*Acer negundo*), speckled alder (*Alnus rugosa*), willows (*Salix* sp.), and white elm (*Ulmus americana*). On some farms, cattle were denied access to the river by electric or barbed-wire fencing. The river is subjected to substantial water level fluctuations during spring run-off. Stream bank erosion was pronounced along both cattle pastures and hay fields. An abundance of sand and gravel banks occurred along the river's edge. Gravel roads, serving local residents, crossed the river at three points. A paved road ran parallel to the river at distances ranging from 20–640 m. Sampling took place between 2–19 May 1995.

The forest site was in Pontiac County, approximately 100 km northwest of the agricultural site, at an elevation of 180 m. The average number of FFD was 113 (based upon 27 years of data between 1951–80). The study area included a meandering stretch of virtually undisturbed floodplain in a transition forest characterized by restricted road access, absence of agricultural development, a minimum of forestry activity, and extensive marshes. Dominant tree species included balsam fir (*Abies balsamea*), speckled alder (*Alnus rugosa*), trembling aspen (*Populus tremuloides*), and white spruce (*Picea glauca*). Five gravel areas suitable for nesting were present within the study site, only one of which was not associated with an old logging road. Overall, the river at the forest site was deeper and narrower than the one at the agricultural site. It was crossed at one point by a highway and had a restricted access gravel road parallel to it. The main human activities along the river included hunting white-tailed deer (*Odocoileus virginianus*) and ruffed grouse (*Bonasa umbellus*) in the fall, as well as fishing for brook charr (*Salvelinus fontinalis*) in the spring. This site has been surveyed sporadically for wood turtles since 1984 (Saumure, 1992). A more intensive sampling for this project took place between 30 May and 1 July 1994 and 22 May to 22 June 1995.

Capture Techniques. — Turtles at both sites were captured by hand or dipnet. The agricultural area was patrolled on foot along the river banks and by canoe. Turtles were usually encountered in open grassy areas several meters from the river. Most specimens did not attempt to flee when approached. The forest site was surveyed by canoe, as the dense thickets of speckled alder along the river banks precluded a silent approach. Wood turtles usually basked at the river's edge and dove into the river at the slightest visual or auditory disturbance. Occasionally, natural openings created by the actions of beaver (*Castor canadensis*) occurred along the river banks. These areas were searched on foot. In

addition, three nesting areas were patrolled during June of 1994 and 1995.

Each turtle was distinctly marked by notching the carapace (Cagle, 1939) using a numerical system similar to the one described by Froese and Burghardt (1975). Hatchlings and small juveniles, not large enough to be notched, were marked by placing 0.018 gauge stainless steel wire rings through the marginal scutes (Layfield et al., 1988).

Mutilation. — Detailed notes, drawings, and photographs were taken of injuries to the limbs, tails, and shells of captured turtles in order to compare rates of mutilation between the two populations. Congenital abnormalities (Harding and Bloomer, 1979) were excluded from our compilations. Traumatic injuries were classified as either due to predation (Fig. 1) or collision (Fig. 2). Collision injuries resulted from encounters with cattle or motorized vehicles, such as passenger vehicles and farm machinery. When trauma was of undetermined origin, it was tabulated separately. Tail injuries were also compiled separately, as these injuries are known to be caused by conspecific wood turtles in captivity (Bell, 1972). Furthermore, contaminants such as PCBs, dioxins, and furans are known to cause tail malformations in common snapping turtle embryos, *Chelydra serpentina* (Shirose et al., 1996).

Morphometrics and Age Structures. — Turtles were sexed based on a combination of their size (Harding and

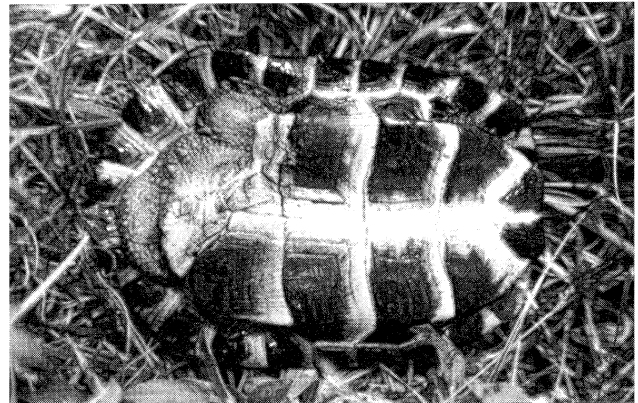


Figure 1. *Clemmys insculpta* from study site with mutilated posterior plastron and partially amputated tail due to predation.

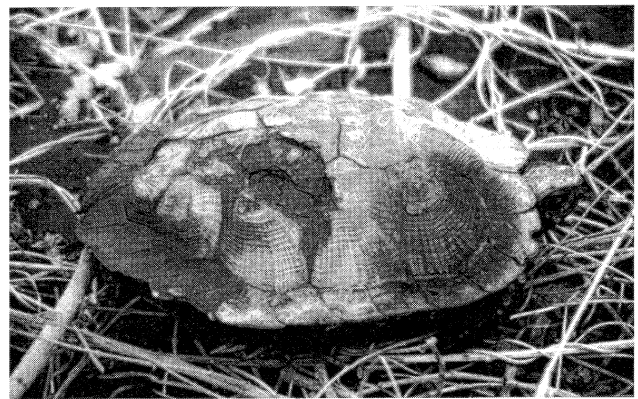


Figure 2. *Clemmys insculpta* from study site with crushed posterior carapace and several damaged marginal scutes due to collision.

Bloomer, 1979; Lovich et al., 1990; Brooks et al., 1992; Kaufmann, 1992a) and the presence or absence of male secondary sex characteristics, such as plastral concavity or a relatively longer preanal tail length (Wright, 1918; Kaufmann, 1992b). Much variability exists in ages at maturity published in the literature (Farrell and Graham, 1991; Harding, 1991; Ross et al., 1991; Brooks et al., 1992; Garber and Burger, 1995), probably because maturity in *C. insculpta* may be more a function of size than age. Juveniles included all turtles of undetermined sex. Our juvenile category included hatchlings, juveniles, and subadults as described by Farrell and Graham (1991).

The maximum length and width of both the carapace and the plastron were determined with Mitutoyo dial calipers (± 0.05 mm). Turtles ≤ 1 kg were weighed using Pesola spring scales accurate to ± 2 or ± 10 g, depending on the mass of the specimen. Turtles in excess of 1 kg were weighed with an Ohaus spring scale (± 25 g).

Growth rings are produced on an annual basis in wild wood turtles for 15 to 20 years (Harding and Bloomer, 1979; Harding, 1985a). Whenever possible, dental stone casts of the anterior right costal scute were made (Galbraith and Brooks, 1983, 1987; Zug, 1991; Brooks et al., 1992). These molds provided us with permanent records of the minimum age and annual growth of each turtle captured (Ewing, 1939). Casts of two preserved (NMC 26568, 33884) and one frozen specimen (RAS-251) from the forest site were included in the analyses. Age estimates were categorized into five classes in order to determine frequency distributions for both populations. In addition, dial calipers were used to measure the width of growth rings on each cast. These measurements enabled the comparison of growth rates between populations. As sexual size dimorphism occurs in *C. insculpta* (Lovich et al., 1990), we also subdivided our growth data by sex to enable us to detect any intrasexual differences that may exist between the two populations.

Statistical Analyses. — As growth measurements from a particular turtle are correlated, and thus not independent, a repeated-measures design was used (Moser et al., 1990; Potvin et al., 1990). Univariate repeated-measures analysis of variance (ANOVAR) were used to interpret the data. As the assumption of sphericity was violated, the Huynh-Feldt (H-F) adjusted F-values were used to detect significance. Data analyses were accomplished using the General Linear Model (GLM) procedure (SAS Institute Inc., 1985).

Table 1. Percentages of male, female, and juvenile *Clemmys insculpta* with mutilated limbs, tail, carapace, and/or plastron from agricultural and forested sites in southern Québec, Canada. No significant differences.

	Agriculture		Forest	
	n	% mutilated	n	% mutilated
Male	16	81.2	10	70.0
Female	13	69.2	10	90.0
Juvenile	4	50.0	11	54.5
Total	33	72.7	31	71.0

Table 2. Percentages of wood turtles with mutilated appendages and/or shells from agricultural ($n = 33$) and forested ($n = 31$) populations in southern Québec, Canada.

	Limbs		Tail		Carapace		Plastron	
	n	%	n	%	n	%	n	%
Agriculture	5	15.2	18	54.5	17	51.5	7	21.2
Forest	10	32.3	16	51.6	8	25.8	4	12.9

We tested for significant differences in annuli growth between sites (site effects), within turtles (time effects), and within turtles between the sites (time-site effects). The effects of time were investigated because annuli measurements were pooled from many turtles to produce a mean value for each year of growth, regardless of the actual age of a given turtle. For example, measurements of the fourth growth ring from 3 turtles of ages 5, 10, and 15 years were pooled. Such pooling of data conceals the possible influences of the environmental conditions present when the growth actually occurred, as was outlined in Tucker et al. (1995).

We tested for significant sexual differences in morphometric parameters and mutilation rates using Student's *t*-tests and χ^2 , respectively. The sexual dimorphism index was calculated from the equation described in Lovich et al. (1990). Statistical significance was set at $p < 0.05$ for all analyses.

RESULTS

A total of 31 individuals (10 males, 10 females, and 11 juveniles) were captured at the forest site, whereas 33 individuals (16 males, 13 females, and 4 juveniles) were sampled from the agricultural population.

Predation and Mutilation. — Turtles exposed to sublethal predation, motorized vehicles, or cattle showed various degrees of mutilation. Mutilated turtles represented 72.7% of turtles sampled from the agricultural population and 71.0% from the forest site (Table 1). No differences in mutilation rates were detected between the sexes for either the agricultural ($\chi^2 = 0.566$, $df = 1$) or forest sites ($\chi^2 = 0.532$, $df = 1$) (Table 1). Furthermore, there were no statistical differences in mutilation rates between males ($\chi^2 = 1.8$, $df = 1$) or females ($\chi^2 = 1.08$, $df = 1$) when comparing the two populations. Approximately 50% of the juveniles from both sites were injured.

Limb amputations were observed on 5 turtles from the agricultural site, and 10 from the forest site (Table 2). Only turtles at the forest site had more than one limb amputated ($n = 4$). Carapace injuries were encountered twice as often at the agricultural site (17 animals), than at the forest site (8 animals) (Table 2). Damage to the plastron was approximately twice as common at the agricultural site (7 animals) as at the forest site (4 animals). Of the shell injuries recorded at the forest site, 6 were the result of predation and 3 the result of collisions. One turtle had healed injuries that could have belonged to either category. The agricultural site had 5 turtles with signs of predation and 8 with trauma that clearly resulted from collisions. Ten turtles at the agricultural site

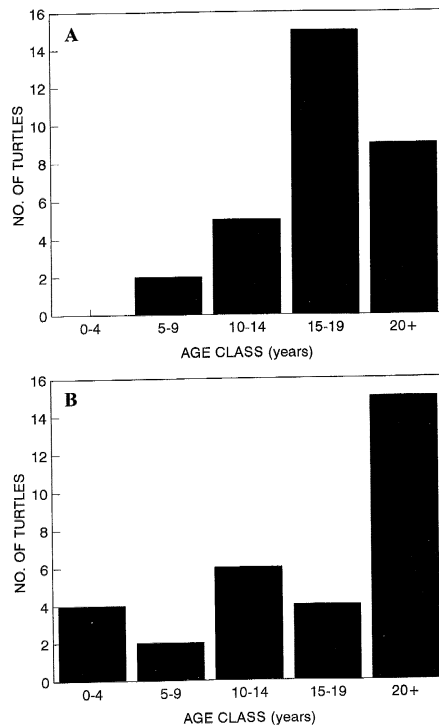


Figure 3. Age-frequency histograms for (A) Brome County agricultural site and (B) Pontiac County forest site.

had various forms of gouges, dents, and scrapes in their marginal scutes and underlying bone that were of undetermined origin. Tail amputations were found on approximately the same number of turtles at both sites (18 at the agriculture site, 16 at the forest site). The exclusion of tail injuries resulted in a decrease in overall mutilation rates to 63.6% and 48.4% for the agricultural and forest populations, respectively. A total of 12.1% ($n = 4$) of turtles from the agricultural site and 22.6% ($n = 7$) from the forest site had no trauma other than tail amputations.

Population Age Structures. — Age frequency distributions for both the agricultural and forest populations are shown in Fig. 3. Turtles in the 0–4 year age class were absent from the agricultural site sample. There was a greater number of juveniles captured at the forest site. The proportion of juvenile turtles located in the agricultural and forest populations were 12.1 and 35.5%, respectively.

Based strictly on counts of annuli, which never exceeded 26 at either site, the minimum average ages for the agricultural and forest populations were 16.7 years ($n = 32$) and 16.8 years ($n = 31$), respectively. The youngest identifiable males were 11 (CL = 157.6 mm) and 10 years (CL = 176.30 mm) for the forest and agricultural sites, respectively. The youngest nesting female at the forest site had 15 annuli (CL = 195.4 mm).

Growth. — Significant differences in growth of turtle scutes in the 10–15 and 15–20 year growth periods were detected between the two study sites (Table 3; Fig. 4). Significant differences in growth among turtles over time were also revealed for all but the 10–15 year growth period (Table 4). Differences in growth between the sites were

Table 3. Repeated measures univariate analysis of variance for site effects, between turtle costal annulus growth, in two populations of wood turtles in southern Québec, Canada. MS is mean square value. Statistically significant difference ($p < 0.05$) indicated by (*).

Year Class	n	df	MS	F	$p > F$
1-5	24	1	0.077	0.08	0.7737
5-10	24	1	2.288	3.20	0.0875
10-15	20	1	9.017	14.02	0.0013*
15-20	14	1	3.751	5.43	0.0381*

Table 4. Repeated measures univariate analysis of variance for the effects of time on costal annulus growth, within turtles from two populations of *Clemmys insculpta*, in southern Québec, Canada. MS is the mean square value, H-F is the probability of the Huynh-Feldt adjusted F-tests. Statistically significant difference ($p < 0.05$) indicated by (*).

Year Class	df	MS	F	$p > F$	H-F
1-5	4	3.130	11.79	0.0001	0.0001*
5-10	5	0.651	3.39	0.0069	0.0069*
10-15	5	0.399	2.24	0.0561	0.0561
15-20	5	1.458	10.07	0.0001	0.0001*

Table 5. Repeated measures univariate analysis of variance for the effects of time on costal annulus growth, between two populations of *Clemmys insculpta*, in southern Québec, Canada. MS is the mean square value, H-F is the probability of the Huynh-Feldt adjusted F-tests. No significant differences.

Year Class	df	MS	F	$p > F$	H-F
1-5	4	0.288	1.08	0.3691	0.3633
5-10	5	0.306	1.59	0.1674	0.1674
10-15	5	0.218	1.22	0.3034	0.3034
15-20	5	0.137	0.95	0.4576	0.4249

Table 6. Repeated measures univariate analysis of variance for site effects, between adult female wood turtle costal annulus growth, in two populations in southern Québec, Canada. MS is mean square value. Statistically significant difference ($p < 0.05$) indicated by (*).

Year Class	n	df	MS	F	$p > F$
1-5	12	1	1.218	0.96	0.3494
5-10	12	1	0.761	1.88	0.2000
10-15	12	1	6.242	22.00	0.0009*
15-20	4	1	0.901	4.16	0.1783

Table 7. Repeated measures univariate analysis of variance for site effects, between adult male wood turtle costal annulus growth, in two populations in southern Québec, Canada. MS is mean square value. Statistically significant difference ($p < 0.05$) indicated by (*).

Year Class	n	df	MS	F	$p > F$
1-5	12	1	0.504	0.97	0.3480
5-10	12	1	1.605	1.70	0.2217
10-15	10	1	2.948	8.15	0.0213*
15-20	10	1	2.860	3.43	0.1010

found to be consistent from one year to the next (Table 5). Significant differences in annuli widths were only detected for the 10–15 year growth period when females from the two sites were compared (Table 6; Fig. 5). The same was true of male growth rates (Table 7; Fig. 6).

Adult males from the forest site were significantly larger than those from the agricultural site (Table 8). Females from the forest site were significantly larger for all measurements recorded (Table 9). In addition, significant differences in maximum carapace lengths ($t = -4.34$, $df = 25$) and widths ($t = -3.89$, $df = 25$), as well as masses ($t = -2.59$,

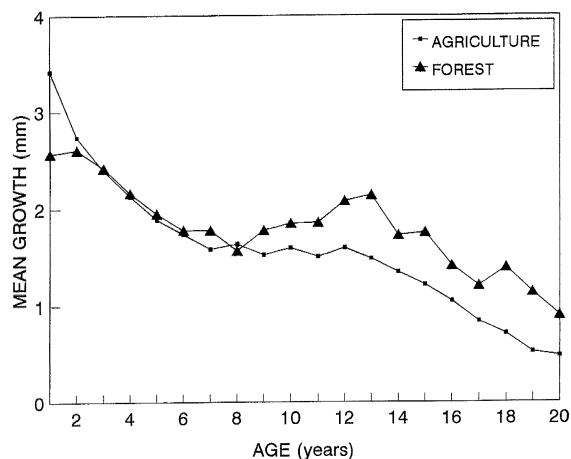


Figure 4. Mean growth of the anterior right costal scute from two populations of wood turtles in southern Québec, Canada.

df = 25) were observed between the sexes for the agricultural population. However, no significant morphometric differences were detected between the sexes for the forest site. The sexual dimorphism index for both populations was -1.07.

Overall decreases in mean annual growth were observed to begin at age 12 for females at the agricultural site and at age 13 in those inhabiting the forest site. Similar decreases were recorded for males at both sites during their twelfth year of growth.

DISCUSSION

Predation and Mutilation. — To date, circumstantial evidence suggests that wood turtle limb amputations occur as a result of predation by raccoons (Harding and Bloomer, 1979; Harding, 1985b; Farrell and Graham, 1991). Congdon et al. (1993) have suggested that recent declines in the fur trade have allowed turtle predators to greatly increase their numbers. Others have found that raccoon numbers have increased in agricultural areas, particularly where corn is grown (Rivest and Bergeron, 1981). The injuries sustained by *C. insculpta* at our sites revealed interpopulational differ-

ences. As we have no evidence to suggest commercial collecting of undamaged specimens at either site, we assumed that the differences observed were real, and not just artifacts of selective poaching. We suspect that the relative abundance and/or density of predatory species accounts for the higher limb mutilation rates at the forest site. One factor which may have a significant impact on predator abundance and density is hunting pressure. Raccoons and fox can only be taken by one licensed trapper on the government land portion of the forest site, whereas they can be legally hunted (without bag limit) at the agricultural site. In addition, Yahner (1996) documented a reduction in predator abundance as a result of increased fragmentation of forest habitats. At the agricultural site, the highly fragmented forest, absence of corn fields, and the greater hunting pressure may have led to a reduction in the number of predator species and densities. We cannot, however, reject the possibility that the differences observed in limb amputation rates were the result of a few individual predators which were particularly efficient hunters (Butler and Sowell, 1996). Predator efficiency may explain the removal of more than one limb from turtles at the forest site, although multiple amputations could just as likely occur as a result of greater predator density.

Some turtles at the forest site may have had their limbs severed in beaver traps, as was suggested by Harding and Bloomer (1979). Although an unlikely event, several researchers have, in fact, documented the capture of turtles in muskrat traps (Lagler, 1943; Meeks and Ultsch, 1990). In addition, wood turtles have been observed by Bloomer (1978) to hibernate in large numbers ($n = 70$) in a pond created by a beaver dam. Another possibility is that beavers (Harding, 1985b) and/or muskrats (Johnson, 1925) gnaw at wood turtles, which are known to use their underwater burrows and runways as hibernacula (Bishop and Schoonmacher, 1921; Bloomer, 1978; Harding and Bloomer, 1979; Ernst, 1986).

Although shell injuries attributed to predators were observed to occur at similar frequencies at both sites, turtles at the agricultural site had 2.7 times more shell mutilations caused by human activity. We were unable to distinguish

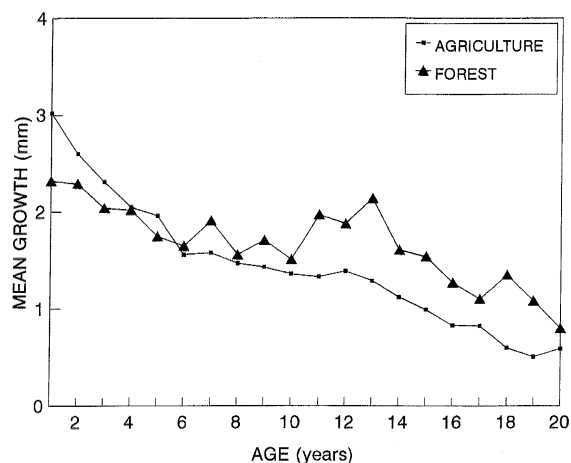


Figure 5. Mean growth of the anterior right costal scute of adult female wood turtles from two populations in southern Québec, Canada.

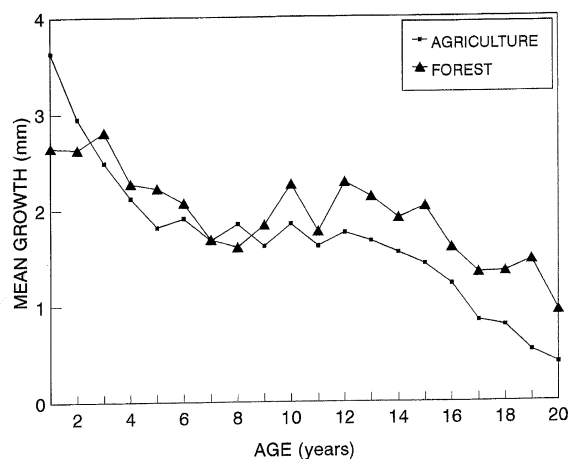


Figure 6. Mean growth of the anterior right costal scute of adult male wood turtles from two populations in southern Québec, Canada.

Table 8. Measurements of adult male wood turtles from agricultural and forested habitats in Brome and Pontiac counties, Québec, Canada. Values are given as mean \pm standard deviation.

	<i>n</i>	Carapace Length (mm)	Carapace Width (mm)	Plastron Length (mm)	Mass (g)
Agriculture	15	193.87 \pm 8.97*	143.72 \pm 6.83	174.71 \pm 6.82**	1008.0 \pm 146.60
Forest	9	215.61 \pm 22.34	149.91 \pm 14.56	194.87 \pm 16.99	1219.4 \pm 361.37

* Significant difference between sites, $t = -2.79$, $df = 9.6$ ** Significant difference between sites, $t = -3.40$, $df = 9.6$ **Table 9.** Measurements of adult female wood turtles from agricultural and forested habitats in Brome and Pontiac counties, Québec, Canada. Values are given as mean \pm standard deviation.

	<i>n</i>	Carapace Length (mm)	Carapace Width (mm)	Plastron Length (mm)	Mass (g)
Agriculture	12	181.03 \pm 5.51*	134.54 \pm 5.00**	171.14 \pm 5.81***	881.7 \pm 92.91****
Forest	10	200.52 \pm 11.63	145.87 \pm 5.14	196.12 \pm 7.85	1060.5 \pm 127.38

* Significant difference between sites, $t = -4.86$, $df = 12.3$ ** Significant difference between sites, $t = -5.23$, $df = 20$ *** Significant difference between sites, $t = -8.57$, $df = 20$ **** Significant difference between sites, $t = -3.80$, $df = 20$

between injuries caused by passenger vehicles and those of agricultural machinery or cattle. Consequently, the relative impact of agricultural machinery and cattle cannot be identified, but agricultural development either directly (i.e., machinery or cattle) or indirectly (i.e., passenger vehicles) resulted in an increase in the number of injured turtles.

Population Age Structures. — Several studies have documented population age structures for wood turtles (Farrell and Graham, 1991; Ross et al., 1991; Brooks et al., 1992; Garber and Burger, 1995). The interpretation of such age-frequency histograms is speculative at best, due to their inherently descriptive nature. Some noteworthy differences between our populations should, however, be mentioned. A comparison between our age-frequency histograms suggests a lower rate of recruitment into the 0–4 year age class at the agricultural site. Our results also indicate that 23% fewer juveniles were captured at the agricultural site than at the forest site.

A number of theories have been put forward to explain the relative absence of juveniles in samples of many chelonian species (Ross et al., 1991; Pappas and Brecke, 1992; Congdon et al., 1992, 1993; Herman et al., 1994; Kaufmann, 1995). These are: 1) failure to search or trap habitats frequented by juveniles; 2) secretive behavior of juveniles; 3) researcher search image; 4) lack of susceptibility of juveniles to trapping; 5) decreased survivorship of nests; and 6) a combination of high juvenile and low adult mortality. Future research should make use of drift fences (Stone et al., 1993), fluorescent pigments (Butler and Graham, 1993), radiotelemetry (Brewster and Brewster, 1991), and/or dogs (Plummer, 1979) to uncover the fate, or refugia, of juvenile wood turtles in agricultural habitats.

Growth and Body Size. — Significant differences in growth rates and body sizes were detected between our sites. Brooks et al. (1992) also reported interpopulation differences in body sizes between wood turtles. Several hypotheses to explain latitudinal variations in body size have been proposed. For instance, larger body size may reduce the metabolic costs per unit weight during reproductive years,

thereby lowering the risk of mortality during hibernation due to energy depletion (Galbraith et al., 1989; Brooks et al., 1992). Female wood turtles from our more northerly forest population had higher growth rates between the ages of 10 and 20 years than did those from the agricultural site 100 km to the southeast, and were also significantly larger for all body size measurements recorded. Graham and Forsberg (1991) presented evidence that supported the theory that large body size reduces metabolic costs. These authors found that subadult wood turtles had oxygen demands ($\mu\text{l O}_2 \text{ g}^{-1} \text{ h}^{-1}$) two to three times greater during hibernation than those of adults twice their size. Ultsch et al. (1985) found that the only adaptation required by *Chrysemys picta bellii* to endure longer winters than *C. p. dorsalis* was a lower metabolic rate and/or an increased ability to eliminate lactate buildup. The larger size of *C. p. bellii* (St. Clair et al., 1994) may therefore allow it to reduce metabolic costs. Northern populations of wood turtles may experience selective pressures to reach larger sizes for the same reason. Moreover, Brenner (1970) found a direct correlation between depletion of fat bodies and ovarian development. Specifically, ovarian fat increased even as the fat content of the liver, heart, and skeletal muscles decreased during a prolonged period of starvation. If starving adult female turtles continued to divert energy to the development of ovarian follicles in late summer and fall (Powell, 1967), then egg production could decrease the fat stores available during long northern winters sufficiently to cause mortality.

Harding (1985b) found that most limb injuries sustained by wood turtles occurred after they had reached sexual maturity (CL = 160 mm). He also documented that turtles with intact limbs survived significantly longer than those with one or more missing limbs. The higher frequency of limb loss observed in adults may also simply be a function of exposure time, as adults can reach the age of at least 33 years in the wild (Ross et al., 1991).

We propose that the mutilations inflicted on turtles at our two sites may have altered the growth rates of individu-

als. Congdon et al. (1983) and McLeod (1994) documented that the injuries sustained by individual turtles impeded growth. Limb loss may reduce mobility and thus reduce foraging efficiency and shell damage may directly inhibit or restrict shell growth. We are, however, unaware of any studies which have adequately addressed the impact of different injuries on growth rates. Our interpopulation differences in growth rates may have resulted from the type or severity of injuries received.

Larger body mass in *C. insculpta* may also confer a thermoregulatory advantage (Brooks et al., 1992). Females at our forest site had significantly greater masses than those to the south, whereas males did not differ significantly in mass between the sites. Female *C. insculpta* are known to bask more frequently prior to their June nesting season than males (Ernst, 1986). Perhaps the increase in mass in northern female wood turtles optimizes thermoregulation and egg development.

Regardless of why a turtle might need to achieve a larger body size, there are only a limited number of ways to increase growth rates. These include changes in diet, temperature, and metabolism (Gibbons, 1970; Parmenter 1980, 1981; Avery et al., 1993). Thornhill (1982), however, did not find significant size differences between turtles in artificially heated lakes and those in unheated lakes. Enhanced juvenile growth rates have been documented for turtles with high levels of animal protein in their diet (Gibbons, 1967; Moll, 1976; Graham and Doyle, 1977; Thornhill, 1982; MacCulloch and Secoy, 1983; Kennett, 1996; Lindeman, 1996). The fact that we detected no significant differences in annuli widths during the first decade of growth in our two populations implies that either juveniles obtained similar amounts of food of similar nutritional levels or that one population consumed more food of a lesser nutritional value.

Owen and Galbraith (1989) found that mean earthworm biomass in Maine was considerably greater in previously farmed land (29.1 g/m²) than in forests which had never been farmed (0.92 g/m²). High biomass was attributed to the introduction of European worms during the 17th century and early agricultural practices that increased organic matter and moisture retention while reducing soil acidity. Earthworms may be an important component of a wood turtle's diet, as witnessed by their specialized foraging behavior known as "stomping" (Zeiller, 1969; Kaufmann, 1986; Kaufmann et al., 1989). Pastures and hay fields are also known to provide an abundance of arthropods (Basore et al., 1987). Consequently, agricultural disturbances may improve foraging and diet of juvenile wood turtles.

In contrast, several authors have noted that biodiversity may be decreased in agricultural areas devoted to monoculture or pasture (Holechek et al., 1982; Odum, 1994; Sietman et al., 1994). Fragmented ecosystems undergo large changes in their physical environment which are particularly pronounced in edge habitats (Saunders et al., 1991). These changes include an increased flux in radiation due to the removal of natural vegetation cover, which results in increased soil temperatures that promote desiccation. Desiccation can, in turn, reduce foraging opportunities as a result

of changes in plant growth and invertebrate numbers (Saunders et al., 1991). These changes could, therefore, lead to fewer suitable prey for adult wood turtles. Should this be the case, the adult turtles would then have an increased reliance on plant matter to meet their energy requirements, as has been documented for *Chrysemys picta* (Gibbons, 1967; Zug, 1993). Consequently, these adult turtles would have lower growth rates and be smaller than their same-age counterparts at the forest site. Future research should attempt to quantify differences in wood turtle diets in natural versus agricultural habitats.

In conclusion, several important differences were detected between agricultural and forested populations of wood turtles. Turtles which inhabited the agricultural area had significantly lower growth rates between years 10 and 20 than those from the forest site. Females at the forest site were significantly larger for all measurements recorded. Males, however, differed only with respect to their carapace and plastron lengths. Overall, 23% fewer juveniles were captured at the agricultural site, with juveniles in the 0–4 year age class being absent. There were relatively fewer adults belonging to the 20+ age class sampled at the agricultural site. Shell injuries were twice as common at the agricultural site when compared to the forest site, whereas limb amputations were twice as frequent at the forest site. Although shell injuries inflicted by predators occurred with similar frequencies at both sites, there were 2.7 times more mutilations resulting from anthropogenic sources at the agricultural site. These differences suggest that agricultural practices may have a negative impact on these wood turtle populations.

Acknowledgments

Funding for this research was provided to the St. Lawrence Valley Natural History Society by the Québec Ministère de l'Environnement et de la Faune. Equipment was provided by the Canadian Museum of Nature, Royal Ontario Museum, World Wildlife Fund, and Ontario Ministry of Natural Resources. We also extend our thanks to Catherine Saumure, Raymond Saumure Sr., Claude Daigle, Christopher Sharp, Isabelle Bellavance, Sylvain Ethier, Gilles Lavoie, and Marlene Featherstone for their notable contributions in the field. Earlier drafts of this manuscript were improved by the comments of Catherine Saumure, Elizabeth Wright, Francis Cook, Rodger Titman, Daniel Gingras, Catherine Guay, and Christopher Shewchuk. This paper was submitted in partial fulfillment of the requirements for the degree of Master of Science to the Department of Natural Resource Sciences of McGill University.

RÉSUMÉ

Les effets du développement de l'agriculture sur la tortue des bois (*Clemmys insculpta*) ont été étudiés au Québec en 1994 et 1995. Les structures d'âge, la croissance, et les taux de mutilation d'une population vivant en milieu agricole ont été comparés à celle d'un site dans une forêt

non-perturbée. Dans l'ensemble, 23% moins de juvéniles ont été capturés en milieu agricole. De plus, un nombre relativement inférieur d'adultes dans la classe d'âge 20+ ont été capturés. Les tortues en milieu agricole ont montré deux fois plus de blessures à la carapace que celles du site forestier. Les blessures de carapace résultant d'actions humaines ont été 2.7 fois supérieures chez les tortues du site agricole. Par contre, le nombre de tortue manquant un membre a été deux fois plus élevé en forêt. Des tortues manquant plus qu'un membre ont seulement été trouvées au site forestier. Des moulages d'anneaux de croissance des plaques costales ont révélé que les tortues du site agricole avaient des taux de croissance significativement inférieures durant la seconde décennie de leur vie. Chez les femelles du site forestier, toutes les mesures enregistrées ont été significativement supérieures, tandis que chez les mâles elles ont été différentes seulement pour la longueur de la carapace et du plastron. Les perturbations agricoles pourraient être une des causes principales de l'augmentation de la mortalité des adultes et de la diminution de la croissance, du recrutement, et des taux de prédation chez ces populations de *C. insculpta*.

LITERATURE CITED

- ALLABY, M. (Ed.). 1991. The Concise Oxford Dictionary of Zoology. Oxford University Press, New York, 508 pp.
- AVERY, H.W., SPOTILA, J.R., CONGDON, J.D., FISCHER, R.U., JR., STANDORA, E.A., AND AVERY, S.B. 1993. Roles of diet protein and temperature in the growth and nutritional energetics of juvenile slider turtles, *Trachemys scripta*. *Physiol. Zool.* 66:902-925.
- BASORE, N.S., BEST, L.B., AND WOOLEY, J.B., JR. 1987. Arthropod availability to pheasant broods in no-tillage fields. *Wildl. Soc. Bull.* 15:229-233.
- BAYLEY, J.R., AND HIGHFIELD, A.C. 1996. Observations on the ecological changes threatening a population of *Testudo graeca graeca* in the Souss Valley, southern Morocco. *Chelonian Cons. Biol.* 2:36-42.
- BELL, V. 1972. Turtle of the month. *N.Y. Turtle Tortoise Soc.* 1:5-7.
- BISHOP, S.C., AND SCHOONMACHER, W.J. 1921. Turtle hunting in midwinter. *Copeia* 1921:37-38.
- BLOOMER, T.J. 1978. Hibernacula congregating in the genus *Clemmys*. *J. NOAH* 4:37-42.
- BRENNER, F.J. 1970. The influence of light and temperature on fat utilization in female *Clemmys insculpta*. *Ohio J. Sci.* 70:233-237.
- BREWSTER, K.N., AND BREWSTER, C.M. 1991. Movement and microhabitat use by juvenile wood turtles introduced into a riparian habitat. *J. Herpetol.* 25:379-382.
- BROOKS, R.J., SHILTON, C.M., BROWN, G.P., AND QUINN, N.W.S. 1992. Body size, age distribution, and reproduction in a northern population of wood turtles (*Clemmys insculpta*). *Can. J. Zool.* 70:462-469.
- BUECH, R.R., HANSON, L.G., AND NELSON, M.D. 1993. Identification, protection, and management of wood turtle nesting areas. (Abstract). *Conservation, Restoration, and Management of Tortoises and Turtles: An International Conference*. Purchase, New York, p. 22.
- BUHLMANN, K. 1992. Legislation and conservation alert. *Herp. Review* 23:66.
- BUHLMANN, K.A. 1993. Legislation and conservation alert. *Herp. Review* 24:125.
- BUTLER, B.O., AND GRAHAM, T.E. 1993. Tracking hatchling Blanding's turtles with fluorescent pigments. *Herp. Review* 24:21-22.
- BUTLER, J.A., AND SOWELL, S. 1996. Survivorship and predation of hatchling and yearling gopher tortoises, *Gopherus polyphemus*. *J. Herpetol.* 30:455-458.
- CAGLE, F.R. 1939. A system of marking turtles for future identification. *Copeia* 1939:170-172.
- CONGDON, J.D., DUNHAM, A.E., AND VAN LOBEN SELS, R.C. 1993. Delayed sexual maturity and demographics of Blanding's turtles (*Emydoidea blandingii*): implications for conservation and management of long-lived organisms. *Conservation Biol.* 7:826-833.
- CONGDON, J.D., GOTTE, S.W., AND MCDIARMID, R.W. 1992. Ontogenetic changes in habitat use by juvenile turtles, *Chelydra serpentina* and *Chrysemys picta*. *Can. Field-Nat.* 106:241-248.
- CONGDON, J.D., TINKLE, D.W., BREITENBACH, G.L., AND VAN LOBEN SELS, R.C. 1983. Nesting ecology and hatchling success in the turtle *Emydoidea blandingii*. *Herpetologica* 39:417-429.
- DEBYLE, N.V. 1981. Songbird populations and clearcut harvesting of aspen in northern Utah. U.S. Dept. Agriculture, Forest Service, Research Note INT-302, 8 pp.
- ERNST, C.H. 1986. Environmental temperatures and activities in the wood turtle, *Clemmys insculpta*. *J. Herpetol.* 20:222-229.
- EWING, H.E. 1939. Growth in the eastern box-turtle, with special reference to the dermal shields of the carapace. *Copeia* 1939:87-92.
- FARRELL, R.F., AND GRAHAM, T.E. 1991. Ecological notes on the turtle *Clemmys insculpta* in northwestern New Jersey. *J. Herpetol.* 25:1-9.
- FROESE, A.D., AND BURGHARDT, G.M. 1975. A dense natural population of the common snapping turtle (*Chelydra s. serpentina*). *Herpetologica* 31:204-208.
- GALBRAITH, D.A., AND BROOKS, R.J. 1983. A simple restraining device for large turtles. *Herp. Review* 14:115.
- GALBRAITH, D.A., AND BROOKS, R.J. 1987. Photographs and dental casts as permanent records for age estimates and growth studies of turtles. *Herp. Review* 18:69-71.
- GALBRAITH, D.A., BROOKS, R.J., AND OBBARD, M.E. 1989. The influence of growth rate on age and body size at maturity in female snapping turtles (*Chelydra serpentina*). *Copeia* 1989:896-904.
- GARBER, S.D., AND BURGER, J. 1995. A 20-yr study documenting the relationship between turtle decline and human recreation. *Ecological Applications* 5: 1151-1162.
- GATES, J.E., AND GYSEL, L.W. 1978. Avian nest dispersion and fledging success in field-forest ecotones. *Ecology* 59:871-883.
- GIBBONS, J.W. 1967. Variation in growth rates in three populations of the painted turtle, *Chrysemys picta*. *Herpetologica* 23:296-303.
- GIBBONS, J.W. 1970. Reproductive dynamics of a turtle (*Pseudemys scripta*) population in a reservoir receiving heated effluent from a nuclear reactor. *Can. J. Zool.* 48:881-885.
- GRAHAM, T.E., AND DOYLE, T.S. 1977. Growth and population characteristics of Blanding's turtle, *Emydoidea blandingii*, in Massachusetts. *Herpetologica* 33:410-414.
- GRAHAM, T.E., AND FORSBERG, J.E. 1991. Aquatic oxygen uptake by naturally wintering wood turtles *Clemmys insculpta*. *Copeia* 1991:836-838.
- HARDING, J.H. 1985a. Comments on age determination and growth in the Michigan population of the wood turtle (*Clemmys insculpta*). (Abstract). Combined meetings of SSAR and HL, Univ. South Florida, Tampa, p. 149.
- HARDING, J.H. 1985b. *Clemmys insculpta*. Predation-mutilation. *Herp. Review* 16:30.
- HARDING, J.H. 1991. A twenty year wood turtle study in Michigan: implications for conservation. In: Beaman, K.R., Caporaso, F., McKeown, S., and Graff, M.D. (Eds.). *Proceedings of the First International Symposium on Turtles and Tortoises: Conservation and Captive Husbandry*, pp. 31-35.
- HARDING, J.H., AND BLOOMER, T.J. 1979. The wood turtle, *Clemmys insculpta*... a natural history. *Herp. Bull. N.Y. Herp. Soc.* 15:9-26.
- HASBROUCK, J.J., CLARK, W.R., AND ANDREWS, R.D. 1992. Factors associated with raccoon mortality in Iowa. *J. Wildl. Manag.* 56:693-699.
- HERMAN, T.B., POWER, T.D., AND EATON, B.R. 1994. Status of

- Blanding's turtle, *Emydoidea blandingii*, in Nova Scotia, Canada. *Can. Field-Nat.* 109:182-191.
- HOLECHEK, J.L., VALDEZ, R., SCHEMNITZ, S.D., PIEPER, R.D., AND DAVIS, C.A. 1982. Manipulation of grazing to improve or maintain wildlife habitat. *Wildl. Soc. Bull.* 10:204-210.
- JOHNSON, C.E. 1925. The muskrat in New York: its natural history and economics. *Roosevelt Wildlife Bull.* 3:205-320.
- KAUFMANN, J.H. 1986. Stomping for earthworms by wood turtles, *Clemmys insculpta*: a newly discovered foraging technique. *Copeia* 1986:1001-1004.
- KAUFMANN, J.H. 1992a. Habitat use by wood turtles in central Pennsylvania. *J. Herpetol.* 26:315-321.
- KAUFMANN, J.H. 1992b. The social behavior of wood turtles, *Clemmys insculpta*, in central Pennsylvania. *Herpetological Monogr.* 6:1-25.
- KAUFMANN, J.H. 1995. Home ranges and movements of wood turtles, *Clemmys insculpta*, in central Pennsylvania. *Copeia* 1995:22-27.
- KAUFMANN, J.H., HARDING, J.H., AND BREWSTER, K.N. 1989. Worm stomping by wood turtles revisited. *Bull. Chi. Herp. Soc.* 24: 125-126.
- KENNETT, R. 1996. Growth models for two species of freshwater turtle, *Chelodina rugosa* and *Elseya dentata*, from the wet-dry tropics of northern Australia. *Herpetologica* 52:383-395.
- LAGLER, K.F. 1943. Food habits and economic relations of the turtles of Michigan with special reference to fish management. *Amer. Midl. Nat.* 29:257-312.
- LAYFIELD, J.A., GALBRAITH, D.A., AND BROOKS, R.J. 1988. A simple method to mark hatchling turtles. *Herp. Review* 19:78-79.
- LINDEMAN, P.V. 1996. Comparative life history of painted turtles (*Chrysemys picta*) in two habitats in the inland Pacific northwest. *Copeia* 1996:114-130.
- LITZGUS, J.D., AND BROOKS, R.J. 1996. Status report on the wood turtle, *Clemmys insculpta*, in Canada. COSEWIC status report, 76 pp.
- LOVICH, J.E., ERNST, C.H., AND MCBREEN, J.F. 1990. Growth, maturity, and sexual size dimorphism in the wood turtle, *Clemmys insculpta*. *Can. J. Zool.* 68:672-677.
- MACCULLOCH, R.D., AND SECOY, D.M. 1983. Demography, growth, and food of western painted turtles, *Chrysemys picta bellii* (Gray), from southern Saskatchewan. *Can. J. Zool.* 61:1499-1509.
- MEEKS, R.L., AND ULTSCH, G.R. 1990. Overwintering behavior of snapping turtles. *Copeia* 1990:880-884.
- MCLEOD, D. 1994. Observations of growth after injury in the slider turtle, *Trachemys scripta elegans*. *Herp. Review* 25:116-117.
- MOLL, D. 1976. Environmental influence on growth rate in the Ouachita map turtle, *Graptemys pseudogeographica ouachitensis*. *Herpetologica* 32:439-443.
- MOSER, E.B., SAXTON, A.M., AND PEZESHKI, S.R. 1990. Repeated measures analysis of variance: application to tree research. *Can. J. For. Res.* 20:524-535.
- ODUM, E.P. 1994. Conservation of biodiversity. In: Majumdar, S.K., Brenner, F.J., Lovich, J.E., Schalles, J.F., and Miller, E.W. (Eds.). *Biological Diversity: Problems and Challenges*, pp. 18-25.
- OWEN, R.B., JR., AND GALBRAITH, W.J. 1989. Earthworm biomass in relation to forest types, soil, and land use: implications for woodcock management. *Wildl. Soc. Bull.* 17:130-136.
- PAPPAS, M.J., AND BRECKE, B.J. 1992. Habitat selection of juvenile Blanding's turtles, *Emydoidea blandingii*. *J. Herpetol.* 26:233-234.
- PARMENTER, R.R. 1980. Effects of food availability and water temperature on the feeding ecology of pond sliders (*Pseudemys s. scripta*). *Copeia* 1980:503-514.
- PARMENTER, R.R. 1981. Digestive turnover rates in freshwater turtles: the influence of temperature and body size. *Comp. Biochem. Physiol.* 70:235-238.
- PEARSON, H.A. 1968. Thinning, clearcutting, and reseeded affect deer and elk use of ponderosa pine forests in Arizona. U.S. Dept. Agriculture, Forest Service, Research Note RM-119, 4 pp.
- PLUMMER, M.V. 1979. Collecting and marking. In: Harless, M., and Morlock, H. (Eds.). *Turtles: Perspectives and Research*. John Wiley and Sons, Inc., New York, pp. 45-60.
- POTVIN, C., LECHOWICZ, M.J., AND TARDIF, S. 1990. The statistical analysis of ecophysiological response curves obtained from experiments involving repeated measures. *Ecology* 71:1389-1400.
- POWELL, C.B. 1967. Female sexual cycles of *Chrysemys picta* and *Clemmys insculpta* in Nova Scotia. *Can. Field-Naturalist* 81:134-140.
- RIVEST, P., AND BERGERON, J.M. 1981. Density, food habits, and economic importance of raccoons (*Procyon lotor*) in Québec agrosystem. *Can. J. Zool.* 59:1755-1762.
- ROSS, D.A., BREWSTER, K.N., ANDERSON, R.K., RATNER, N., AND BREWSTER, C.M. 1991. Aspects of the ecology of wood turtles, *Clemmys insculpta*, in Wisconsin. *Can. Field-Nat.* 105:363-367.
- ST. CLAIR, R., GREGORY, P.T., MACARTNEY, J.M. 1994. How do sexual differences in growth and maturation interact to determine size in northern and southern painted turtles? *Can. J. Zool.* 72:1436-1443.
- SAUMURE, R.A. 1992. *Clemmys insculpta* (Wood Turtle). *Size. Herp. Review* 23:116.
- SAUNDERS, D.A., HOBBS, R.J., AND MARGULES, C.R. 1991. Biological consequences of ecosystem fragmentation: a review. *Conservation Biol.* 5:18-32.
- SHIROSE, L., BISHOP, C., AND GENDRON, A. 1996. Amphibians and reptiles in Great Lakes wetlands: threats and conservation. *Environment Canada: Great Lakes Fact Sheet En 40-222/4-1996E*, 12 pp.
- SIETMAN, B.E., FOTHERGILL, W.B., AND FINCK, E.J. 1994. Effects of haying and old-field succession on small mammals in tallgrass prairie. *Amer. Midl. Nat.* 131:1-8.
- STATISTICAL ANALYSIS SYSTEMS INSTITUTE, INC. 1985. SAS user's guide. Version 6 ed. SAS Institute Inc., Cary, N.C.
- STONE, P.A., HAUGE, J.B., SCOTT, A.F., GUYER, C., AND DOBIE, J.L. 1993. Temporal changes in two turtle assemblages. *J. Herpetol.* 27:13-23.
- TEMPLE, S.A. 1987. Predation on turtle nests increases near ecological edges. *Copeia* 1987:250-252.
- THOMPSON, F.R., AND FRITZELL, E.K. 1990. Bird densities and diversity in clearcut and mature oak-hickory forest. U.S. Dept. Agriculture, Forest Service, Research Paper NC-293, 7 pp.
- THORNHILL, G.M. 1982. Comparative reproduction of the turtle, *Chrysemys scripta elegans*, in heated and natural lakes. *J. Herpetol.* 16:347-353.
- TUCKER, J.K., MAHER, R.J., AND THEILING, C.H. 1995. Year-to-year variation in growth in the red-eared turtle, *Trachemys scripta elegans*. *Herpetologica* 51:354-358.
- ULTSCH, G.R., HANLEY, R.W., AND BAUMAN, T.R. 1985. Responses to anoxia during simulated hibernation in northern and southern painted turtles. *Ecology* 66:388-395.
- WALLMO, O.C. 1969. Response of deer to alternate-strip clearcutting of lodgepole pine and spruce-fir timber in Colorado. U.S. Dept. Agriculture, Forest Service, Research Note RM-141, 4 pp.
- WRIGHT, A.H. 1918. Notes on *Clemmys*. *Proc. Biol. Soc. Wash.* 31: 51-58.
- YAHNER, R.H. 1996. Forest fragmentation, artificial nest studies, and predator abundance. *Conservation Biol.* 10:672-673.
- ZEILLER, D. 1969. Turtle sanctuary. *Int. Turt. Tort. Soc. J.* 3:6-9, 30-31.
- ZUG, G.R. 1991. Age determination in turtles. *SSAR Herp. Circular* 20:1-28.
- ZUG, G.R. 1993. *Herpetology. An introductory biology of amphibians and reptiles*. Academic Press, Inc., New York, pp. 123-146.

Received: 25 August 1997

Reviewed: 21 April 1998

Revised and Accepted: 10 June 1998