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Demography and Ecology of an Ornate Box Turtle (*Terrapene ornata*) Population in South-Central Wisconsin

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We studied a population of ornate box turtles (*Terrapene ornata*) during 1977–87 in south-central Wisconsin, and intensively monitored ($\geq$20 relocations) 53 radio-marked individuals during 1986–87. Egg laying occurred mainly in June; eggs in four nests hatched after 79–84 d. Twenty-one of 37 adult females (57%) laid during 1986–87, mean clutch size was 3.5, and hatchlings per adult female averaged 0.7. Mean annual survival of marked adults (age $\geq$10 yr) was 0.81 during 1977–87 (Jolly-Seber analysis). We estimated a total of 54–56 adults on four occupied sites within our 8 km^2 study area. Adult densities at these sites ranged from 2.9–5.0/ha. Most (84%) turtles entered hibernation during Sept.; all emerged during April. Known periods of hibernation averaged 216 d (n = 9); burrow depths were between 0.5–1.8 m (n = 26). Mean home range size of adults was 8.7 ha (n = 47) annually, but varied greatly among individuals and did not differ significantly with sex or year. Home ranges of juveniles and subadults were much smaller. Areas of remnant prairie on deep sandy soil were frequented disproportionately, whereas agricultural cropland was clearly avoided. We compared demographic parameters of this and other turtle populations, and explored requisites for numerical stability with observed and hypothetical survival and recruitment rates. Our study area population will likely continue to decline because the average rate of adult survival (0.81 annually) is well below that (about 0.95) which would, with normal recruitment, stabilize numbers. Results of this study are discussed from a management perspective.

THE ornate box turtle (*Terrapene ornata*) is widely distributed throughout the southern half of the Grassland Biome, part of the Desert Biome, and the Prairie-Forest Ecotone of the Temperate Deciduous Forest Biome. On the northern extreme of its range are isolated populations in South Dakota and south-central Wisconsin (Legler, 1960). *Terrapene ornata* displays remarkable versatility in occupying microhabitats which differ greatly in food supply, temperature, moisture and soil type (Legler, 1960).

A detailed life-history study of the ornate box turtle was conducted in Kansas during 1953–57 by Legler (1960). Blair (1976) supplemented Legler's work with a 5 yr study of *T. ornata* in Texas. Little is known, however, about the ecology and population dynamics of *T. ornata* in northern sections of its range.

Small, disjunct populations of ornate box tur-

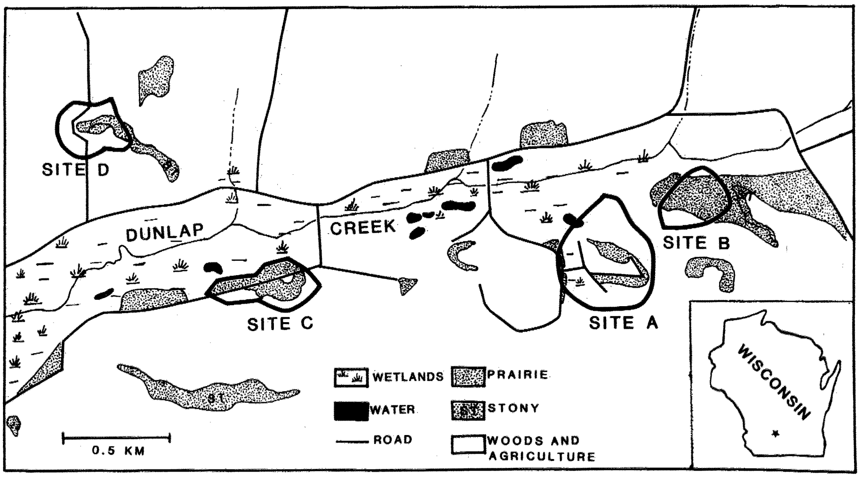

Fig. 1. The study area in Dunlap Hollow, northwestern Dane County, Wisconsin. Location shown on inset map of the state. Sites A through D were most heavily frequented by ornate box turtles (*Terrapene ornata*). These population centers are designated in text as core areas.

tles exist along the Wisconsin River flood plain in six counties in south-central Wisconsin (Vogt, 1981). These populations are primarily associated with remnants of native prairie, and their declining distribution and abundance have prompted an endangered listing in Wisconsin (Wisconsin Natural Resource Laws 1985–86; Chapter NR 27, Wisconsin Administrative Rules). Information on survival, dispersal, reproduction, and critical habitat components is needed for effective management.

During 1977–85 we marked and released box turtles captured on about 100 ha in western Dane County, Wisconsin. Our encounters with turtles were largely incidental to other activities. The objective of this part-time study was to determine numbers, movements, survival rates and other aspects of box turtle life history and ecology. In mid-summer 1985 we radio-tagged and monitored movements of five adults. The study was greatly intensified during 1986–87 through additional radio tagging, an enlarged study area, and full-time field work. This paper summarizes the population's demography and ecology, and discusses implications for its management.

Study Area

Our study was conducted on a 2 by 4 km area in Dunlap Hollow, south-central Wisconsin, at the junction of Roxberry, Berry, and Mazomanie townships in Dane County (Fig. 1). The area is hilly, well drained and covered by a mixture of woodland (59%), wetland (12%), remnant prairie (6%) and cropland (22%). Roads comprise the remaining 1%.

Soils range from silt loams underlying wetlands to loamy sands, sandy loams and fine sands on drier locations. Shallow rocky soils and frequent outcrops of sandstone bedrock occur on some hillsides.

The climate is continental: summers tend to be warm with recurrent periods of high humidity; minimum temperatures in winter often drop to −20 C during surges of arctic air. Mean July and Jan. temperatures are 21.9 C and −8.6 C, respectively. Annual precipitation averages 78.5 cm. Snow depths of 2.5 cm or greater are present during 60% of the time from 10 Dec.–25 Feb. in an average winter. Mean frost penetration is 64–76 cm, and growing seasons average 175 d (National Oceanic and Atmospheric Administration [N.O.A.A.], Local Climatological Data, 1986).

Box turtles were found within the study area on four sites, 0.5--3.1 km apart (Fig. 1). Some individuals moved among the three closest sites; it was on site A that most turtles were marked during 1977–85.

Methods

Measurements and marking.—Turtles were initially found through intensive searching or fortuitous encounters. Upon first capture, sex, weight, and plastron length and width were recorded. Age was estimated by counting annual rings on the carapace (Legler, 1960). We designated four age classes: hatchlings (≤1 yr), juveniles (1–<7 yr), subadults (7–<10 yr), and adults (≥10 yr).

All individuals were permanently marked by notching marginal scutes on the carapace, each notch or combination of notches yielding a unique code number (Schwartz and Schwartz, 1974). As a temporary but more conspicuous marking, we used red nail polish to paint code numbers on the carapace of adults.

Radio transmitters on frequencies 150.7–151.8 MHz, weighing 10–13 g, and with ranges up to approx. 0.5 km were attached to 42 different adult and nine different subadult and juvenile turtles during 1986–87. A stainless-steel barrel swivel was first attached to a loop on the transmitter, then clipped to the rear of the carapace through a small drilled hole. The transmitters were simply dragged along. Transmitters were also glued with rubber silicon sealant to the carapace of several adults and subadults. Two-gram transmitters with ranges of approx. 50 m were glued to the carapace of juveniles. A receiver (Merlin-12, Custom Electronics, Carbondale, Illinois) and H-shaped (150–154 MHz) antenna (Telonics, Inc., Mesa, Arizona) were used to relocate radio-marked turtles. The sequence of individual relocations was largely random. Date, hour, location, sky condition, ambient air temperature, vegetation type and turtle activity were recorded.

Rings from pull-tab aluminum cans were glued to the carapace of hatchlings in spring 1987. These rings were painted black, numbered, and bent slightly to conform to carapace shape. The hatchlings were subsequently relocated by intensive searching with a Fisher metal detector. Hatchlings were also marked by notching outer scutes.

Nesting.—We x-rayed females (Gibbons and Greene, 1979) in late May to determine if they were gravid, and if so, size of the clutch. Radio-tagged females were relocated and weighed at least twice daily during late May–June 1986 and 1987, to determine nest locations. Because each egg weighs approx. 10 g (Legler, 1960), and there were several per clutch, abrupt weight reductions of >30 g indicated females had laid. Hardware cloth and welded-wire fencing were used to protect five of nine nests from predators in 1986–87.

In 1987, nests were excavated at least twice during the summer-fall incubation period. The first excavation (May–June) was to determine nest depth and verify clutch size, the second (Sept.) to determine hatching success. Excavation began with a teaspoon, then continued with a stiff paint brush when evidence of an egg or egg-shell fragment was uncovered.

In 1987 we fortuitously determined incubation periods by excavating two nests and finding hatchlings pipping. A third clutch was excavated, placed in a wire-mesh basket (8 × 5 × 5 cm), and reburied at nest depth. Thermocouple wires were anchored to the basket, and soil temperatures recorded with a thermocouple reader three times weekly, near noon. The basket was brought to the surface twice to examine the eggs for signs of hatching. After this nest was destroyed by a predator, another was excavated and its noon-day temperatures similarly monitored.

Hibernation.—Hibernating radio-tagged turtles were recovered from burrows by removing soil, a few shovels at a time, while continually monitoring radio-signal strength. We recorded depth of hibernation, soil consistency and temperature, body weight, and cloacal temperature.

Turtles were replaced in their burrows; eight were reburied with paired thermocouple wires in 1986 to record burrow temperatures monthly overwinter. Five pairs of thermocouple wires were placed in one hibernation burrow at depths of 0.1, 0.2, 0.4, 0.6, and 0.85 m to monitor frost depth.

Wire-mesh enclosures were built above hibernating turtles that were not excavated. This assured their recapture in spring so inactive transmitters could be removed or replaced.

Vegetation classification.—We classified plant communities on the study area as prairie (native and disturbed), woodland, wetland and agricultural (Fig. 1). Prairie consisted of remnants of native prairie, and areas of former prairie that had been converted to pasture and lawn. Ground cover was often incomplete on native prairie remnants, and soil depths ranged from >1 m on lower ground to ≤10 cm on ridges and hilltops. Plant species typically included prickly pear (*Opuntia humifusa*), spiderwort (*Tradescantia ohiensis*), panic grass (*Panicum perlongum*), gramma grass (*Bouteloua curtipendula* and *B. hirsuta*), and bluestem (*Andropogon gerardi* and *A. scoparius*). Ground cover in pastures and lawns was complete, with little or no exposed soil. Grass height varied from 5–20 cm depending on grazing intensity or mowing.

Woodland was either deciduous forest or 20–

30 yr old pine plantation. The former was predominantly a mixture of red and white oak (*Quercus borealis* and *Q. alba*), hickory (*Carya ovata*), black cherry (*Prunus serotina*) and white birch (*Betula papyrifera*), with a brushy understory of prickly ash (*Zanthoxyllum americanum*), blackberry (*Rubus* sp.) and gooseberry (*Ribes* spp.). Red, white and scotch pines (*Pinus resinosa*, *P. strobus*, and *P. sylvestris*) comprised the plantations; all were devoid of understory vegetation.

Wetlands had standing water during all or part of the summer. Most were sedge (*Carex* spp.) meadows with swamp milkweed (*Asclepias incarnata*), Joe-pie weed (*Eupatorium maculatum*), meadow aster (*Aster lucidulus*) and other forbs. Agricultural areas were planted with annual or perennial crops, primarily corn (*Zea maize*), oats (*Avena sativa*) and alfalfa (*Medicago sativa*).

Density, available habitat and home range.—To determine densities on our four study sites, we estimated the area frequented by turtles at each by plotting all observations (radio locations and accidental encounters), and thereby obtained a site-specific range for each subpopulation. We used a computer program that generated geographic isopleths encompassing given percentages of all known locations (Dixon and Chapman, 1980). We used the 50% isopleth to estimate the core area occupied at each site, and calculated density as turtle numbers divided by core area (ha). Several turtles moved between two sites and were arbitrarily assigned to the one most commonly frequented.

Availability of major plant communities was also determined by obtaining the site-specific range of each subpopulation, but we used the 100% isopleth of distribution rather than the 50% isopleth. Percentages of prairie, woodland, wetland, and agricultural cropland within the 100% isopleth at each study site were considered to reflect relative availability of these major plant communities.

Home ranges were calculated (Dixon and Chapman, 1980) for individuals for which we had at least 20 locations annually during 1986–87. All locations were verified by visual contact.

Experimental releases.—We conducted two experimental releases to determine if adult box turtles translocated to typical habitat, currently without box turtles, would settle or disperse. In the first release, five radio-tagged turtles (two males, three females) were translocated 30 km from our Dunlap Hollow study area to the Aldo Leopold Memorial Reserve on 18 July 1986. All were released at a single site in mixed habitat resembling our study area, then monitored daily for 3 wk and every third day thereafter.

Turtles from the Valentine National Wildlife Refuge in Cherry County, Nebraska, were held in an outdoor enclosure on our study area for 16 d. On 17 Aug. 1987, three males and three females were radio-tagged and released into habitat formerly containing box turtles approximately 4 km west of the enclosure. The area had been surveyed in 1985, and again immediately prior to release, without finding turtles or their burrows, but an unmarked subadult was encountered on 27 Aug. 1987. Locations of the Nebraska turtles were determined daily for 2 wk and every third day thereafter.

RESULTS

Reproduction.—We observed instances of copulation among turtles from 28 May–6 Sept., during 1978–87: 10 copulating pairs were seen in May–June, three in July, and 13 in Aug.–Sept. Nest excavation and egg-laying occurred during 10–26 June in 1986, and 29 May–23 June in 1987. Nine (50%) of the 18 radio-tagged females were known to have produced a clutch in 1986, and 12 (63%) of 19 in 1987 (Table 1). Twelve of the 16 nests located in 1986 and 1987 were on remnants of native prairie; the remaining four were on disturbed prairie. All nests were in loose sandy soil, and all eggs were laid within the period from 2 h before sunset to 2 h after sunrise. Nests were flask-shaped; the neck of each was 5–8 cm deep, and mean nest-cavity depth was 13 cm ($n = 14$).

Clutch size in 1986 averaged 4.1 ($n = 8$)—based on three females x-rayed before laying in June, and five nests of other females examined during 4–15 Nov. Clutch sizes for nests first examined in Nov. were determined by counting unhatched eggs, egg-shell fragments, or hatchlings.

Mean clutch size was 2.8 ($n = 8$) in 1987. Fifteen radio-tagged females were each x-rayed twice in 1987; eight were gravid. Nests of five of these eight gravid females were examined and their clutch sizes verified. Nests of three additional females were located without radiotelemetry. Gibbons and Greene (1979) reported the x-ray technique as 100% accurate in determining clutch size; however, one of our females,

TABLE 1. REPRODUCTIVE PARAMETERS OF ADULT FEMALE BOX TURTLES, DUNLAP HOLLOW, WISCONSIN.

	Adult females		Nests		Eggs		Natality	
Year	Number monitored	% Laying eggs	Number monitored	% With hatched eggs	Number monitored in nests with hatched eggs	% Hatched	Hatchlings/ laying adult female[a]	Hatchlings/adult female[b]
1986	18	50	5	100	19	58	2.4	1.2
1987	19	63	8	50	26	42	0.7	0.4
Totals and weighted means	37	57	13	69	45	49	1.2	0.7

[a] (Proportion of laying adult females producing hatched eggs) (mean clutch size) (proportion of eggs hatching): e.g., for 1986, (1.0) (4.1) (0.58) = 2.4.

[b] (Proportion of adult females nesting) (proportion producing hatched eggs) (mean clutch size) (proportion of eggs hatching): e.g., for 1986, (0.50) (1.0) (4.1) (0.58) = 1.2.

shown as nongravid by x-ray, laid at least one egg 3 wk later.

Of the nine females monitored in both 1986 and 1987, four laid a clutch each year, three laid in 1 of the 2 yr, and two did not lay. Two females producing the largest clutches (seven and five eggs) in 1986 did not lay in 1987.

Mean incubation period for three nests in the wild was 80 d, (range 79–81 d) in 1987. A clutch of seven eggs was taken to the laboratory on 20 Aug. 1986. These eggs had been incubated 55 d in the wild, and subsequently hatched after 29 d of further incubation at 29 C in the laboratory (total incubation of 84 d). One or more eggs hatched in nine of 13 nests (69%) monitored in 1986–87 (Table 1).

In 1986, eight nest sites were checked daily for 4.5 mo for signs of predation and hatchling emergence. None of the nests were disturbed by predators. All nests were excavated during 4–15 Nov. Two had hatchlings at nest depth (13–15 cm) or below. At the first, one hatchling was still in the nest cavity and another was 12 cm beneath. At the second, both hatchlings had dug to bedrock, 18 cm below the soil surface. Hatchlings from two additional nests containing egg-shell fragments had probably burrowed below the nest cavity, but could not be located. Hatchlings may have emerged above-ground in fall 1986 from the one nest where bedrock was at approx. 20 cm. The remaining three sites had no eggs or egg-shell fragments and their fates were unknown.

In 1987, two of the eight clutches monitored were destroyed by prairie moles (*Scalopus aquaticus machrinus*) after the eggs had incubated approx. 69 d. A third clutch, protected by a wire-mesh basket, was dug up by an unknown predator that destroyed three of five eggs. The area around a fourth nest (protected by welded wire fencing) was disturbed, but the eggs were untouched. On 24 Sept. we examined the latter two nests and four other intact nests. Hatchlings were present at three of these nest sites. At one nest, hatchlings were 17, 22, and 27 cm below the surface—the latter was on bedrock; a fourth hatchling was not located. At a second nest, the single hatchling was 19 cm below the surface; a third nest site had hatchlings at 19, 30, and 34 cm. Above-ground emergence of two hatchlings from a fourth nest occurred in fall. The two other nests contained complete unhatched clutches.

Midday incubation temperatures during June, July and Aug. 1987 averaged 22.3 C (n = 3), 26.3 C (n = 11), 26.4 C (n = 3) at a depth of 10–12 cm in one nest, and 27.6 C (n = 5) during Aug. in another. These nest temperatures did not differ (t = 1.02, $P = 0.32$) from air temperatures recorded concomitantly at ground level.

Mortality.—Automobiles (four deaths), farm machinery (two deaths) and lawn mowers (one death) were the only known causes of adult mortality in the marked population during 1977–87. The mean annual survival rate of adults at site A, as estimated by a Jolly-Seber analysis (Jolly, 1965; Seber, 1965), was 0.81 for both males and females, but ranged from 0.51–1.00 among years (Table 2). May–Sept. survival of our radio-tagged adults was 0.96 (one death in 4126 transmitter days) during 1986, and 0.91 (two deaths in 3315 transmitter days) during 1987. None died during hibernation over winters 1985–86 (n = 5) and 1986–87 (n = 26). There were no known deaths among the 11 juveniles and subadults marked during 1977–

TABLE 2. SURVIVAL RATES AND NUMBERS OF ADULT ORNATE BOX TURTLES ON 5.4 HA, DUNLAP HOLLOW, WISCONSIN.

Year May–April	Annual survival rate ± SE		Estimated population size ± SE	
	Female	Male	From Jolly-Seber[a] analysis	From intensive searching
1977–78	0.71 ± 0.14	0.70 ± 0.11		
1978–79	1.00 ± 0.15	1.00 ± 0.27	25 ± 2	
1979–80	0.80 ± 0.08	0.69 ± 0.14	50 ± 4	
1980–81	1.00 ± 0.15	0.90 ± 0.08	32 ± 1	
1981–82	0.75 ± 0.10	1.00 ± 0.15	40 ± 3	
1982–83	1.00 ± 0.24	0.87 ± 0.23	40 ± 2	
1983–84	0.54 ± 0.14	0.77 ± 0.40	45 ± 6	
1984–85	0.81 ± 0.13	0.84 ± 0.14	27 ± 2	
1985–86	0.73 ± 0.05	0.55 ± 0.04	35 ± 1	
1986–87			25 ± 0.4	27
1987–88				25
Means	0.816	0.813	36	26
95% Confidence limit	(0.69–0.94)	(0.70–0.93)		

[a] Jolly (1965), Seber (1965).

87, but two marked in 1982 and 1985 were never reobserved.

We hatched a clutch of eggs in the laboratory, held the hatchlings overwinter, and on 27 March 1987 returned them to their original nest cavity. We excavated this site on 24 April: three hatchlings were dead in the nest, two were alive approx. 2 cm below the soil surface, another was alive 4 m from the nest site, and one hatchling was never recovered. The three known survivors were relocated throughout summer. One was last seen on 19 July, and the others on 19 Sept.

Two hatchlings from a clutch laid on 12 June 1986 emerged on 28 April and 1 May 1987 through the same hole. They weighed 6.4 and 7.4 g, and yolk sacs were not fully absorbed. The first to emerge was lost (we believe to a predator) within an hour; the second was last seen on 28 May. Two dead hatchlings were found in the nest. Overwinter temperatures in this nest ranged from −8.1 C to 11.8 C, being lowest in Jan.

Four other nests thought to contain hatchlings in fall 1986 were excavated on 9 May 1987. Two dead hatchlings were found in one nest; none were found in three others, but crescent-shaped holes appearing at two nest sites on 2 June and 13 June, indicated hatchling emergence. Two of six young that hatched in the wild during fall 1986 were known to have survived overwinter. First-year survival of 14 young hatched in 1985–86 (including seven experimentally released as hatchlings) was just 21%.

Adult numbers and densities.—The number of marked adult turtles observed on site A (Fig. 1) was 27 in 1986 and 25 in 1987. The core area occupied (50% isopleth) was 5.4 ha; adult densities were thus 5.0 and 4.6/ha, respectively. We believe that few if any adults were overlooked during our intensive field work. The total of 27 encountered in 1986, for example, compares with a Jolly-Seber population estimate of 25 individuals (Table 2). The number of adult turtles at sites B–D (Fig. 1) during both 1986 and 1987 was estimated to be 15, 8, and 6; and densities were 4.5, 3.4, and 2.9/ha. The total adult population of 54–56 on all four sites is likely close to that on the entire 8 km² study area. None of the radio monitored turtles dispersed from our study sites during 1985–87.

Sex ratio.—The observed sex ratio of adults within our study-area population during 1978–88 was 39 males : 61 females (n = 102 individuals). We believe this ratio is representative because the Jolly-Seber estimates of population size were similar to the total number of individuals seen by us during 1986–87 (see Adult numbers and densities). Although adult males and females had similar survival rates (Table 2), this may not have been the case with juveniles and subadults.

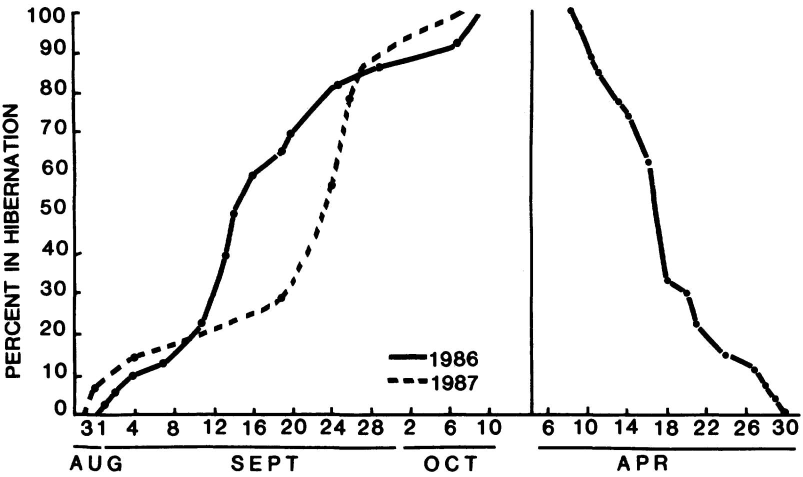

Fig. 2. Percentage of radio-tagged box turtles in hibernation during 31 Aug.–9 Oct. (1986 and 1987), and 9–30 April (1987).

Hibernation.—Turtles entered hibernation during the 39 d period 1 Sept.–9 Oct. in 1986, and the 38 d period 31 Aug.–7 Oct. in 1987. By 14 Sept. 1986, half (14) of the 29 radio-tagged individuals had hibernated; and by 16 April 1987, half had emerged (Fig. 2). All emerged during the 22 d between 9–30 April.

We knew the exact dates that nine turtles entered and emerged from hibernation; for 11 others, we knew one date exactly and the second within ±5 d; in one other case we knew neither date more precisely than ±10 d. The mean known hibernation period was 216 d (n = 9); that estimated with less precision was 209 d (n = 12).

Twelve of the 29 radio-tagged adult turtles followed to hibernation sites in 1986 were excavated during 25 Oct.–5 Nov. Differences in mean hibernation depths of males (0.7 m, n = 6) and females (1.1 m, n = 6) were statistically significant (t = 2.29, $P = 0.05$). All hibernation burrows were in loose sandy soil: nine within woodland and 20 on native prairie.

Soil temperatures in fall hibernacula of 12 turtles were recorded eight times between 22 Nov. and 6 April 1986–87. Burrow depth ranged from 0.5–1.8 m. Mean temperatures differed significantly (F = 2.61, $P < 0.01$) among sites. We classified shading of hibernation burrows as complete, partial and none, and examined effects of shading and depth on burrow temperatures overwinter. During late Nov.–late Feb., burrow temperatures declined from an average of 5.0 C (range, 3.6–7.5 C) to 1.2 C (range, −0.3 to 2.7), with deeper burrows tending to have higher temperatures (r = 0.70; df = 10, $P = 0.01$). There was no significant effect of shading during this period. From late Feb.–early April, mean burrow temperature rose to 3.9 C (range, 2.2–5.0 C). Burrow temperatures by early April were lowest in complete shade, intermediate in partial shade and highest without shade (F = 3.80; $P = 0.07$). The impacts of shading and depth thus differ over time—depth primarily determining temperature overwinter, and degree of shading determining how rapidly burrow temperature rises in spring. Temperatures in 11 of the 12 burrows remained above freezing over the winter, but in one burrow dropped to −0.3 C during Jan. All 12 turtles emerged in spring.

Fourteen turtles were tracked to hibernation sites in 1987, then excavated 13–45 d later. The mean depth (0.51 m) of four turtles after 13–21 d in hibernation did not differ (t = 0.94, $P = 0.38$) from that of five others (0.66 m) after 37–45 d. Eight of the 14 turtles hibernated within 1 m of their 1986 hibernation sites; five of these turtles were within 0.5 m of each other. Two sites were in pine plantations and 12 were on native prairie. The known time between spring emergence and fall hibernation averaged 155 d for five radio-tagged turtles, and was approx. 161 d for six others.

Home range.—Home range size varied greatly among adults, ranging from 0.2–58.1 ha. A square-root transformation was used to nor-

TABLE 3. PERCENT USE (WITH 95% CONFIDENCE LIMITS) OF MAJOR PLANT COMMUNITIES BY RADIO-TAGGED ADULT BOX TURTLES AT STUDY SITE A.[a]

Year and site size	Plant community	Percentage of site covered by plant community	Prenesting and nesting periods (April–June)			Mid-summer (July)			Late-summer and fall (Aug.–Sept.)	
			Nesting female	Non-nesting female	Male	Postnesting female	Non-nesting female	Male	Female	Male
1986	Woodland	53	17 ± 6	31 ± 5	19 ± 11	33 ± 15	34 ± 12	47 ± 12	7 ± 5	35 ± 9
(448 ha)	Agricultural	24	0	0	0	0	0	0	0	0
	Wetland	13	12 ± 5	13 ± 5	1 ± 3	48 ± 16	33 ± 12	7 ± 6	11 ± 6	4 ± 4
	Prairie	9	71 ± 8	56 ± 7	80 ± 11	19 ± 13	33 ± 12	48 ± 12	82 ± 8	61 ± 9
	Total locations		199	307	70	54	97	105	150	156
1987	Woodland	63	16 ± 8	21 ± 8	37 ± 10	29 ± 19	51 ± 18	33 ± 11	25 ± 8	18 ± 8
(113 ha)	Agricultural	3	0	0	0	0	0	0	0	0
	Wetland	24	2 ± 3	31 ± 10	19 ± 8	0	31 ± 17	15 ± 9	2 ± 3	7 ± 5
	Prairie	10	82 ± 8	48 ± 10	44 ± 10	71 ± 19	18 ± 14	52 ± 12	73 ± 8	75 ± 9
	Total locations		122	136	130	31	45	41	168	138

[a] See text for calculation of site size and description of plant communities.

malize distribution of home range sizes and to stabilize variance before comparing means. Male home ranges averaged 8.2 ha (n = 13) in 1986 and 3.4 ha (n = 5) in 1987; whereas female home ranges averaged 12.0 ha (n = 17) and 6.9 ha (n = 12). These means did not differ significantly either between years (t = 1.01, $P = 0.32$ for females; t = 1.16, $P = 0.27$ for males) or between sexes (t = 0.76, $P = 0.46$ in 1986; t = 1.68, $P = 0.12$ in 1987). Mean home range size of five individuals, age 3–7 yr in 1987, was just 1.5 ha, significantly less than that of adult females (t = 3.41, $P = 0.006$), and adult males (t = 2.49, $P = 0.04$).

Three hatchlings from a single nest were each relocated at least 40 times throughout summer 1987. All locations were within a 16 m^2 area that included the nest site. These hatchlings were often near or under rocks in dense vegetative cover.

Habitat use and availability.—At site A, adult turtles avoided agricultural cropland in 1986–87 (Table 3). The frequency with which adults used prairie was higher at all times than was its frequency of occurrence. Nesting females were present on prairie areas to a greater degree than non-nesting females during prenesting and nesting periods. During mid-summer, reduced use of prairie coincided with increased use of woodland and wetland (Table 3).

Juveniles and subadult turtles at site A also tended to use prairie areas disproportionately, and were never located in agricultural cropland or wetlands in 1987 (Table 4). Subadults used woodland extensively but juveniles did not.

At sites B–D adult turtles also frequented prairie areas at a disproportionately high rate and avoided agricultural cropland. Unlike site A, however, there was no tendency for increased use of woodland and wetland during mid-summer (Table 5).

Experimental releases.—Three of the five radio-tagged adults (two males, three females) released by us at the Aldo Leopold Memorial Reserve on 18 July 1986 were returned to our Dunlap Hollow study area on 23 Aug. after we lost radio contact with one female and another had died. Home ranges and number of fixes (in parentheses) during 19 July–22 Aug. were: 0.6 (21), 16.0 (23), 17.9 (23), 22.4 (23) and 24.7 ha (23). Home ranges during the month prior to translocation were calculated for three of these individuals. In two cases home range size

TABLE 4. PERCENT USE (WITH 95% CONFIDENCE LIMITS) OF MAJOR PLANT COMMUNITIES BY RADIO-TAGGED JUVENILE AND SUBADULT BOX TURTLES AT STUDY SITE A.[a]

Year and site size	Plant community	Percentage of site covered by plant community	Prenesting and nesting periods (April–June)		Mid-summer (July)		Late-summer and fall (Aug.–Sept.)	
			Juvenile	Subadult	Juvenile	Subadult	Juvenile	Subadult
1987 (113 ha)	Woodland	63	13 ± 12	82 ± 10	38 ± 25	76 ± 20	28 ± 19	32 ± 13
	Agriculture	3	0	0	0	0	0	0
	Wetland	24	0	0	0	0	0	0
	Prairie	10	87 ± 12	18 ± 10	62 ± 25	24 ± 20	72 ± 19	68 ± 13
	Total locations		46	83	21	25	29	69

[a] See text for calculation of site size and description of plant communities.

changed little—i.e., from 0.2–0.6 ha and from 31.6–24.7 ha. The other decreased from 58.1–17.9 ha. None of the five transplants seemed inclined to disperse.

Of the six Nebraska box turtles (three males, three females) released 4 km west of study site A (Fig. 1) on 17 Aug. 1987, contact with one female was lost immediately due to transmitter failure, and four of the remaining five individuals dispersed. We lost contact with two of these four after 3 wk, during which time they had moved 0.4 and 1.7 km from where released. Within 37 d of release the third turtle moved 4 km. The fourth traveled a straight-line distance of 3.7 km in 14 d to within 25 m of the outdoor enclosure where it had initially been held for 16 d. It remained there for 7 d, then continued northeast. This turtle was last located on 27 Sept. along State Highway 12; no signal was received thereafter. It was likely run over. The total straight-line distance traveled was 8.8 km. The fifth turtle remained at the release site, moving a maximum distance of 0.8 km. It entered hibernation on 27 Sept., 0.44 km from its point of release. It selected a south-facing slope with sandy loam friable to a depth of 1.5 m.

DISCUSSION

Comparative demography and ecology

Sex ratio.—The adult sex ratio within our study area population (39 males : 62 females) was similar to the 37:63 ratio (n = 162) reported by Legler (1960) for ornate box turtles in Kansas. Unbalanced adult sex ratios favoring females have been noted in other turtle populations but were attributed to sampling bias (Gibbons, 1970). However, when several methods were used to sample two map turtle (*Graptemys ouachitensis* and *G. pseudogeographica*) populations in Wisconsin, observed adult and hatchling sex ratios were 20:80 and 25:75, respectively (Vogt and Bull, 1982). On the other hand, during extensive mark-recapture studies of eastern box

TABLE 5. PERCENT USE (WITH 95% CONFIDENCE LIMITS) OF MAJOR PLANT COMMUNITIES BY RADIO-TAGGED BOX TURTLES AT SITES B–D[a] DURING APRIL–SEPT. 1986.

Total area	Plant community	Mean percentage of site covered by plant community	Prenesting and nesting periods (April–June)			Midsummer (July)		Late-summer and fall (Aug.–Sept.)	
			Nesting female	Non-nesting female	Male	Female	Male	Female	Male
378 ha	Woodland	47	13 ± 4	8 ± 7	16 ± 11	10 ± 6	3 ± 5	11 ± 6	9 ± 6
	Agriculture	26	0	6 ± 6	2 ± 4	5 ± 4	0	4 ± 4	0
	Wetland	16	5 ± 2	9 ± 7	16 ± 11	6 ± 5	1 ± 3	0	0
	Prairie	9	82 ± 4	76 ± 10	66 ± 14	79 ± 8	96 ± 6	85 ± 7	91 ± 6
	Total locations		468	109	77	168	71	169	127

[a] See text for calculation of site and description of plant communities.

turtles (*Terrapene carolina*), Stickel (1950) and Schwartz and Schwartz (1974) found equal adult sex ratios. Wilbur (1975) likewise reported a balanced sex ratio among adult painted turtles (*Chrysemys picta*).

Among chelonians, including *T. ornata*, sexual differentiation is commonly influenced by egg temperature during the middle third of incubation (Peau, 1974; Vogt and Bull, 1982; Packard et al., 1985). Thus, the sex ratio at hatching may vary with temperatures during this critical period as determined by annual differences in: 1) ambient temperatures; 2) dates of egg laying; and 3) location of nest sites (Vogt and Bull, 1982).

Reproduction.—During 1986–87, an average of 57% of adult females present on our study area produced a clutch of eggs. Legler (1960) examined ovaries of adult females in Kansas and concluded that ovulation occurred annually in all cases. He did not know, however, if all females actually nested each season. Among Blanding's turtles (*Emydoidea blandingi*), an estimated 23–48% of adult females nested in any 1 yr (Congdon et al., 1983); among painted turtles a maximum of 70% nested (Tinkle et al. 1981).

Mean clutch size was 3.5 in Wisconsin box turtles vs 4.7 in Kansas (Legler, 1960). We have no evidence that box turtles in Wisconsin produced two clutches within a single season. Legler (1960) reported that about one-third may do so in Kansas. Length of incubation is temperature dependent, and averaged 80 d for three clutches incubated naturally on our Wisconsin study area, but just 51 d for clutches from Nebraska incubated in a laboratory at 29 C (Packard et al., 1985).

Hibernation.—Depth of hibernation averaged 0.76 m (range, 0.47–1.78 m) in Wisconsin; the reported range in Kansas was 0.05–0.56 m (Legler, 1960). Our data suggest that turtles will burrow to 0.51–0.66 m upon first entering hibernation: average frost penetration in Wisconsin is 0.64–0.76 m. Legler (1960) stated that hibernating turtles will gradually deepen their burrows during the winter. Fifty-seven percent of the turtles monitored by us used the same hibernation site in 1987 as in 1986. This tendency was also noted in Kansas (Metcalf and Metcalf, 1979). The mean numbers of frost-free days annually at study sites in Wisconsin, Kansas and Texas (175, 180 and 270, respectively) reflected the mean number of days during which box turtles were not hibernating (155, 162 and 270) (N.O.A.A., 1986; Legler, 1960; Blair, 1976).

Mortality.—Known predators of adult box turtles are few. Legler (1960) reported only two instances of adult turtles found in coyote stomachs, (*Canis latrans*) and one case where the remains of 10 turtles (eight adult, two juvenile) were found outside a striped skunk (*Mephitis mephitis*) den. These turtles were presumably hibernating when discovered by the skunk. Neill (1948) reported that many *T. carolina* in Georgia die from exposure to cold prior to hibernation, or freeze to death following emergence in early spring. We found no evidence of such mortality among *T. ornata* in Wisconsin. The only known causes of adult mortality in our study were automobiles, farm machinery and lawn mowers. Automobiles were a major cause of adult mortality in Kansas (Legler, 1960; Metcalf and Metcalf, 1979) and Texas (Blair, 1976).

There are records of hatchlings consumed by: white necked ravens (*Corvus cryptoleucus*), crows (*C. brachyrhynchos*), copperheads (*Agkistrodon contortrix*), and raccoons (*Procyon lotor*) (Legler, 1960).

DEMOGRAPHIC PARAMETERS AND POPULATION TREND

There is a general consensus that distribution and abundance of box turtles in Wisconsin have declined markedly. Although no consistent downward trend occurred during 1978–87 on our most intensive study site (Table 2), interviews with long-time residents of Dunlap Hollow indicated that box turtles had become much less common over the past 10–30 yr. An aspect of turtle demography which concerned us was the apparent lack of recruitment to the adult cohort: during 1977–87 only four subadults (age 7–<10 yr) were encountered vs 102 adults (age ≥10 yr).

We explored probable long-term population trends through life-equation analyses (Table 6) that used demographic parameters from Dunlap Hollow (Tables 1–2). Our calculations were restricted to the female cohort; conclusions that follow should, however, apply equally well to both sexes.

Because we had good estimates of adult survival and reproductive rates, but little knowledge of juvenile and subadult survival, our ap-

TABLE 6. DEMOGRAPHIC PARAMETERS FOR HYPOTHETICAL STATIONARY BOX TURTLE POPULATIONS IN WHICH FEMALES FIRST REPRODUCE AT AGE 10 YR.

Demographic input						
Annual survival and reproductive rates			Demographic output in stationary population			
			Interval survival rates[e]			
Survival of adults (age ≥10 yr)	Survival of adults and subadults (age ≥7 yr)	Female hatchlings per adult female	Hatching to age 10 yr	Hatching to age 7 yr	Mean annual to age 10 or 7 yr	Percent subadults among individuals age ≥7 yr
0.81[a]		0.35[b]	0.54 (0.44)		0.94 (0.92)	
0.81		0.52[c]	0.37 (0.30)		0.90 (0.89)	
	0.81	0.52		0.69 (0.57)	0.95 (0.92)	47
	0.95[d]	0.52		0.112 (0.093)	0.73 (0.71)	14
	0.98[d]	0.52		0.041 (0.034)	0.63 (0.62)	6

[a] Calculated from reobservations of marked turtles on a 5.4-ha site within the Dunlap Hollow study area during 1978–87 (Table 2).

[b] Based on the mean number of eggs that hatched per adult female within the Dunlap Hollow study area during 1986–87 (Table 1, column 9); and assumes a sex ratio at hatching of 50 males : 50 females.

[c] Observed at site A within the Dunlap Hollow study area during 1986–87; and assumes a sex ratio at hatching of 50 males : 50 females.

[d] Hypothetical survival rates.

[e] Unparenthesized survival rates assume a sex ratio at hatching of 50 : 50 (see Footnote b). Survival rates in parentheses assume a sex ratio at hatching of 39 males : 61 females as observed among adults on the Dunlap Hollow study area.

proach was to ask what level of juvenile and subadult survival would produce a stationary population. We began with the mean annual survival rate of 0.81 for adults during 1978–86, and the mean annual reproductive rate of 0.35 female hatchlings (50:50 sex ratio) per adult female annually during 1986–87. With these parameter values, overall survival from hatching to age 10 yr would have to be 0.54, or a mean annual survival rate of 0.94, to prevent a population decline. That level of survival is clearly improbable.

We next used 0.52 female hatchlings per adult female, the maximum observed on our study area (in the core of site A). Survival to age 10 yr would then be 0.37, and mean annual survival 0.90, in a stationary population. Such survival is still improbable in light of the 0.81 annual survival of adults at site A, and low survival of hatchlings.

It seemed to us that subadult survival might resemble adult survival, whereas survival rates from hatching to age 7 would likely be considerably less. Our next calculation assigned adult survival to subadults; juvenile survival was thereby estimated at 0.95 annually—again higher than that of adults.

We think the maximum reproductive rate cited above (0.52 female hatchlings per adult female) will not often be surpassed elsewhere in Wisconsin. It follows, therefore, that adult survival in stationary populations must be higher than the annual rate of 0.81 measured by us in Dunlap Hollow. Given a reproductive rate of 0.52 female hatchlings per adult female, adult survival would have to average about 0.95 or higher to yield juvenile survival rates that begin to appear likely (Table 6), and percentages of subadults that approach those observed by us. This level of adult survival may well occur under pristine conditions, but is unlikely where box turtle populations are now exposed to automobiles, farm machinery, and lawn mowers. We conclude from the foregoing analysis that the study-area population will continue to decline. This conclusion is unaffected if the sex ratio at hatching is actually 39:61 (as among adults), rather than the assumed 50:50, because the calculated survival rates change very little (Table 6).

MANAGEMENT IMPLICATIONS

Information from the present study is relevant to management of box turtle populations in Wisconsin. Our demographic analyses (Table 6) indicated that steps to improve adult survival could be highly significant in stemming further population declines. All known deaths of adult box turtles on our study area were human related; there as elsewhere (Legler, 1960; Blair, 1976; Schwartz et al., 1984), the primary cause was automobiles. Roads fragment habitat, thereby increasing the likelihood of turtles being run over or collected as pets. Such fragmentation also increases the amount of ecological edge and thus the probability of predation on turtle nests (Temple, 1987). Given the foregoing risks, turtle home ranges of ≤14 ha, and the observed distribution of remnant populations in Dunlap

Hollow, we tentatively suggest that roadless areas of at least 100 ha, where collecting is effectively forbidden, will be required to sustain viable box turtle populations.

We doubt the practicality of attempting to improve nesting success. Although nest sites might be protected from predators, the initial effort to find a significant proportion of the nests would clearly be too great.

Areas of native prairie with deep sandy soils appear to constitute critical habitat. We do not know if the strong association between turtle distribution and prairie vegetation reflected the presence of a vital food source, or simply the occurrence of prairie remnants on sandy soils that were unsuitable for agricultural crops but attractive to turtles. However, we often observed box turtles feeding on prickly pear cactus and the fleshy bases of spiderwort—species common on our study-area prairies.

The attractiveness of deep sandy soils is easier to understand. Such soils greatly facilitate burrowing—a necessity for hibernation, nesting and thermoregulation. Although adult box turtles can survive freezing temperatures for short periods (Legler, 1960), they must hibernate below frost depth. Hatchlings typically burrow beneath the nest, hibernate there, and first emerge the following spring. Without exception, our radio-tagged females deposited their eggs in loose sandy soil.

Burrowing appears also to provide an important option for thermoregulation. Turtles invariably spent the night in burrows, and frequently buried themselves during midday heat or on unusually cool days. Optimal environmental temperatures for active adult box turtles on our study area were 21–25 C; at about 28 C the turtles sought cover in burrows or dense vegetation (L. R. Han, unpubl.).

Further research is needed to test the feasibility of transplanting box turtles to establish new populations. Our limited experiments suggest that timing of such transplants may be extremely important: none of the five adults released at the Leopold Reserve in mid-July attempted to disperse, whereas five of six released near Dunlap Hollow in mid-Aug. dispersed immediately. Mid-July is normally a time of minimal movement following nesting in June; the mid-Aug. transplant immediately preceded the period of most intensive mating. We doubt the Wisconsin vs Nebraska origin of these two groups was responsible for their sedentary vs dispersal tendencies.

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Seasonal Variations in Plasma and Tissue Chemistry in Water Snakes, *Nerodia sipedon*

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Although reptiles that become dormant during the winter show seasonal adaptations similar to those found in hibernating mammals, few unifying characteristics of hibernation in ectotherms have been established. I therefore examined seasonal chemical changes in plasma and tissue of northern water snakes in order to characterize chemical changes typical of hibernation in this reptile. I held snakes outdoors under ambient conditions and animals either chronically or acutely exposed to winter or summer conditions. I analyzed plasma and tissue samples for water content, Na, K, Ca, Mg and Cl and measured whole organ weights (liver, ventricle, kidney and abdominal fat body). There were no seasonal variations in total body water or plasma or tissue water contents. Plasma magnesium concentrations were higher in winter than in summer snakes. There were no seasonal variations in fat body weight, suggesting that lipids may not be an important source of energy during hibernation in this species. The chemical profiles of snakes kept outdoors under ambient conditions were different from those of snakes experimentally acclimated to either winter or summer conditions. The variations in some electrolyte concentrations along with a lack of change in others indicated that hibernating snakes continue to osmoregulate and ionoregulate and could maintain essentially normal electrolyte and water concentration gradients across cell membranes in winter.

REPTILES that live in northern temperate regions must cope with a widely varying range of temperature and photoperiod conditions. During winter months these reptiles are exposed to extreme conditions of cold. In response to these conditions, some mammals hibernate: a complex physiological response that involves both metabolic and biochemical adjustments in most, if not all, of the animal's organ systems. A great deal of work has been