
Nesting ecology of the Eastern box turtle (*Terrapene carolina carolina*) in central Virginia, USA

GORDON L. WILSON¹ and CARL H. ERNST²

¹ *New Saint Andrews College, 405 South Main Street, Moscow, Idaho 83843, USA.*
gwilson@nsa.edu

² *Division of Amphibians & Reptiles, MRC 162, Smithsonian Institution, P.O. Box 37012, Washington, D.C., 20013-7012, USA.* chernst@frontiernet.net

ABSTRACT — The Eastern box turtle, *Terrapene carolina carolina*, was studied in an 11 ha woods in Lynchburg, Virginia, USA. There was evidence that moderate to heavy precipitation in June–July induced nesting behaviour by gravid females. We found that 86–92% of telemetered, gravid females oriented toward open areas (fields, road/trail borders, and yards) to oviposit. Of the observed 13 nestings, 11 (85%) occurred between 17:00 and 01:00 h. Forty-seven percent of eggs hatched in enclosed, predator-proof nest enclosures. Because of migration to and from nesting sites, gravid females had a mean bivariate normal activity range almost five times greater than that of nongravid females. This finding has negative implications regarding the conservation of the species in road-fragmented habitats due to the potential for increased road mortality or other human disturbance of the wider ranging gravid females.

TERRAPENE *carolina carolina* (Testudines: Emydidae) ranges in the eastern USA from southern Maine south to Georgia and west to Michigan, Illinois, and Tennessee (Ernst *et al.*, 1994). The species occurs predominately in mixed oak-pine forests, pine flatwoods, marshy meadows, maritime oak forests, hardwood swamps, and agricultural areas. Moreover, it is frequently found in residential areas and upland forests of the Appalachian Mountains.

Because *T. c. carolina* is the most common terrestrial turtle within its geographic range, it is a convenient subject for research (see Ernst *et al.*, 1994; and Dodd, 2001; for reviews of previous studies); however, a disproportionate amount of data is anecdotal. Consequently, there is still need for more information on the turtle's nesting ecology. Previous studies with data, some anecdotal or incidental, on nesting include Ewing (1933), Allard (1935), Stickel (1950), Congello (1978), Boucher (1999), and Wilson & Ernst (2005). Because of the lack of quantitative analysis on several aspects of the turtle's nesting ecology, we decided to explore them more thoroughly, particularly the relationships between nesting and time of day, precipitation, relative humidity, and nest site habitat.

MATERIALS AND METHODS

Field-site description

All data were collected in an approximately 20 ha, undisturbed, oak-pine (*Quercus-Pinus*) woodlot adjacent to the Blackwater Creek Natural Area in the city of Lynchburg, Virginia, USA. The area used for most studies was a flagged area of approximately 11 ha. The habitat ranged from predominately open deciduous woods to dense thickets of brush (mostly raspberry, *Rubus* sp.) and a mowed grassy field. The study area was bordered by the Odd Fellows/Rebekah Nursing Home of Virginia to the northeast and east, the Blackwater Creek bike path to the south and west, and residential homes to the north. To the southeast and northwest, the boundaries were marked with flags based on the relative ease in which the area could be surveyed. The woodland is the property of the Odd Fellows Home, and is within the Blackwater Creek watershed.

Field materials and methods

Virginia *T. c. carolina* may emerge from hibernation as early as late February (Boucher, 1999; Wilson, pers. obs.), but significant activity does not usually begin until April, so studies were begun in that month and extended into the fall

during the years 2000–2002. Microenvironmental variables such as air temperature (AT, dial Enviro-Safe Thermometers), surface litter temperature (LT) and soil temperature (ST) (both taken with Taylor soil thermometers), local daily weather conditions (including precipitation data obtained from the United States National Oceanic and Atmospheric Administration [NOAA] website), relative humidity (sling psychrometer), location description (i.e., canopy cover, microhabitat, and landmarks), time and date were recorded at the location of each capture. Each capture point was marked with a flag on which the individual turtle's number, date, and time of capture were recorded. These flags were relocated during the winter and their positions (UTM coordinates) recorded using a Garmin GPS unit. These data were analyzed using Calhome Software (Kie *et al.*, 1996) to calculate home ranges for each female using several different methods: minimum convex polygon (MCP), adaptive kernel (AK), harmonic mean (HM), and bivariate normal (BVN). Results from these methods were compared to ascertain which was the least sensitive to sample size and which was most useful for the objectives of this study (Warkentien, 2001).

The turtle's straight-line carapace length (CL), carapace width (CW), and carapace height (CH) were recorded with dial calipers accurate to 0.5 mm, and mass (BM) to the nearest g with a Pesola spring scale. Each turtle was shell notched for future identification using the coding system of Ernst *et al.* (1974).

Twelve reproductive age females captured during the springs of 2000–2002 were equipped with SOPB-2190 radio-transmitters (Wildlife Materials, Inc.; see Wilson and Ernst, 2005, for attachment procedure), and were tracked for approximately the same annual length of time during the study. Three size categories, usually with four females per category, were captured to span a range of CLs of mature turtles (small, 10.0–11.5 cm; medium, 11.6–12.5 cm; large, 12.6 cm or larger). The females were released at the place of capture, and then radio-located every few days.

Belzer (1999a) and Congello (1978) reported that Pennsylvania *T. c. carolina* generally oviposit in the late afternoon and into the night on overcast or stormy days. We located our females daily, or on

every other day, during 16:00 to 20:00 h, especially those females that were determined to contain shelled oviductal eggs through palpation or X-radiographs. If a female was observed nesting, her behaviour was recorded during nest excavation, oviposition, and placement of the eggs within the nest cavity. Once oviposition was completed, she was weighed and set aside. The eggs were then carefully retrieved; their lengths (EL), widths (EW) and masses (EM) recorded (data analyzed in Wilson & Ernst, 2005); they were replaced in the nest as closely as possible to their original positions. The female was then set back in her nesting position to allow her to finish filling and tamping the nest cavity so the soil was compacted in the normal way. Once she finished and moved away, a plywood enclosure 45 cm x 45 cm x 15 cm) with a screen top was placed over the nest to prevent nest predation during the incubation period of approximately 70–80 days (Ernst *et al.*, 1994). The base of the enclosure was partially buried to retain the neonates upon hatching. Also, the enclosure was secured by tent stakes to prevent disturbance by predators or harsh weather conditions. Hatchling retention was brief, as the site was checked daily when the estimated hatching date approached. Once the eggs hatched, the nest enclosure was removed, the hatchlings were measured (CL, CW, BM), and notched. The fate of each egg was recorded (hatched, desiccated, rotted, etc.). By monitoring the 12 females, it was determined if any had laid more than one clutch per year. Nest characteristics were also described (mowed lawn, trail or dirt road border, open, or woodland, etc.), and nest site locations (UTM coordinates) were recorded. Since nesting migrations are not considered part of an animal's home range by most investigators (Burt, 1943; Brown & Orians, 1970), we have combined locational data of both home range and nesting excursions and will refer to this as activity range. Combining all locational data for each female allows us to demonstrate if any temporal differences exist in the mean activity range of females of different reproductive statuses.

Data analysis

Data gathered were used to determine relationships between nestings (date, time, precipitation, relative humidity, and habitat). The

Open area nesters	Forest nesters
#107	#51
#112	
#37	
#53	
#6 (aborted)	
#108 (aborted)	
Probably open area nesters	
#19 (3 years)	
#77	
#67	
#60	

Table 1. Nest site selection of *Terrapene c. carolina* at Lynchburg, Virginia: open area nesters versus forest nesters.

activity range method that was least sample dependent was determined using Calhome Software (see above; Kie *et al.*, 1996). Seven females were chosen (with relatively large UTM data sets), and randomly generated subsets of data points were taken from the total UTM data set of each turtle. Activity range calculations were performed using subset sample sizes of $N = 5, 10,$ and 15 (Warkentien, 2001). BVN was the calculation method that best suited the study. Although BVN is not sample size dependent, each BVN activity range was calculated using females that had UTM sample sizes of at least 10. Once it was chosen, *t*-test comparisons were made between the means of female activity range size depending on reproductive status (gravid or nongravid). Gravid female BVN activity ranges were calculated using location data from home range plus nesting migration movements. Nongravid female BVN activity ranges were calculated using location data from home range movements. Activity range data gathered from radio-tracked females and other individuals encountered on multiple years were averaged.

RESULTS AND DISCUSSION

Nesting, incubation period, and hatching

During 2000 (1), 2001 (7), and 2002 (6), data was gathered from 14 nestings during 15th June–3rd July (12) and 18th July (2). The times of nesting were

07:45 (1), 1130 (1), and 17:30–01:00 (12) h. Clutch size averaged 3.1 (1–5) eggs. Of the 49 eggs, 47 (95.9%) were known or assumed to be fertile and two (4.1%) were extremely small and infertile. Twenty-two (47%) of the 47 fertile eggs hatched; known causes of egg destruction were: desiccation (4); plant penetration (1); predation, probably by ants (2); torn egg shell (investigator error) resulting in embryo death (1); fungal rot (5); and causes unknown (8). Another clutch of four eggs perished with a road-killed female. Hatching occurred between 30th August and 24th September; duration of incubation was 64–94 days.

Our results suggest that most gravid females about to oviposit orient toward open areas, corroborating the observations of Allard (1935), Belzer (1999a), Congello (1978), Ernst *et al.* (1994), and Messinger and Patten (1995). From confirmed nestings, 86% of radio-monitored females selected open areas for nesting (Table 1). This percentage was even higher (92%) if all monitored females that most likely nested in an open area were included. Even the nest found in the woods suggests a preference for solar exposure, having been dug in an open patch. However, it should be noted that there were no successful hatchlings from this clutch.

There are several possible advantages of females choosing open areas for nesting. Open areas receive more solar radiation, and have a higher ST, which speeds up embryonic development and shortens the incubation period (Dodge *et al.*, 1978). This may enable the hatchlings to find suitable overwintering sites before cold weather becomes a threat. Although this may seem advantageous, differential survivorship of short versus long incubation times has not been determined in *T. c. carolina*. Also, the females may seek a ST that straddles the temperature threshold at which the hatchling's sex is determined (temperature sex determination, TSD), somewhere between 27°C and 28.5°C (Dimond, 1983; Ewert & Nelson, 1991), assuring a close to 1:1 male to female ratio.

Precipitation and nesting

It has been reported that *T. c. carolina* nesting behaviour is evoked by rainfall (Congello, 1978; Belzer, 1999; pers. obs.), but such observations

have not been quantified or analyzed. It has also been noted that heavy midday rainfall stimulates nesting activity in the semi-terrestrial wood turtle, *Glyptemys insculpta* (Walde *et al.*, 2007). When the Odd Fellows/Rebekah field and nearby yards were discovered to be hot spots for nesting *T. c. carolina*, surveys were focused there when it had rained or was raining, usually in the late afternoon or evening. When it was dry or experienced only a light, short-lived sprinkle, females did not migrate to nest, even in the peak of the nesting



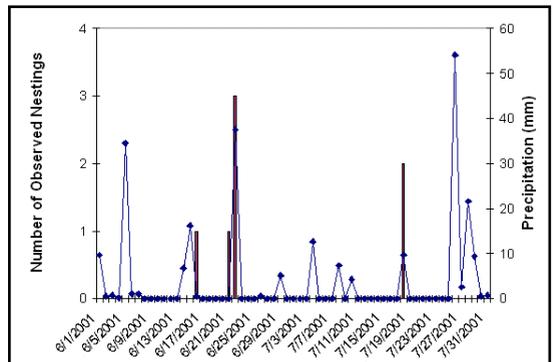
Figure 1. Female #53 ovipositing in Odd Fellows field the evening of 18th July 2001. © G. Wilson.

season. In the summer of 2000, one nesting was observed on 16th June after a heavy afternoon thunderstorm. On 5th June 2001, a heavy rainfall of 34.5 mm apparently did not evoke a surge of nesting, possibly it was too early in the season. None of the radio-equipped, gravid females moved toward their nesting areas until mid- to late June. The first good rain during the typical nesting season was on 14th June (6.8 mm) and female 51 was found excavating a nest, but she abandoned the site. Whether our presence disturbed her or she was merely digging a trial cavity, could not be determined. She was monitored again the following evening after a heavier rain, but showed no nesting behaviour. However, female 9 was observed that evening apparently searching for a suitable nest site in the Odd Fellows/Rebekah field. Also, female 112 was digging a trial nest there, which she aborted after investing considerable time and effort in soil that was not very moist. Female 51 successfully nested either later that night or on 16th June. The next four nests were found after a rainfall on 21st–22nd June. A nesting by female 107 occurred on 21st June and females 80, 112 and 117 nested on 22nd June, when there was a much heavier rain event (37.6 mm). No other nestings occurred until 18th July (9.7 mm), when female 122a nested in the morning and

female 53 nested that night (Figure 1). Periodic rains occurred early in July, but no completed nests were found. Female 53 was seen digging a trial nest on 4th July after a rainfall, but quit after nightfall. Even though nestings did not necessarily follow every precipitation, one or more nesting attempts always occurred on the same day as a rain event or on the following day while the substrate was still moist (Figures 2–3).

There are several possible advantages of nesting after a substantial rainfall. One advantage is that

Figure 2. Number of observed nestings by *Terrapene c. carolina* (bars) relative to daily precipitation (lines) in June–July 2001.



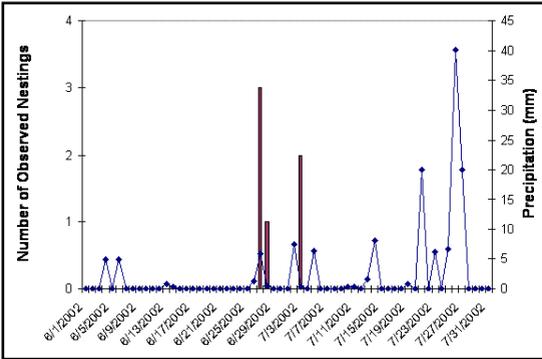


Figure 3. Number of observed nestings by *Terrapene c. carolina* (bars) relative to daily precipitation (lines) in June-July 2002.

rain softens the substrate, making it more friable during the excavation process (Ernst *et al.*, 1994). When females were observed digging in dry or only slightly moist ground, the excavation was slow and laborious, and the attempt was usually aborted. Conversely, in well-saturated soils, excavation was more rapid and usually completed (*pers. obs.*). Moist soil also decreases the chances of egg desiccation (Packard *et al.*, 1985); ovipositing in a wet soil allows the eggs to imbibe additional moisture (Lynn & von Brand, 1945). This water would presumably provide a margin of safety against future water loss during drought conditions. Another possible advantage is that of rehydrating the female after water loss during migration and the nesting process. Although striped mud turtles do not require rainfall to nest, Wilson (1998) found that striped mud turtles (*Kinosternon baurii*) select nest sites having higher soil moisture content than randomly selected sites in the same area. This seems to indicate that the females can physically monitor water content in the soil and use it as an indicator for nest site suitability.

Other purported advantages have to do with predator avoidance; predators are not usually as active during rainfall events. However, turtle scent may be more traceable on a moist substrate, due to the cohesiveness of water. Moist soils may also be more impressionable for leaving visible tracks than dry soils. These factors need to be researched to see if they significantly increase predation. Possibly, with regard to predators, nesting in wet conditions may be more of a liability than an advantage.

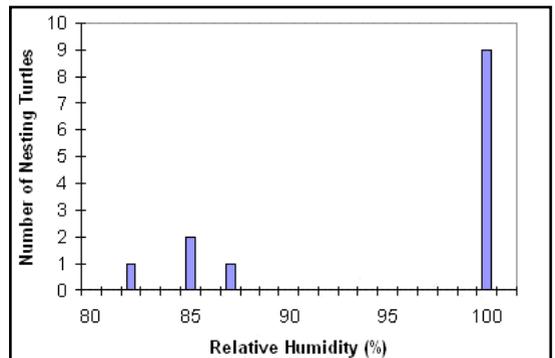
Nesting and relative humidity

Most nestings occurred during or after a significant rain event, so the relative humidity was very high for the majority of them. Nine (64%) of the 14 observed nestings occurred at 100% relative humidity. A relative humidity reading of 87% occurred while female 122a nested. She was found at 07:45 h, which was during a light morning rain but preceding a heavier rainfall later that day. In addition, female 137 nested at 87% relative humidity at 11:30 h on a sunny day after a heavy rainfall the preceding day of 27th June. The nestings by females 37 and 111 took place on 3rd July 2002 after a modest but not soaking rain. Consequently, the humidity was relatively lower compared to those nine nestings that occurred after heavy downpours (Figure 4).

Nest site use

Of the total 15 nests observed, 14 (93%) were in open areas (mowed field, backyards, trail/road borders, woodland clearings). These results could be attributed to a sampling bias because open areas were selectively sampled during optimal egg laying times; however, for all of the gravid and radio-monitored females either found nesting or for which the nest site (7) was found, six (86%) were in open areas with little canopy cover. Two of the six females aborted their attempts at nest excavation, possibly due to the observer's presence. Nevertheless, they had moved to an open area and at least started to excavate a nest. There was also good reason to suspect that four other radio-equipped gravid females nested at

Figure 4. Number of nesting *Terrapene c. carolina* in relation to relative humidity.



open sites; although they were not observed nesting, they engaged in a pre-oviposition migration out of their woodland home ranges toward open areas. Three were found in backyards just prior to oviposition. If these four females are included in the analysis, the open area nestings increased to 92.3% of total nestings of radio-monitored females. The only radio-monitored female that nested in the woods did so about 15–20 m from the edge, and her nest was located in a light gap in the canopy. Overall, six observed nestings (two of which aborted) and six probable nestings occurred in the open, versus only one woodland nesting.

Nesting and time of day

Most observed nestings took place between 17:00 and 01:00 h, but the majority of nesting activity occurred after dusk between 19:00 and 24:00 h. A few females, although they started to dig at a typical time, took longer to excavate their nests and finished after midnight. The only exception to this was the nesting of female 137 at 11:30 h, 28th June. This nesting was unusual in that only one other mid-day nesting has been reported for *T. c. carolina* (Lee, 2002). Figure 5 shows the times that females were first encountered at various points in the nesting process.

The majority of nestings occur at night, probably because most periods of heavy precipitation in this region occur in the afternoon or late afternoon (*pers. obs.*). The gravid female is most likely incited to nest by rainfall (Congello, 1978; Belzer, 1999; *pers. obs.*), or possibly the drop in barometric pressure that usually accompanies it, rather than simply the onset of darkness. Allard (1948) observed that females generally nest on clear evenings and begin earlier if it is dark and cloudy. He assumed that the key factor was decreased light intensity and not pre- or post rainfall conditions, but mentioned that thunderstorms and showers intervened not infrequently while the females were nesting. He did not indicate, however, whether or not clear-evening nesters excavated prior to or after a rain event.

Until Lee's (2002) report, no mid-day nesting had been previously reported, only early morning (Allard, 1948; Belzer, 1999b; Ernst *et al.*, 1994). The earliest reported afternoon nesting was at

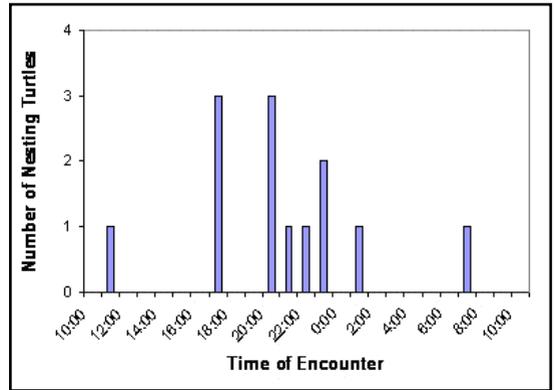


Figure 5. Number of nesting *Terrapene c. carolina* relative to the time initially encountered.

15:45 h (Ewing, 1935). However, Virginia female 137 had an unusual nesting time between 11:30 and 15:00 h; Ernst (unpubl. data) has observed an Alabama *T. carolina major* nesting at 10:30 h. If darkness is an essential factor in box turtle nesting, these records and that of Lee (2002) are inexplicable. However, the mid-day Virginia nesting is understandable, because the soil was still very moist from the heavy rain of the previous day. Unfortunately, Lee (2002) did not mention the weather conditions preceding or following this mid-day nesting. Because darkness without precipitation, or factors associated with it, did not evoke nesting behaviour during our study, it was tentatively concluded that darkness is not the major cue for nesting.

Effects of reproductive status on home range

In a peripheral study on the same population of *T. c. carolina*, Warkentien (2001) calculated the activity ranges using four different methods (see above) of 12 radio-equipped females using UTM data collected in 2000. HM was the most sample size dependent. At a sample size of 15, five of seven turtles had home ranges significantly smaller than the original HM activity ranges calculated from each turtle's entire data set; however, it was not clear whether or not the entire data set was large enough to use this method. The next most sample size dependent method was MCP. The sample size of 15 was almost large enough in that only two out of the seven turtles had significantly smaller activity ranges when compared to their original MCPs. The AK method

Gravid Females		Nongravid Females	
Turtle-year(s)	Activity range size (ha)	Turtle-year(s)	Activity range size (ha)
77-02	48.7	108-02	9.1
112-01	9.8	60-02	2.7
19-00, 01, 02	31.6	59-00, 01, 02	0.6
122-02	6.8	33-00, 01	3.8
51-01	11.7	24-02	5.0
6-02	16.1	125-02	2.1
16-01	6.4	101-01	4.2
107-01	40.2	37-00	2.5
108-01	11.9	38-00	3.9
42-00	15.9	45-00	1.0
60-00	24.6	51-00	12.1
67-00	1.6	53-00	1.1
		65-00	1.6
	Mean = 18.8		Mean = 3.8
	SD = 14.6		SD = 3.3
t-statistic = 3.6	df = 23	p = 0.0015	

Table 2. The effects of reproductive status on home range size in female *Terrapene c. carolina* in Lynchburg, Virginia (Home range calculated using the bivariate normal method).

ranked third in sample size dependency. Only one of seven turtles showed a significantly smaller activity range when compared to the original AK activity ranges. Of the four methods tested, BVN was the least sample size dependent. In spite of the sample size (5, 10, 15), no turtle BVN activity range differed significantly from the original BVN estimation. Thus, BVN was selected for determining the activity range of the radio-equipped females. This method gives a very liberal estimate in that it draws a generous ellipse around the data points and has several assumptions that cannot be met. It is the least sample size dependent because it exaggerates the actual activity range size. Nevertheless, our purpose was to select a method that would be useful in showing relative differences in activity range size between turtles of different reproductive status. BVN activity ranges for radio-monitored females for all three years were categorized according to reproductive status (gravid, nongravid). The mean gravid female activity range was 18.8 ha and the mean nongravid female activity range was 3.8 ha. The difference

was significant (t -statistic = 3.6, $df = 23$, $P = 0.0015$, Table 2).

Gravid freshwater turtles and sea turtles migrate outside their home range during the nesting season (Ernst *et al.*, 1994). Their home range is mostly aquatic, but, because the eggs must be laid on land to be adequately aerated, gravid females must come ashore to nest, often extending beyond their home range by large distances. Although migration to nesting sites outside of the home range is well documented in aquatic turtles, it is not so understood in *T. c. carolina*. As it lives in the same general habitat as its terrestrial nest site, it could be assumed that females would not necessarily have to relocate far, if at all, to lay eggs.

Therefore, migration extending beyond home range would not necessarily be predicted during the nesting season, but in our Virginia population gravid females had a significantly larger mean activity range (18.8 ha) than nongravid females (3.8 ha). Stickel (1950) anecdotally supported these findings in stating that a female may not find a suitable nest site within her home range and may have to make an excursion beyond it to lay her eggs. It was very apparent that our gravid radio-monitored females moved various distances to nest in open areas. The monitored gravid females moved toward open areas to nest, and other gravid nontelemetered females were also observed moving toward or in open areas. As the migration route and nest site are usually outside of the home range, such movement results in a temporal expansion of the female's activity range. The monitored females did not always move to the nearest clearing. Several moved through multiple open areas to reach a distant clearing to nest. After depositing their eggs and subsequently resting a short time, each female returned to her home range.

It can not be assumed that the intervening clearings were marginal nest sites, because other females nested in some of them. Although not

conclusive, these excursions possibly indicate movement to a general natal ground. This has been clearly established in several sea turtle species (Ernst *et al.*, 1994). Future research should determine if this is true in the genus *Terrapene*. If it is true, the orientational and navigational cues used to find such areas should be investigated. Do particular females use the same nest sites repeatedly (nest site fidelity)? Virginia female 117 was observed nesting about 20 m apart at the same site in two consecutive years, and female 53 searched for a suitable place to excavate in about the same location in which she had nested the year before. However, if nest site fidelity occurs in *T. carolina*, it is not rigid. The general areas chosen by female 19 for three years are known, although she was never observed nesting. All were in different locations within a several hectare area. These areas were well outside and in the same compass direction from her home range.

Gravid females instinctively migrate, not only toward clearings, but also toward areas peripheral to their home ranges. The following are three possible advantages for this behavior which would require further research to be confirmed. 1) Peripheral nesting may promote dispersal of the offspring. This could possibly extend the population's range into other uninhabited suitable areas, thus avoiding or lessening vulnerability to regional perturbations that could cause population decline or extirpation. 2) Peripheral nesting could over time increase gene flow between adjacent populations if the hatchlings take up residence outside of the parental home ranges. Unfortunately, movement or dispersal patterns of Eastern box turtle hatchlings are poorly known. 3) Peripheral nesting may reduce predation on eggs and hatchlings. Nesting outside parental home ranges may make it more difficult for predators to locate them

Conservation implications

Apart from the possible ecological and genetic advantages of nesting outside a home range, there are implications for conservation of *T. c. carolina* occurring in human habitats. The data show that females moved beyond their home ranges to nest in open areas. Since *T. carolina* is the most terrestrial emydid turtle in the USA, its habitat is often shared with humans. The turtle

can often be found in residential, suburban, and rural human communities, provided there is adequate woodland nearby. In these shared areas, most open areas that may serve as nesting sites are anthropogenic. Such clearings may be positive for nesting if they are not frequently disturbed. However, as gravid females are drawn into these areas instinctively, they are exposed to a number of threats not usually encountered in their home ranges. These include encountering motorized vehicles while crossing roads, predators hunting along forest edges, and humans who may collect or harass them. One behaviour pattern that mitigates these threats is the temporal separation that usually occurs between turtle nesting times and human activity, as the turtles normally nest at night after or during rainfall. This behavior aids in the avoidance of humans.

Habitats that are fragmented by roads, trails, developments, and other inhospitable tracts create a number of smaller isolated patches of suitable habitat and possibly increase nest site availability (Meffe & Carroll, 1997). In such fragmented habitats, turtles often make road-crossing forays while normally moving about their home ranges, searching for mates, or seeking nest sites, and are at greater risk of being struck by motorized vehicles or disturbed by passing humans. For instance, Dodd *et al.* (1989) observed 160 turtles on northcentral Alabama roads in 1985; 74.4% were dead, and of these, 85% were *T. carolina*. Because the mean BVN activity range of gravid female box turtles in this study is almost five times larger than their mean BVN activity range when not gravid, the chance of crossing roads seeking a nest site is greatly increased in a road-fragmented habitat. It is generally observed that a box turtle population along roads will decline due to unsuccessful road crossings (Anderson, 1965; Klemens, 2000; Mitchell, 1994). Consequently, gene flow is accordingly reduced (Klemens, 2000). If movement patterns between females of different reproductive statuses were the same it could be assumed that road-kills would result in equal numbers of gravid and nongravid females being killed. Even though road-kills are not random and indiscriminate (Ashley *et al.*, 2007) those that do purposefully target turtles are not likely distinguishing between

sex or reproductive status in choosing their next victim. Our data suggests that the highly significantly different activity ranges between the two female reproductive classes would result in more gravid females being killed than nongravid ones during the June–July nesting season. Gibbs & Steen (2005) found that there was a trend toward a male-biased sex ratio in areas of increasing road networks since 1930. This trend was apparent in all turtles species surveyed but was the most pronounced in aquatic species and progressively less in semiaquatic and terrestrial species. Steen *et al.* (2006) found that a larger fraction of road-kill turtles were female and concluded that females are indeed more likely to make road-crossing forays. They suggested that their finding may explain the skewed sex ratio toward a male bias. Our study did not radio-monitor male turtles so we could not determine if there was a difference in the activity ranges of male turtles and gravid or nongravid female turtles. Our findings however did suggest that gravid females would be the most likely female reproductive class encountering roads. Our finding that gravid females have a much larger mean activity range corroborates the view of Steen & Gibbs (2004), Gibbs & Steen (2005), and Steen *et al.* (2006) that gravid females are more susceptible to vehicular death due to terrestrial nesting migrations. It appears that those females responsible for the reproductive output of the population have a much greater chance of being killed, thus reducing the population's reproductive effort yearly, and resulting in an eventual decline in numbers. Such selection is opposite of typical selection in that those females that have the highest clutch frequency (not necessarily largest clutch size) are selected against. If the trait of low clutch frequency is heritable, then road fragmentation not only directly accelerates population decline by killing individual turtles, but also by the selection of low clutch frequency females because they are less likely to be road-killed. Wilcove *et al.* (1986), Wilcox (1980), and Wilcox & Murphy (1985) observed that isolated islands of habitat support fewer individuals than expanses of habitat interconnected by habitat corridors. Obviously vehicular traffic kills turtles (Dodd *et al.*, 1989; Ashley & Robinson, 1996; Klemens, 2000; Ashley *et al.*, 2007), but we also think the male-biased sex

ratios in areas of higher road densities (Steen *et al.*, 2006) and widespread box turtle decline in road fragmented habitats (Klemens, 2000) may be amplified by the movement patterns of gravid females.

A holistic approach to the conservation of *T. c. carolina* must be ecologically circumspect. If policy makers are to make informed decisions, they need to have access to pertinent information on the ecology of the box turtle. These include its habitat use and home range characteristics; movement patterns; activity range; population sex ration; age and size structures; range of threats to the population and habitat; spatial arrangement of suitable habitat; and the relationship of these habitats to the landscape. This study has addressed important aspects of the first points, but only regarding adult turtles, especially the activity ranges of gravid and nongravid females in relation to threats encountered along anthropogenic edges.

Important questions answered in this study are the following: the reproductive output of the population (Wilson & Ernst, 2005), nest site selection, environmental conditions for nesting, timing of nesting, and the differential movement of gravid versus nongravid females. However, obvious gaps in our knowledge remain: the fate of unprotected nests, the proportion of hatchlings that survive to reproductive age, and the movement patterns (including home range size) and dispersal behaviour of hatchlings. These poorly understood facets of Eastern box turtle ecology are needed to advance conservation management strategies for populations intimately associated with human development.

Finally, conservation strategies need to consider box turtle management on the broader scale of landscape ecology. Only a few niche requirements of *T. c. carolina* need to be understood and conserved in order to maintain healthy populations. These include the maintenance of quality habitat patches of adequate size, the development or maintenance of corridors that in some way span roads and interconnect such patches, and the creation and maintenance of undisturbed open area buffer zones either external or internal to these patches. The corridors (probably under road culverts, which are used by *T. carolina*; Ernst, *pers. obs.*) would provide

pathways for gene flow among adjacent populations and would minimize road kills. To devise and construct effective road crossing corridors for turtles on a large scale will require much creativity if they are to be considered economically feasible. However, even if cost-effective small wildlife culverts (and drift fences directing small animals into them) are designed, they still might not be constructed until the public understands and values the movements of wildlife. Currently, successful road crossings are accomplished by determined lucky turtles that have run the gauntlet of traffic (Steen & Gibbs, 2004) or by concerned citizens providing a temporary shuttle service for other turtles attempting to cross. The open buffer zones will provide gravid females suitable nesting areas relatively free from human threats.

We should continue ecological and behavioural studies to fill in the gaps in our knowledge, not only to satisfy human curiosity but also to fine-tune conservation efforts. We do not, however, have to wait until all these knowledge gaps are filled to formulate an adequate conservation strategy. Innovative and knowledgeable biologists are needed to instill within local citizens an appreciation for *T. c. carolina* and other wildlife, and to also devise feasible conservation strategies that are implemented by the public rather than imposed on them.

ACKNOWLEDGEMENTS

We thank Paul Sattler (Chairman) for allocating Liberty University Biology Funds for the purchase of much of the necessary field equipment. Thanks also go to Thomas Akre for his training in radiotelemetry, and to the Odd Fellows/Rebekah Nursing Home for allowing us to conduct the study on their property. We are grateful to Tyler Warkentien, Seth Anderson, David Perault, and all members of the Wilson family for field assistance. Finally, we are grateful for Norman Reichenbach for his statistical assistance and advice.

REFERENCES

Allard, H. A. (1935). The natural history of the box turtle. *Science Monthly* **41**, 325–338.
 Allard, H. A. (1948). The eastern box turtle and its behavior. *J. Tennessee Acad. Sci.* **23**, 307–321.

Anderson, P. (1965). *The Reptiles of Missouri*. Columbia: Univ. Missouri Press.
 Ashley, E. P. & Robinson, J. T. (1996). Road mortality of amphibians, reptiles and other wildlife on the Long Point Causeway, Lake Erie, Ontario. *Can. Field-Nat.* **110** (3):403–412.
 Ashley, E. P., Kosloski, A., & Petrie, S. A. (2007). Incidence of intentional vehicle-reptile collisions. *Hum. Dimen. Wildl.* **12**:137–143.
 Belzer, B. (1999a). Predictor of nesting onset by eastern box turtles. *Box Turtle Conserv. Newsl.* **8**, 11–12.
 Belzer, B. (1999b). Morning nesting by *Terrapene carolina carolina*. *Box Turtle Conserv. Newsl.* **8**, 12–13.
 Boucher, T. P. (1999). Population, growth and thermal ecology of the eastern box turtle, *Terrapene carolina carolina* (L.), in Fairfax County, Virginia. *Ph.D. Dissertation*. Fairfax, Virginia: George Mason University.
 Brown, J. L. & Orians, G. H. (1970). Spacing patterns in mobile animals. *Ann. Rev. Ecol. Syst.* **1**, 239–262.
 Burt, W. H. (1943). Territoriality and home range concepts as applied to mammals. *J. Mammal.* **24**, 346–352.
 Congello, K. (1978). Nesting and egg laying behavior in *Terrapene carolina* in Pennsylvania. *Proc. Pa. Acad. Sci.* **52**, 51–56.
 Dimond, M. T. (1983). Sex of turtle hatchlings as related to incubation temperature. *Proc. 6th Reptile Symp. Captive Prop. Husbandry*, pp. 88–101. Thurmont, Maryland: Zoology Conservation.
 Dodd, C. K., Jr. (2001). *North American Box Turtles: A Natural History*. Norman: Univ. Oklahoma Press.
 Dodd, C. K., Jr, Enge, K. M., & Stuart, J. N. (1989). Reptiles on highways in north-central Alabama. *J. Herpetol.* **23**, 197–200.
 Dodge, C. H., Dimond, M. T., & Wunder, C. C. (1978). Effect of temperature on the incubation time of eggs of the eastern box turtle (*Terrapene carolina carolina* Linné). *Florida Mar. Res. Publ.* **33**, 8–11.
 Ernst, C. H., Lovich, J. E. & Barbour, R. W. (1994). *Turtles of the United States and Canada*. Washington, DC: Smithsonian Inst. Press.

- Ernst, C. H., Hershey, M. F. & Barbour, R. W. (1974). A new coding system for hardshelled turtles. *Trans. Kentucky Acad. Sci.* **35**, 27–28.
- Ewert, M. A. & Nelson, C. E. (1991). Sex determination in turtles: diverse patterns and some possible adaptive values. *Copeia* **1991**, 50–69.
- Ewing, H. E. (1933). Reproduction in the eastern box turtle *Terrapene carolina carolina* (Linné). *Copeia* **1933**, 95–96.
- Ewing, H. E. (1935). Further notes on the reproduction of the eastern box turtle, *Terrapene carolina* (Linne'). *Copeia* **1935**, 102.
- Gibbs, J. P. & Steen, D. A. (2005). Trends in sex ratios of turtles in the United States: implications of road mortality. *Conserv. Biol.* **19**, 552–556.
- Kie, J. G., Baldwin, J. A. & Evans, C. J. (1996). CALHOME: a program for estimating animal home ranges. *Wildl. Soc. Bull.* **24**, 342–344.
- Klemens, M. W. (Ed.). (2000). *Turtle conservation*. Washington, DC: Smithsonian Inst. Press.
- Lee, D. S. (2002). A note on box turtle reproduction. *Turtle Tortoise Newsl.* **6**, 27.
- Lynn, W. G. & von Brand, T. (1945). Studies on the oxygen consumption and water metabolism of turtle embryos. *Biol. Bull.* **88**, 112–125.
- Meffe, G. K. & Carroll C. R. (Eds.). (1997). *Principles of Conservation Biology*. 2nd. ed. Sunderland, Massachusetts: Sinauer.
- Messinger, M. A. & Patton, G. M. 1995. Five year study of nesting of captive *Terrapene carolina triunguis*. *Herpetol. Rev.* **26**, 193–195.
- Mitchell, J. C. (1994). *The Reptiles of Virginia*. Washington, DC: Smithsonian Inst. Press.
- Packard, G. C., Packard, M.J. & Gutzke, W.H.N. (1985). Influence of hydration of the environment on eggs and embryos of the terrestrial turtle *Terrapene ornata*. *Physiol. Zool.* **58**, 564–575.
- Steen, D. A. & Gibbs, J. P. (2004). Effects of roads on the structure of freshwater turtle populations. *Conservation Biol.* **18**, 1143–1148.
- Steen, D. A., Aresco, M. J., Beilke, S. G., Compton, B. W., Condon, E. P., Dodd, C. K. Jr., Forrester, H., Gibbons, J. W., Greene, J. L., Johnson, G., Langen, T. A., Oldham, M. J., Oxier, D. N., Saumure, R. A., Schueler, F. W., Sleeman, J. M., Smith, L. L., Tucker, J. K., & Gibbs, J. P. (2006). Relative vulnerability of female turtles to road mortality. *Anim Conserv.* **9**, 269–273.
- Stickel, L. F. (1950). Populations and home range relationships of the box turtle *Terrapene c. carolina* (Linnaeus). *Ecol. Monogr.* **20**, 351–378.
- Walde, A. D., Bider, J. R. Masse, D., Saumure, R. A., & Titman, R. D. (2007) Nesting ecology and hatching success of the wood turtle, *Glyptemys insculpta*, in Quebec. *Herpetol. Conserv. Biol.* **2**, 49–60.
- Warkentien, T. E. (2001). A comparison of home range estimation techniques using the eastern box turtle, *Terrapene carolina*. *Honors Thesis*. Lynchburg, Virginia: Liberty University.
- Wilcove, D. S., McLellan, C. H. & Dobson, A. P. (1986). Habitat fragmentation in the temperate zone. In: *Conservation Biology: The Science of Scarcity and Diversity*, pp. 237–256. Soule, M. E. (Ed.). Sunderland, Massachusetts: Sinauer.
- Wilcox, B. A. (1980). Insular ecology and conservation. In: *Conservation Biology: An Evolutionary-ecological Perspective*, pp. 95–117. Soule, M. E. & Wilcox, B. A. (Eds.). Sunderland, Massachusetts: Sinauer.
- Wilcox, B. A. & Murphy, D. D. 1985. Conservation strategy: the effects of fragmentation on extinction. *Amer. Midl. Nat.* **125**, 879–887.
- Wilson, D.S. (1998). Nest-site selection: microhabitat variation and its effects on the survival of turtle embryos. *Ecology* **79**, 1884–1892
- Wilson, G. L. & Ernst, C. H. (2005). Reproductive ecology of *Terrapene carolina carolina* (eastern box turtle) in central Virginia. *Southeast. Nat.* **4**, 689–702.