Herpetological Conservation and Biology 1(1):9-15
Submitted: 18 April 2006; Accepted: 18 June 2006

ROAD SURVEYS FOR TURTLES: CONSIDERATION OF POSSIBLE SAMPLING BIASES

DAVID A. STEEN[1] AND LORA L. SMITH

Joseph W. Jones Ecological Research Center
Route 2, Box 2324
Newton, GA, 39870, USA
[1]*e-mail:* David.Steen@jonesctr.org

***Abstract.*—Herpetofaunal surveys often rely on observations obtained via road cruising. The ease with which many species of amphibians and reptiles can be observed on roads makes this a useful technique. However, road surveys have inherent limitations and biases, particularly for turtles. Observations of turtles along roads are likely biased towards large, adult female freshwater turtles on nesting forays and male terrestrial turtles that typically have a large home range. Turtles may also use roadsides as habitat and their presence on roads may not necessarily be reflective of their abundance in adjacent natural habitats. Researchers who use road surveys to examine demographic parameters of a turtle population (e.g., sex ratio or age class structure), or to describe a turtle community (e.g., species richness) should consider these biases in their conclusions and explicitly note the role of road cruising in data collection.**

Key Words.— road cruising; road survey; sampling technique; spatial ecology; tortoise; turtle

OVERVIEW

Road surveys have been used to monitor the populations of a wide variety of taxa (e.g., Ashley and Robinson 1996; Goosem 2000). This technique has been used primarily to determine road mortality rates of birds and mammals, and biases of this methodology have been identified for these groups (e.g., Rolley and Lehman 1992; Loughry and McDonough 1996). Road surveys have also been used in similar ways to describe amphibian and reptile communities (Fitch 1949; Kauffeld 1957) and are effective to observe a diverse array of squamates (Rodda 1990; Bernardino and Dalrymple 1992), chelonians (Haxton 2000), anurans (Hels and Buchwald 2001) and caudates (Mazerolle 2004).

Unlike in avian and mammalian studies, herpetological surveys often use observations of living and dead amphibians and reptiles on roads to make inferences about populations. Amphibian and reptile road survey data have been used to document the status of populations (Busby and Parmalee 1996), identify activity patterns (Henke and Montemayor 1998) and to quantify species diversity (Turner et al. 2003) as well as road mortality rates (Ashley and Robinson 1996; Smith and Dodd 2003). Although biases of other sampling methodologies have been identified for reptiles (e.g., Ream and Ream 1966; Prior et al. 2001) and amphibians (Dodd 1991), an evaluation of the inherent biases and limitations of road surveys has yet to be thoroughly discussed.

There are several aspects of road surveys that make them attractive to researchers. Driving roads is not labor intensive and allows the observer to cover a large area relatively quickly. The open areas on the road and the road shoulder provide opportunities to observe wildlife which may otherwise be obscured by vegetation or other landscape features. Furthermore, road surveys may be an effective tool for locating species that are difficult to trap and otherwise record such as aquatic snakes (Bernardino and Dalrymple 1992) and fossorial or cryptic species.

The magnitude of amphibian and reptile road mortality has been well documented (e.g., amphibians and snakes, Dodd et al. 2004; and turtles, Aresco 2005a) and carcasses collected on roads may serve as an important source of museum specimens. Road-killed animals can be useful for obtaining ecological and life history data such as geographic distribution, morphology, reproductive condition, and dietary components, for example, of a particular species (e.g., Case 1975).

THE ROAD SURVEY TECHNIQUE

Road survey methods (road cruising) are straightforward. The road serves as a transect and the number of organisms encountered on a specified route is expressed per unit time or distance (e.g., kills per km). Ideally, the speed of travel is standardized and is slow enough that most individuals of the target taxa are observed and identified. The number of observers should also be consistent, as the total individual animals detected along the road will likely be influenced by the effort invested. Furthermore, observer experience should be standardized as much as possible. If target species are particularly small it may be necessary to conduct counts on foot (Enge and Wood 2002).

Efforts should be scheduled such that they incorporate patterns of activity, with an emphasis on whether the target organism is nocturnal, diurnal or crepuscular. Animal movements may also be highly seasonal. For example, snake migrations to and from hibernacula may lead them to cross roads in great numbers during the fall and the spring (Chan 1993).

In this paper we critically examine the use of road surveys to sample turtles. Many of the potential biases associated with road surveys apply equally to other organisms; therefore, the discussion may prove useful to a wider audience interested in the strengths and limitations to the methodology. Use of road surveys for population has been well described (Campbell and Chrisman 1977). Numerous studies have employed road surveys to obtain information on population structure, relative abundance, or mortality of herpetofauna in Alabama (Dodd 1989), Arizona (Turner et al. 2003), Florida (Duellman and Schwartz 1958; Seigel et al. 2002; Smith and Dodd 2003), Kansas (Busby and Parmalee 1996), Ontario (Ashley and Robinson 1996), and South Carolina (Leiden et al. 1999). Researchers used the technique with various turtles including the Common Snapping Turtle (*Chelydra serpentina*) (Haxton 2000), Desert Tortoise

(*Gopherus agassizii*), Northern Diamondback Terrapin (*Malaclemys terrapin terrapin*) (Szerlag and McRobert 2006), Gopher Tortoise (*Gopherus polyphemus*) (McRae et al. 1981; Boarman and Sazaki 1996; Pike et al. 2005), Madagascar Radiated Tortoise (*Geochelone radiata*) (Goodman et al. 1994), Painted Turtle (*Chrysemys picta*) (Whilans and Crossman 1977; Marchand and Litvaitis 2004; Fowle 1996), Striped Mud Turtle (*Kinosternon baurii*) (Wygoda 1979), and the Texas Tortoise (*Gopherus berlandieri*) (Bury and Smith 1986; Hellgren et al. 2000). Turtle life history traits and ecology may interact with certain characteristics of roads and seasonal weather patterns to promulgate important biases in the use of this technique. Turtle life history traits and ecology may interact with certain characteristics of roads and seasonal weather patterns to promulgate important biases in the use of this technique.

ASSUMPTIONS OF ROAD SURVEYS

To use road surveys to draw general references about animal populations, the following assumptions must be met: 1) roads should not form a barrier to dispersal; 2) roads should not attract animals; 3) animals should not learn to avoid roads; 4) roads, and associated elements, should not influence species richness or abundance in the immediate area; and 5) individuals should be counted only once per sampling period (Shaffer and Juterbock 1994). Typically, many of these assumptions are violated when road surveys are used to study chelonians.

Roads can form a barrier to turtle dispersal (Gibbs and Shriver 2002; Aresco 2005b). Features like fences, curbs, and retaining walls are often associated with roads and can obstruct the dispersal corridors of many species (Mitchell and Klemens 2000). Researchers should consider the mobility and behavior of the organism in question and consider whether any features associated with roads in their study area might influence the ability of turtles cross (Goodman et al. 1994) and potentially reduce the species' detectability.

The second and third assumptions that roads do not attract or are avoided by animals are important because if either is true, samples from roads will not be representative of the population. Although there is no evidence to suggest that turtles learn to avoid roads, conventional wisdom suggests that individuals that cross roads may be at a selective disadvantage relative to those that avoid roads. If this behavior has a genetic component, vehicular-induced mortality would eventually create a population of turtles with a genetically controlled tendency to avoid roads. This is important for female freshwater turtles whose nesting migration routes are often intersected by roads (Steen and Gibbs 2004), because they tend to show fidelity to nest sites across years (Lindeman 1992). Terrestrial turtles whose home ranges encompass roads are also more vulnerable to mortality relative to those whose home ranges are displaced from vehicle throughways. Under these conditions, one could misinterpret a population's status when using road counts. The long term effects of this road mortality in turtles are discussed elsewhere (Gibbs and Steen 2005) but may eventually lead to population declines.

There are several characteristics of roads that serve to attract turtles. As poikilotherms, turtles may be attracted to paved roads for thermoregulation. The open canopy above roads coupled with the heat radiating from asphalt (Asaeda and Ca 1993) may provide excellent conditions for basking. This is of particular importance when roads are located in the proximity of wetlands, although heavy traffic volume or extreme temperatures may discourage this behavior. In addition, the soil, vegetation, and thermal properties of roadsides may attract nesting turtles (Seigel 1980; Szerlag and McRobert 2006). Freshwater turtles often nest near ecological edges (Kolbe and Janzen 2002), and may perceive dirt roads and roadsides as suitable nesting habitat. Gopher tortoises, *Gopherus polyphemus*, often nest in dirt roads (Lora Smith, pers. obs.) which may function as population sinks for turtle populations that demonstrate similar behavior. Egg mortality and increased risk of depredation may result due to road maintenance (e.g., Jackson and Walker 1997).

Another assumption, implicit in road surveys, is that features associated with the road itself do not affect species richness or abundance in the vicinity of the road (Shaffer and Juterbock 1994). The vegetation surrounding roads may attract terrestrial turtles due to the increased foraging opportunities relative to other adjacent habitat (Boarman et al. 1997). Roadside ditches may offer habitat to aquatic and semi-aquatic species. For example, Mud Turtles, *Kinosternon subrubrum*, use roadside ditches as dispersal corridors (David Steen, pers. obs.) and Common Snapping Turtles, *Chelydra serpentina*, are often found in freshwater drainage culverts on barrier islands (David Steen, pers. obs.).

In contrast, high levels of mortality from collisions with vehicles can substantially decrease local populations of turtles (Gibbs and Shriver 2002) and tortoises (Nicholson 1978; Luckenbach 1982), whereas populations distant from roads are stable. Further, predators of turtle eggs and juvenile turtles, particularly subsidized predators such as raccoons, may be relatively abundant in the edge habitat surrounding roadsides (McDougal 2000), potentially limiting turtle populations (Temple 1987). Ravens, known predators of juvenile tortoises, are drawn to roads (Knight and Kawashima 1993; Boarman and Heinrich 1999). Consequently, roads may have an influence on adjacent turtle populations.

Road surveys are often conducted under the assumption that live individuals are only counted once. Most movements of turtles are not uni-directional (Gibbons 1986), whether they be nesting migrations (Obbard and Brooks 1980), or movements toward a food source or while searching for mates (Stickel 1950). Migrating turtles may risk road mortality two or more times during a single foray as it becomes necessary to repeatedly traverse a road that intersects its route. Female freshwater turtles may make multiple terrestrial movements during the nesting season, potentially resulting in repeated counts of a single individual within a general area. For example, female Pacific Pond Turtles, *Actinemys marmorata*, have been known to make up to 11 overland nesting migrations within a season (Reese and Welsh 1997), which could, if a road transected this route, lead to one individual being recorded up to 22 times. This potential bias can be remedied by individually marking turtles (Cagle 1939), although processing time should be considered when quantifying sampling effort.

OBSERVATIONAL BIAS

There are several disadvantages intrinsic to road surveys. When driving, even at slow speeds, it is inevitable that some individuals (particularly small or cryptic species) will be misidentified or may escape observation altogether. In many historical road surveys amphibians and reptiles are either absent from species lists or are lumped into broad taxonomic categories (Dickerson 1939; Main and Allen 2002). Such generalizations could lead to errors in estimates of population parameters. Adult and sub-adult individuals of most turtle species are more often observed on roads than juveniles (Steen et al., unpubl. data), although the reverse may be true in localized areas following emergence of hatchlings from nests (e.g., McCallum 2003). Observations of relatively high numbers of large individuals may be due to the size discrepancy between young and adult animals, but also may be influenced by disparate movement patterns among different size classes (Loughry and McDonough 1996). Additionally, the size of an individual may influence the likelihood that it is scavenged prior to observation (Kimberly M. Andrews, pers. comm.). These observational biases should be noted when discussing turtle communities and species richness determined via road surveys.

Bias Due to the Spatial Ecology of Turtles

The species observed during road surveys are a reflection of the surrounding habitat, road density, and behavior of that particular species, as well as the skill of the investigator. Habitat specialists may be underrepresented unless a particular habitat is transected by a road. Depending on road density, turtles with small home ranges, highly specific habitat requirements, and limited mobility, (e.g., Bog Turtles, *Glyptemys muhlenbergii*, Chase et al. 1989) are less likely to cross roads than those with large home ranges (e.g., *Gopherus* spp., Diemer 1992). Among freshwater turtles, highly aquatic species, (e.g., Musk Turtles, *Sternotherus* spp.) will be recorded with less regularity than species that frequently undergo terrestrial movements (e.g., *Glyptemys insculpta*).

Furthermore, the sex ratio or age structure of a population may appear biased due to disparities in the movement patterns of aquatic and terrestrial turtles. Within a population, turtles typically exhibit a 1:1 sex ratio (Gibbons 1970; but see Lovich and Gibbons 1990). However, due primarily to their nesting migrations, female freshwater turtles are more likely to be encountered on roads and are often found in greater proportion on roads than in samples based on trapping efforts in wetlands (Steen et al. 2006). The opposite trend is observed among populations of the terrestrial genus *Gopherus* (Steen et al. 2006). Perhaps due to the large home ranges of male tortoises, relative to those of females (Eubanks et al. 2002, 2003), males are more commonly observed along roadways (e.g., McRae et al. 1981) and thus their relative abundance could be easily overestimated within the population.

In addition to seasonality, weather conditions may play a role in how representative a particular sample is of the population as a whole. Freshwater turtles may undertake terrestrial movements, and therefore cross roads, to escape unfavorable habitat conditions related to weather (Gibbons 1986; Aresco 2005b). A road survey conducted during a drought may indicate that a population is increasing relative to previous surveys. However, this may be indicative of individuals undertaking mass migrations to find suitable aquatic habitat (Aresco 2005b), rather than a shift in abundance. Aresco (2005b) found significant differences in the sex ratios and abundances of turtles on roads in drought versus non-drought years and Turner et al. (2003) found annual precipitation may have influenced the species composition of reptiles and amphibians detected in the Whetstone Mountains of Arizona.

Bias due to Aspects of Roads

As described, aspects of the natural history of animals may result in sampling bias during road surveys. However, aspects of the roads themselves may also lead to important biases. For example, caution must be exercised when comparing results of road surveys implemented in different geographic areas and on different types of roads. While a turtle may be less likely to approach and cross a high-traffic volume, four-lane highway than a road with less traffic, the highway encompasses more area than a rural two-lane road due to its greater width. Consequently, animals may be observed more readily on these larger roads. When designing studies that aim to compare results from different areas, traffic volume, road type, and width should be considered. The interaction of these factors and their potential influence on wildlife populations is a field that has received little attention.

Potential Consequences of Road Survey Bias

The purpose of this section is not to dismiss or reject previous research, but rather to suggest how biases associated with road surveys may influence data collection and interpretation. Aresco (2005b) found populations of freshwater turtles were biased towards males within wetlands in northwestern Florida (Florida Cooter, *Pseudemys floridana*, 80% male; Yellow-bellied Slider, *Trachemys scripta*, 73% male; and Stinkpot, *Sternotherus odoratus*, 65% male). However, turtles intercepted at the roadside exhibited a sex ratio biased towards females (57-72% annual proportion of female turtles). Had only road cruising been employed, an inaccurate estimate of population structure may have been obtained.

Hellgren et al. (2000) employed road surveys while studying the demography of the Texas Tortoise, *Gopherus berlandieri*, but did not specify the percentage of the sample captured with this method. The authors noted juveniles were not as vulnerable to capture with road surveys and were therefore underrepresented. Also, the sex ratio of adults was increasingly male biased with age class; older individuals were more likely to be males. This was attributed to higher male survival rates relative to females, the latter experiencing higher mortality due to complications resulting from calcium deficiencies. However, disparate movement patterns relative to the sex and age of an individual may influence the observed sex ratio on roads. The cumulative average yearly movements of young male Texas Tortoises <150 mm are smaller than those of similar sized females (Auffenberg and Weaver 1969). However, adult males occupy larger home ranges than adult females (Judd and Rose 1983); these individuals may search longer distances for mates, leading to an increased likelihood that they will be encountered on roads than will females of similar age.

Bury and Smith (1986) walked along roads in Texas to detect the same species. They found significantly more male tortoises (n = 67) than females (n = 39) on the roads and in the surrounding vegetation and noted that their results differed from a study conducted ca. 40 km away where 1:1 sex ratios of adults were observed (Judd and Rose 1983). In addition, only 1/107 (0.9%) tortoises captured was a juvenile (Bury and Smith 1986); this differs markedly from the nearby population that contained nearly 25% juveniles (Judd and Rose 1983). While Bury and Smith (1986) walked linear transects along dirt roads to characterize Texas Tortoise populations, Judd and Rose (1983)

TABLE 1. Potential biases associated with using roads surveys to draw inference about turtle populations.

Biases	Effect
Abundance estimates	
Influenced only by individuals found on the road	Sample may not be representative of the local population
Individuals may be attracted to the road	Abundance estimates will be inflated
Road mortality and predators may limit populations	Abundance estimates will be low
Features associated with the road may prohibit animals from crossing	Abundance estimates will be low
Essential to mark individuals observed	Processing time and effort will be increased
Community descriptions	
Small species will not be observed as readily	Certain species will not be represented in their true proportion
Cryptic species will not be observed as readily	Certain species will not be represented in their true proportion
Habitat specialists may not be observed along roads	Certain species will not be represented in their true proportion
Demographic parameters	
Small individuals will not be observed as readily	Age class distribution will be biased towards adults
Disparate movements between the sexes	A population's sex ratio will be biased towards a particular sex that moves more
General	
Seasonality of movements	Observations may not be representative of the population on a year-round basis
	Between year comparisons may not be valid if weather conditions or sampling season differed

searched study plots over a five year period. The varying sex ratios and age structure may be due to biases inherent in linear transects, such as road surveys, as females and juvenile terrestrial turtles are less likely to be encountered with this method. However, differing habitat types between the two sites may have also influenced perceived or actual population parameters.

CONCLUSIONS AND RECOMMENDATIONS

There are strategies to minimize potential biases when using road survey data to examine population parameters. Encompassing the entire activity season of a particular species will reduce the influence of seasonal movement patterns. Studies that include road surveys conducted during atypical or varying environmental conditions should identify these events and consider how they may influence observed parameters.

There are clearly biases associated with making inferences about population demography of amphibians and reptiles based on road surveys, and many of these limitations pertain to any type of line transect survey methodology. However, road cruising can still be a useful tool for detecting amphibians and reptiles. By accounting for the inherent limitations of road surveys (Table 1) and employing them in conjunction with various other standardized collecting and trapping techniques, one might obtain a more accurate description of turtle populations. Researchers that incorporate multiple sampling methods should explicitly address the potential biases of each method, and differentiate among data collected using different techniques.

Acknowledgments.—James P. Gibbs, K.M. Andrews, C. Kenneth Dodd, Jr., J.M. Stober, J.L. Gagnon, and anonymous reviewers provided helpful comments on the manuscript. E.P. Cox provided assistance obtaining references.

LITERATURE CITED

Aresco, M.J. 2005a. Mitigation measures to reduce highway mortality of turtles and other herpetofauna at a north Florida lake. Journal of Wildlife Management 69:549-560

_____. 2005b. The effect of sex-specific terrestrial movements and roads on the sex ratio of freshwater turtles. Biological Conservation 123:37-44.

Asaeda, T., and V.A. Ca. 1993. The subsurface transport of heat and moisture and its effect on the environment: a numerical model. Boundary Layer Meteorology 65:159-179.

Ashley, E.P., and J.T. Robinson. 1996. Road mortality of amphibians, reptiles, and other wildlife on the Long Point causeway, Lake Erie, Ontario. Canadian Field-Naturalist 110: 403-412.

Auffenberg, W., and W.G. Weaver, Jr. 1969. *Gopherus berlandieri* in southeastern Texas. Bulletin Florida State Museum Biological Sciences 13:141-203.

Bernardino, F.S., and G.H. Dalrymple. 1992. Seasonal activity and road mortality of the snakes of the Pa-hay-okee wetlands of Everglades National Park, USA. Biological Conservation 62: 71-75.

Boarman, W.I., and B. Heinrich. 1999. Common Raven. Pp. 1-32 *In* The Birds of North America, No. 476. Poole, A., and F. Gill, (Eds.). The Birds of North America, Inc, Philadelphia, Pennsylvania, USA.

_____, and M. Sazaki. 1996. Highway mortality in desert tortoises and small vertebrates: success of barrier fences and culverts. Pp. 169-173 *In* Highways and movement of wildlife: improving habitat connections and wildlife passageways across highway corridors. Evink, G., D. Zeigler, P. Garrett, and J. Berry (Eds.). Proceedings of the transportation-related wildlife mortality seminar of the Florida Department of Transportation and the Federal Highway Administration. Report FHWA-PD-96-041. State of Florida, Department of Transportation, Orlando, Florida, USA.

_____, M. Sazaki, and W.B. Jennings. 1997. The effect of roads, barrier fences and culverts on desert tortoise populations in California, USA. Pp. 54-58 *In* Proceedings, Conservation, Restoration, and Management of Tortoises and Turtles: an international conference. Abemma, J.V. (Ed.). Purchase, New York, USA.

Bury, R.B., and E.L. Smith. 1986. Aspects of the ecology and management of the tortoise, *Gopherus berlandieri*, at Laguna Atascosa, Texas. The Southwestern Naturalist 31:387-394.

Busby, W.H., and J.R. Parmalee. 1996. Historical changes in a herpetofaunal assemblage in the Flint Hills of Kansas. American Midland Naturalist 135:81-91.

Cagle, F.R. 1939. A system of marking turtles for future identification. Copeia 1939:170-173.

Campbell, H.W., and S.P. Christman. 1977. Techniques for herpetofaunal community analysis. Herpetological Review 8:3.

Case, R.M. 1975. Interstate highway road-killed animals: a data source for biologists. Wildlife Society Bulletin 6:8-13.

Chan, J. 1993. Evaluation of methods to reduce road mortality of red-sided garter snakes at Narcisse Wildlife Management Area. M.S. Thesis, University of Manitoba, Winnipeg, Manitoba Canada. 106 p.

Chase, J.D., K.R. Dixon, J.E. Gates, D. Jacobs, and G.J. Taylor. 1989. Habitat characteristics, population size, and home range of the bog turtle, *Clemmys muhlenbergii*, in Maryland. Journal of Herpetology 23:356-362.

Dickerson, L.M. 1939. The problem of wildlife destruction by automobile traffic. Journal of Wildlife Management 3:104-116.

Diemer, J.E. 1992. Home range and movements of the tortoise *Gopherus polyphemus* in northern Florida. Journal of Herpetology 26:158-165.

Dodd, C.K. Jr. 1989. Reptiles on highways in north-central Alabama, USA. Journal of Herpetology 23:197-200.

_____. 1991. Drift fence-associated sampling bias of amphibians at a Florida sandhills temporary pond. Journal of Herpetology 25:296-301.

_____, W.J. Barichivich, and L.L. Smith. 2004. Effectiveness of a barrier wall and culverts in reducing wildlife mortality on a heavily traveled highway in Florida. Biological Conservation 118:619-631.

Duellman, W.E., and A. Schwartz. 1958. Amphibians and reptiles of southern Florida. Bulletin of the Florida State Museum 3:627-709.

Enge, K.M., and K.N. Wood. 2002. A pedestrian road survey of an upland snake community in Florida. Southeastern Naturalist 1:365-380.

Eubanks, J.O., J.W. Hollister, C. Guyer, and W.K. Michener. 2002. Reserve area requirements for gopher tortoises (*Gopherus polyphemus*). Chelonian Conservation and Biology 4:464-471.

_____, W.K. Michener, and C. Guyer. 2003. Patterns of movement and burrow use in a population of gopher tortoises (*Gopherus polyphemus*). Herpetologica 59:311-321.

Fitch, J.S. 1949. Road counts of snakes in western Louisiana. Herpetologica 5:87-90.

Fowle, S.C. 1996. Effects of roadkill mortality on the western painted turtle (*Chrysemys picta belli*) in the Mission valley, western Montana. Pp. 205-223 *In* Highways and movement of wildlife: improving habitat connections and wildlife passageways across highway corridors. Evink, G., D. Zeigler, P. Garrett, and J. Berry (Eds.). Proceedings of the transportation-related wildlife mortality seminar of the Florida Department of Transportation and the Federal Highway Administration. Report FHWA-PD-96-041. State of Florida, Department of Transportation, Orlando, Florida, USA.

Gibbons, J.W. 1970. Sex ratios in turtles. Research in Population Ecology 12:252-254.

_____. 1986. Movement patterns among turtle populations: applicability to management of the desert tortoise. Herpetologica 42:104-113.

Gibbs, J.P., and W.G. Shriver. 2002. Estimating the effects of road mortality on turtle populations. Conservation Biology 16:1647-1652.

_____, and D.A. Steen. 2005. Historic trends in the sex ratio of turtle populations: implications for road mortality. Conservation Biology 19:552-556.

Goodman, S.M., M. Pidgeon, and S. O'Connor. 1994. Mass mortality of Madagascar radiated tortoise caused by road construction. Oryx 28:115-118.

Goosem, M. 2000. Effects of tropical rainforest roads: edge changes in community composition. Wildlife Research 27:151-163.

Haxton, T. 2000. Road mortality of snapping turtles, *Chelydra serpentina*, in central Ontario during their nesting period. Canadian Field-Naturalist 114:106-110.

Hellgren, E.C., R.T. Kazmaier, D.C. Ruthven, and D.R. Synatzske. 2000. Variation in tortoise life history: demography of *Gopherus berlandieri*. Ecology 8:1297-1310.

Hels, T., and E. Buchwald. 2001. The effect of road kills on amphibian populations. Biological Conservation 99:331-340.

Henke, S.E., and M. Montemayor. 1998. Diel and monthly variations in capture success of *Phrynosoma cornutum* via road cruising in southern Texas. Herpetological Review 29:148-150.

Jackson, D.R., and R.N. Walker. 1997. Reproduction in the Suwanee cooter, *Pseudemys concinna suwanniensis*. Bulletin of the Florida Museum of Natural History 41:69-167.

Judd, F.W., and F.L. Rose. 1983. Population structure, density and movements of the Texas tortoise, *Gopherus berlandieri*. Southwestern Naturalist 28:387-398.

Kauffeld, C. 1957. Snakes and Snake Hunting. Hanover House, Garden City, New Jersey, USA.

Knight, R., and J. Kawashima. 1993. Responses of raven and red-tailed hawk populations to linear right-of-ways. Journal of Wildlife Management 57:266-271

Kolbe, J.J., and F.J. Janzen. 2002. Spatial and temporal dynamics of turtle nest predation: edge effects. Oikos 99:538-544.

Leiden, Y.A., M.E. Dorcas, and J.W. Gibbons. 1999. Herpetofaunal diversity in coastal plain communities of South Carolina. The Journal of the Elisha Mitchell Scientific Society 115:270-280.

Lindeman, P.V. 1992. Nest-site fixity among painted turtles (*Chrysemys picta*) in northern Idaho. Northwestern Naturalist 73:27-30.

Loughry, W.J., and C.M. McDonough. 1996. Are road kills valid indicators of armadillo population structure? American Midland Naturalist 135:53-59.

Lovich, J.E., and Gibbons, J.W. 1990. Age at maturity influences adult sex ratio in the turtle *Malaclemys terrapin*. Oikos 59:126-134.

Luckenbach, R. 1982. Ecology and management of the desert tortoise (*Gopherus agassizii*) in California. Pp. 1-37 *In* North American Tortoises: Conservation and Ecology. Bury, R.B.

(Ed.), Washington, D.C., United States Department of the Interior Fish and Wildlife Service. Wildlife Research Report 12.

Nicholson, L. 1978. The effects of roads on desert tortoise populations. Proceedings of 1978 Desert Tortoise Council Symposium 1978:127-129.

Main, M.B., and G.M. Allen. 2002. Landscape and seasonal influences on roadkill of wildlife in southwest Florida. Florida Scientist 65:149-158.

Marchand, M.N., and J.A. Litvaitis. 2004. Effects of habitat features and landscape composition on the population structure of a common aquatic turtle in a region undergoing rapid development. Conservation Biology 18:758-767.

Mazerolle, M.J. 2004. Amphibian road mortality in response to nightly variations in traffic intensity. Herpetologica 60:45-53.

McCallum, M.L. 2003. *Graptemys geographica* (Northern Map Turtle). Nest Over Wintering. Herpetological Review 34:241.

McDougal, J. 2000. Tortoises and terrestrial turtles. Pp. 180-206 *In* Turtle Conservation. Klemens, M.W. (Ed.). Smithsonian Institution Press, Washington, D.C., USA.

McRae, W.A., J.L. Landers, and J.A. Garner. 1981. Movement patterns and home range of the gopher tortoise. The American Midland Naturalist 106:165-179.

Mitchell, J.C. and M.W. Klemens. 2000. Primary and secondary effects of habitat alteration. Pp. 5-32 *In* Turtle Conservation. Klemens, M.W. (Ed.). Smithsonian Institution Press, Washington, D.C., USA.

Obbard, M.E., and R.J. Brooks. 1980. Nesting migrations of the snapping turtle (*Chelydra serpentina*). Herpetologica 36:158-162.

Pike, D.A., A. Dinsmore, T. Crabill, R.B. Smith, and R.A. Seigel. 2005. Short-term effects of handling and permanently marking gopher tortoises (*Gopherus polyphemus*) on recapture rates and behavior. Applied Herpetology 2:139-147.

Prior, K.A., G. Blouin-Demers, and P.J. Weatherhead. 2001. Sampling bias in demographic analyses of black rat snakes (*Elaphe obsoleta*). Herpetologica 57:460-469.

Ream, C., and R. Ream. 1966. The influence of sampling methods on the estimation of population structure in painted turtles. American Midland Naturalist 75:325-338.

Reese, D.A. and H.H. Welsh. 1997. Use of terrestrial habitat by western pond turtles, *Clemmys marmorata*: implications for management. Pp. 352-357 *In* Proceedings, Conservation, Restoration, and Management of Tortoises and Turtles: an international conference. Abemma, J.V. (Ed.). Purchase, New York, USA.

Rodda, G.H. 1990. Highway madness revisited: roadkilled *Iguana iguana* in the Llanos of Venezuela. Journal of Herpetology 24: 209-211.

Rolley, R.E., and L.E. Lehman. 1992. Relationships among raccoon road-kill surveys, harvests, and traffic. Wildlife Society Bulletin 20:313-318.

Seigel, R.A. 1980. Nesting habits of diamondback terrapins (*Malaclemys terrapin*) on the Atlantic coast of Florida. Transactions of the Kansas Academy of Science 83:239-246.

_____, R.B. Smith, J. Demuth, L.M. Ehrhart, and F.F. Snelson, Jr. 2002. Amphibians and reptiles of the John F. Kennedy Space Center, Florida: A long-term assessment of a large protected habitat (1975-2000). Florida Scientist 65:1-12.

Shaffer, H.B., and J.E. Juterbock. 1994. Night Driving. Pp. 163-166 *In* Measuring and Monitoring Biodiversity: Standard Methods for Amphibians. Heyer, W.R., M.A. Donelly, R.W. McDiarmid, L.C. Hayek, and M.S. Foster (Eds.). Smithsonian Institution Press, Washington, D.C., USA.

Smith, L.L., and C.K. Dodd, Jr. 2003. Wildlife mortality on U.S. highway 441 across Paynes Prairie, Alachua County, Florida. Florida Scientist 66:128-140.

Steen, D.A., and J.P. Gibbs. 2004. Effects of roads on the structure of freshwater turtle populations. Conservation Biology 18:1143-1148.

_____, M.J. Aresco, S.G. Beilke, B.W. Compton, E.P. Condon, C.K. Dodd, Jr., H. Forrester, J.W. Gibbons, J.L. Greene, G. Johnson, T.A. Langen, M.J. Oldham, D.N. Oxier, R.A. Saumure, F.W. Schueler, J.M. Sleeman, L.L. Smith, J.K. Tucker, and J.P. Gibbs. 2006. Relative vulnerability of female turtles to road mortality. Animal Conservation 9:269-273.

Stickel, L.F. 1950. Populations and home range relationships of the box turtle, *Terrapene c. carolina* (Linnaeus). Ecological Monographs 20:353-378.

Szerlag, S., and S.P. McRobert. 2006. Road occurrence and mortality of the northern diamondback terrapin. Applied Herpetology 3:27-37.

Temple, S.A. 1987. Predation on turtle nests increases near ecological edges. Copeia 1987:250-252.

Turner, D. S., P.A. Holm, E.B. Wirt, and C.R. Schwalbe. 2003. Amphibians and reptiles of the Whetstone Mountains, Arizona. The Southwestern Naturalist 48:347-355.

Whillans, T.H., and E.J. Crossman. 1977. Morphological parameters and spring activities in a central Ontario population of midland painted turtle, *Chrysemys picta marginata* (Agassiz). Canadian Field-Naturalist 91:47-57.

Wood, R.C., and R. Herlands. 1997. Turtles and Tires: the impact of roadkills on northern diamondback terrapin, *Malaclemys terrapin terrapin*, populations on the Cape May Peninsula, southern New Jersey, USA. Pp. 46-53 *In* Proceedings, Conservation, Restoration, and Management of Tortoises and Turtles: an international conference. Abemma, J.V. (Ed.). Purchase, New York, USA.

Wygoda, M.L. 1979. Terrestrial activity of striped mud turtles, *Kinosternon baurii* (Reptilia, Testudines, Kinosternidae) in west-central Florida. Journal of Herpetology 13:469-480.

DAVID A. STEEN has been the lead research technican of the herpetology laboratory at the Joseph W. Jones Ecological Research Center at Ichauway since 2004. He obtained his Bachelor of Science in Zoology from the University of New Hampshire in 2001 and his Masters degree in Ecology and Conservation Biology from the State University of New York-College of Environmental Science and Forestry in 2003. His thesis described the effects of roads on turtle populations. His current research interests generally pertain to the ecology and conservation biology of vertebrates, particularly snakes and freshwater turtles. David is actively involved with The Gopher Tortoise Council, serving as a co-chair of the Upland Snake Conservation Initiative and newsletter editor.

LORA L. SMITH has been an assistant scientist at the Joseph W. Jones Ecological Research Center since 2001. She received her Bachelor of Science degree from Eckerd College in 1982 and her Masters degree in Wildlife Ecology and Conservation from the University of Florida in 1992. Her Masters research focused on the reproductive ecology of gopher tortoises in north central Florida. For her Ph.D. she studied the status and ecology of the ploughshare tortoise, a rare species endemic to the island of Madagascar. After completing her Ph.D. in 1999, she worked for the U.S. Geological Survey as a research wildlife biologist. Her research while at U.S.G.S. included an assessment of the effectiveness of an ecopassage for wildlife at Paynes Prairie State Preserve in north Florida and development and implementation of an amphibian monitoring program at the Okefenokee Swamp. Her current research interests include conservation biology of pond-breeding amphibians, management of longleaf pine forests for amphibian and reptile diversity, and the natural history of amphibians and reptiles.