

Literature Synthesis of the Effects of Roads and Vehicles on Amphibians and Reptiles

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EXECUTIVE SUMMARY

This report contains a summary of ongoing work on the behavioral, physiological, and ecological effects of roads and vehicles on amphibians and reptiles (herpetofauna). Roads are the ultimate manifestation of urbanization, providing an essential connectivity within and between rural and heavily populated areas. However, the continual expansion of this infrastructure is not without ecological consequences. Road impacts extend across temporal and spatial scales beginning during the early stages of construction, progressing through final completion, and continuing with daily use. The most obvious effects are direct; injury or death of wildlife during road construction or from contact with vehicles and the destruction of habitat. In addition to these readily measurable effects, road impacts are compounded further by a variety of indirect effects of roads on herpetofauna that can be pervasive through habitat fragmentation and alteration that extend to population and community levels. This report further identifies potential threats to amphibians and reptiles by noting and discussing previous research in road ecology that is applicable. The report also provides examples of physiological, ecological, and behavioral traits inherent among herpetofauna that enhance their susceptibility to habitat alterations and environmental changes associated with development and roads, emphasizing areas in which impacts have not yet been documented but are likely. Thus, an ecological framework is presented that can serve to suggest research questions and encourage investigators to pursue goals that relate to direct and indirect effects of road development and subsequent urbanization on herpetofauna. The current and possible approaches for resolving and preventing conflicts between wildlife and roads are also presented. The literature synthesis is the most up-to-date bibliographic reference source for consideration of road effects on U.S. amphibians and reptiles to the best of our knowledge. This report will be of interest to government officials responsible for highway planning, road construction, and environmental impact assessments, and to anyone concerned with incorporating ecological research related to environmental concerns, mitigations, and modifications applicable to U.S. roads and the vehicles that use them.

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INTRODUCTION

“The important thing in science is not so much to obtain new facts as to discover new ways of thinking about them.”

-William Bragg

Human societies, whether urban or rural in population density, depend on transportation networks to establish conduits for people and products. Roads are the ultimate manifestation of urbanization, which occurs in progressive stages across multiple temporal and spatial scales. Between 1950 and 1990, urban land area increased more than twice as fast as population growth (White and Ernst 2003). In 1990, suburban households represented 40% of all U.S. households but accounted for 47% of motor vehicle travel, whereas city households comprised 37% of American households and 29% of vehicular travel (NRC [National Research Council] 1997). As development sprawls outward from the city core, existing transportation corridors are supplemented to support increased traffic volumes (e.g., Forman et al. 2003). Long distance and commercial travel was facilitated by the construction of the U.S. interstate system which consisted of 16,000 km (10,000 mi) of divided multi-lane highway that grew by almost 100,000 km (60,000 mi) in less than 20 years (NRC 1997). Freeway development peaked in 1965 and then slowed, increasing by only 19,200 km (12,000 mi) between 1965 and 1975 (NRC 1997). Approximately 6.4 million km (~ 4 million mi) of public roads spanned the U.S. by the mid-1990s (Fig. 1); between 1998 and 2003, the total increased by 112,654 km (69,845 mi, National Transportation Statistics 2004, www.transtats.bts.gov).

The mass production of vehicles in the 1900s created demand for expansion and efficiency of the road network, particularly in the United States (Forman et al. 2003). This was followed by a 1.6% growth of the population between 1950 and 1965 during the baby boom, with the number of children increasing by 20 million and accounting for half of the population increase (NRC 1997). Consequently, the number of licensed drivers doubled from 1960-1980 as adults comprised 75% of the U.S. population in 1980 compared to 64% in 1965 (NRC 1997). The driver base increased yet again with the entry of women into the labor force. In the mid-60s, only 55% of women were licensed drivers, increasing to 80% by 1985 with 90% of them under the age of 50 (NRC 1997).

Roads facilitate future development of an area, increasing use of surrounding habitats by humans for hunting, collection, and observation of wildlife (Andrews 1990; White and Ernst

2003). The extension of the U.S. road system permits vehicle access to most areas, as evidenced by the fact that 73% of all land lies within only 800 m of a road (Riitters and Wickham 2003). More broadly, the human footprint (i.e., area of impact) has been estimated to cover 83% of the planet's land surface (Vitousek et al. 1997). In fact, anthropogenic activity has transformed between one-third and one-half of the earth's terrestrial surface (Vitousek et al. 1997). A recent analysis identifies land transformation, including road development, as the single greatest threat to conservation of intact natural communities (Sanderson et al. 2002). The authors further noted that the current population of 6 billion people is projected to reach 8 billion by 2020.

The U.S. Bureau of Transportation Statistics (2004, www.transtats.bts.gov) defines an urban area as "a municipality . . . with a population of 5,000 or more." By this definition, many national parks and wildlife refuges have daily visitation levels equivalent to populations of small urban areas and during months of peak visitation have traffic volumes comparable to some cities (National Park Service 2004, www.nps.gov). Therefore, recreational activities in these natural areas may detrimentally impact species that should otherwise be protected (e.g., Seigel 1986). Furthermore, an estimated 10% of roads occur in national forests (~611,420 km, Forman 2000), an amount that could encircle the earth approximately 15 times. In an analysis of road fragmentation in national parks by Schonewald-Cox and Buechner (1992), even the largest parks (up to 9000 km²) encompassed few areas that lie greater than 10 km from roads. Further, 30% of the land area within highly fragmented parks is within 1 km of a road and all land parcels comprising 100 km² were within 500 m of roads. Road management in the parks system should consider not only the division of land within their jurisdiction, but the nature of the landscape surrounding the parks as many wildlife species will cross park boundaries into unprotected habitat.

Roads generate an array of ecological effects that disrupt ecosystem processes and wildlife movement. Road variables that potentially affect wildlife, both directly and indirectly, include size, substrate, age, accessibility, and density. Road placement within the surrounding landscape is possibly the most important factor determining the severity of road impacts on wildlife, because it influences roadkill locations and rates, the presence or absence of species, and the diversity and intensity of indirect effects.

The combined environmental effects generated by roads (e.g., thermal, hydrological, pollutants, noise, light, invasive species, human access), referred to as the "road-effect zone"

(Forman 2000), extend outward from 100-800 m beyond the road edge (e.g., Reijnen et al. 1995). Considered independently, each factor influences the surrounding ecosystem to varying extents and is further augmented by road type and environmental processes including wind, water, and animal behavior (Forman et al. 2003). Based on a conservative assumption that effects permeate 100-150 m from the road edge, an estimated 15-22% of the nation's land area is projected to be ecologically affected by roads (Forman and Alexander 1998), an area about 10 times the size of Florida (Smith et al. 2005). However, some effects appear to extend to 810 m (i.e., 0.5 mi), resulting in 73% of U.S. land area that would be susceptible to impacts (Riitters and Wickham 2003).

Conflicts continually arise because of issues related to roads, wildlife, and adjacent habitats. These conflicts have led experts from multiple fields (e.g., transportation planners and engineers, federal, state, and local governments, land managers and consultants, non-profit organizations, environmental action groups, and landscape and wildlife ecologists) to contribute their knowledge in an effort to explain the "complex interactions between organisms and the environment linked to roads and vehicles" in the field of road ecology (Forman 1998; Forman et al. 2003). The field continues to grow, as evidenced by the increase in scientific publication (Fig. 2) of reviews, bibliographies, and texts that focus on the general effects of roads on natural systems (e.g., Andrews 1990; Forman et al. 1997; Forman and Alexander 1998; Spellerberg 1998; Spellerberg and Morrison 1998; Trombulak and Frissell 2000; Forman et al. 2003; White and Ernst 2003; NRC 2005). Further, there are also brief reviews that elaborate on the specific effects that roads have on wildlife. These reviews are published online (FHWA [Federal Highway Administration] 2000), in conference proceedings (Jackson 1999; Jackson 2000), as unpublished reports (Noss 1995; Watson 2005), and in a peer-reviewed journal (Trombulak and Frissell 2000). However, little attention has been given specifically to amphibians and reptiles (herpetofauna) with the exception of the following: 1) a report that highlights road issues in regard to the influence of development activities on herpetofauna in British Columbia and provides guidelines to improve management practices (Ovaska et al. 2004); 2) a review evaluating the effects of recreation on Rocky Mountain wildlife (Maxell and Hokit 1999); 3) a review focused on Florida herpetofauna by Smith et al. (2005); and 4) a comprehensive synthesis by Jochimsen et al. (2004) with emphasis on direct effects and mitigation efforts for herpetofauna. In this document we elaborate on how roads may cause numerous subtle yet

pervasive effects through indirect processes, and provide an ecological framework for future research on herpetofaunal road ecology (see also Andrews et al. in press).

The extent to which roads are linked to the widespread decline of amphibian and reptile populations (Gibbons et al. 2000; Stuart et al. 2004) is unresolved. Nonetheless, the prospect of mitigating and, even more ideally, preventing the adverse effects that can be attributed to roads seems attainable. A better understanding of how roads affect herpetofauna and the subsequent application of this knowledge will minimize detrimental effects on these taxa. Our objective here is threefold: 1) identify biological characteristics of herpetofauna that increase their susceptibility to roads; 2) discuss how roads and vehicles directly and indirectly affect amphibian and reptile individuals, populations, and communities through direct mortality, habitat loss, fragmentation, and ecosystem alterations; and 3) provide examples of post-construction mitigation and long-term solutions of pre-construction transportation planning and public awareness.

SUSCEPTIBILITIES AND VULNERABILITIES OF HERPETOFAUNA TO ROAD IMPACTS

“I am worried primarily about our ignorance of the ecology and behavior of most extant organisms, a knowledge gap that is so large that, for most species, even in the best-studied regions on Earth, we cannot specify the most basic aspects of their biology.”

-Harry Greene

Considerations of the biological distinctiveness of a taxonomic group are always important for predicting and ultimately addressing potential impacts of environmental alterations. The breadth and diversity of ecological traits and behaviors of amphibians and reptiles enhance their vulnerability to environmental changes associated with road construction and modifications, as well as environmental impacts generated thereafter (e.g., direct mortality, petroleum runoff, road noise). Further, susceptibilities unique to certain species may place herpetofauna at particularly high risk to road impacts. A thorough evaluation of road effects on herpetofauna has not been available heretofore, and documentation of the direct and, particularly, the indirect effects of roads on most species of amphibians and reptiles does not exist. Therefore, it is important to identify vulnerabilities and provide an ecological framework

for how herpetofauna can be expected to respond to both direct and indirect road impacts at the individual and population levels.

A general overview of traits characteristic of amphibians and reptiles can be acquired from standard herpetological textbooks (e.g., Zug et al. 2001; Pough et al. 2004) and does not require the specific citation of published articles. Nonetheless, in the following section we provide specific references for traits that make some species or groups susceptible to various road features, especially those we believe to be sensitive but for which no current data are available. For instance, physiological traits coupled with various behavior patterns can increase susceptibility to the indirect environmental effects of roads in a variety of ways. Further, for many amphibians and reptiles, road features (e.g., traffic density and periodicity) can interact with the seasonal timing of specific movements thereby increasing susceptibility to direct mortality. Such movements are related to migration or dispersal, to the spatial relationships of breeding, hibernation, and foraging sites, and to inherent behaviors. In addition, individual longevities that are characteristic of some species, as well as population size and demographic structure, may determine how roads influence population size and persistence. Finally, the attitude of many people toward herpetofauna needs to be addressed in the context of its potential to increase or decrease the susceptibility of these taxa to roads. We elaborate on examples below of biological traits of amphibians or reptiles that could potentially result in roads causing complications directly or indirectly at individual or population levels.

MORPHOLOGICAL AND PHYSIOLOGICAL ECOLOGY

A wide variety of notable biological characteristics such as moisture requirements of amphibians, temperature requirements of reptiles, and locomotion of both taxa make herpetofauna susceptible to the altered micro-environmental conditions correspondent with road construction, maintenance, and standard use. These traits should be taken into consideration in areas where roads could potentially affect endangered, threatened, or other sensitive species.

Dependence on Moisture

Most amphibians require moist conditions and standing water for breeding, metamorphosis, and hydration (e.g., Pough et al. 2004); therefore, any road features that affect soil moisture or aquatic habitats could potentially affect some species. Skin permeability and

vulnerability to water loss also make it difficult for organisms, such as amphibians, to maintain optimal moisture levels. Desiccation rates increase during dispersal, particularly in altered environments that do not retain natural moisture levels (e.g., Rothermel and Semlitsch 2002), and therefore may be accelerated for some species when they traverse roads. Alternatively, drier soils surrounding the road due to reduced cover and leaf litter could influence the abundances of some amphibian species, particularly woodland salamanders (e.g., Marsh and Beckman 2004). These reduced moisture levels are possibly confounded by problems of chemical run-off and siltation (Semlitsch et al. 2006) in influencing species abundances. Pough and colleagues (1987) found that some salamander species were not significantly affected given that microhabitat disturbance levels were low. No studies have been specifically conducted to evaluate how the direct or indirect effects of roads influence rates of evaporative water loss in amphibians and reptiles.

Temperature Requirements

Herpetofauna are ectothermic (body heat derived primarily from external sources) and are therefore highly sensitive to thermal conditions. According to the thermal coadaptation hypothesis (Bennett 1980; Blouin-Demers et al. 2003) reptiles that naturally experience a narrow range of environmental temperatures will evolve to perform best over that narrow range, relative to temperatures outside the range. Consequently, road temperatures that vary (usually by being higher) from the surrounding natural habitats and ambient conditions, may modify the behavior of some species, especially reptiles (Bennett 1980), at night as well as during the day (Huey et al. 1989; Autumn et al. 1994). In fact, numerous studies have documented that flight behavior and performance of amphibians and reptiles can be affected by body temperature (e.g., Hertz et al. 1982; Rocha and Bergallo 1990; Huey and Stevenson 1979).

Some temperature-related behaviors might actually increase susceptibility of some species to direct mortality on roads, especially among lizards and snakes. For example, gravid female lizards and snakes of some species prefer narrow temperature ranges within which to thermoregulate (e.g., Shine 1980; Brown and Weatherhead 2000) and may be more likely to use edge habitats alongside roads than juveniles, males, or non-gravid females (Blouin-Demers and Weatherhead 2002). This habitat selection is not only influenced by thermoregulatory preferences and site availability but foraging opportunities and predation risk (e.g., Huey and

Slatkin 1976). When road surface temperatures increase and ambient environmental temperatures remain cooler, some species of snakes may remain on the road longer than necessary to cross, or may even be attracted to warm roads at night in order to thermoregulate (Klauber 1939; McClure 1951; Sullivan 1981a; Ashley and Robinson 1996). Andrews and Gibbons (2005) have challenged the geographical ubiquity of this concept, although acknowledge the feasibility of the road to serve as a thermal attractant in some situations where peripheral substrates cool more rapidly than the road.

Focused studies testing the responses of herpetofauna to heating patterns of roads should be investigated. Although behavioral performance may be only subtly affected in most instances, the consequences may be profound and could extend beyond the individual level. For example, thermal-adjusting behaviors that differ among sexes or age classes could lead to differential road mortality.

Sensitivity to Chemical Pollution

High skin permeability exacerbates the susceptibility of amphibians in particular to the alteration of microhabitat conditions on roads and in adjacent habitats. Toxic chemicals emitted from vehicles and compounds used during road maintenance may act as endocrine disruptors in amphibians that reduce reproductive abilities and survivorship (e.g., Lodé 2000; Hayes et al. 2006; Rohr et al. 2006). In a review of toxicological impacts on amphibians, Harfenist (1989) reported that potassium and sodium chloride were highly toxic, but high concentrations of calcium chloride were required to cause mortality. Furthermore, road salts induced the impairment of respiration and osmoregulatory balance.

Although less is known regarding physiological effects of roads on reptiles, it is feasible that there could be similar issues with the uptake of pollutants either from prey items or directly from the environment (e.g., selenium, western fence lizards, *Sceloporus occidentalis*, Hopkins et al. 2005), which can vary with sex and body size (e.g., organochlorine pesticides and mercury, cottonmouths, *Agkistrodon piscivorus*, Rainwater et al. 2005). In snakes, there is large variation in length-mass relationships among species (Kaufman and Gibbons 1975), which suggests that pollutant effects may vary interspecifically and be dependent on concentration. Terrestrial pollution can also affect marine turtles as observed with heavy metal contamination

from prey items (e.g., Caurant et al. 1999), which has been shown to bioaccumulate variably relative to species (Sakai et al. 2000).

Sensory Traits

Although limited investigations have been carried out, the sensory mechanisms underlying communication and environmental awareness of amphibians and reptiles may be disrupted by the construction or presence of roads or by traffic activity. Potential effects on sound, sight, tactile sensations, and smell are all conceivable; thus, any features attributable to roads that directly or indirectly affect acoustic, visual, tactile, or chemical signals of individuals qualify as road impacts on the species. A recent study reported that noise can penetrate up to 350 m from a road and light up to 380 m (Pocock 2006).

Vocalization is critical during breeding for most species of frogs and toads (Gerhardt and Huber 2002), and increased noise levels from traffic could clearly compromise the effectiveness of breeding choruses. This effect could be especially problematic for small populations in which only one or a few males are calling, or for species whose vocalizations are easily overridden by the intensity and frequencies of vehicle noise. A secondary and more subtle impact of traffic-created lighting and noise confusion is that some species may rely on darkness for concealment and use sound as a cue in predator detection. Thus, populations of some species associated with roads may become more vulnerable to predation due to alterations of sight and sound.

Most species of amphibians and many reptiles are partially or strictly nocturnal. Hence, stationary lights associated with highway systems as well as vehicle headlights almost surely influence behavior and activity patterns. There may also be secondary effects if light pollution influences the foraging patterns of prey species (e.g., mice, Bird et al. 2004). Basic ecological research and field experiments should be instructive for determining how increased lighting associated with roads affects different herpetofaunal groups.

Another uninvestigated area is the effect of roadside vibrations on both crossing individuals and those in adjacent habitats. A mechanism for predator detection among many aquatic amphibian larvae is a lateral line system that is sensitive to vibrations. Disruption of the detection capabilities of individuals could reduce their effectiveness at predator avoidance. Another sensory faculty that may be important for some species of herpetofauna, especially

snakes, is tactile stimulation. Snakes cannot hear airborne sounds but are sensitive to surface vibrations. Although few studies have been conducted to determine the sensitivity of snakes to substrate-borne sounds, presumably some species would be aware of and responsive to ground vibrations created by vehicles on and adjacent to road systems.

A further topic demanding research, especially among salamanders and snakes, is the role of roads in influencing chemical signals as sensory mechanisms of intraspecific communication and for detection of prey. The ability to detect odors and pheromones is unquestionably a critical sensory trait for some species, playing a primary role in amphibian migration and orientation (e.g., Duellman and Trueb 1986), and the detection of cues to locate mates (e.g., LeMaster et al. 2001), prey items (e.g., Chiszar et al. 1990), and ambush sites (e.g., Clark 2004) in reptiles. Amphibians have been noted to follow chemical trails (Hayward et al. 2000), which is a possible explanation for the observation of congeners sharing terrestrial refuges (Schabetsberger et al. 2004). Some naïve neonate snakes trail conspecific adults to hibernacula (e.g., Cobb et al. 2005). Pheromone scent trailing, observed in a variety of species, could conceivably be altered by some contaminants, such as oil residues on roads (Klauber 1931) or road substrate type (Shine et al. 2004). Whether road systems might disrupt certain detection abilities because of increased petroleum products on the road itself and in contiguous habitat has been virtually unexplored.

BEHAVIORAL ECOLOGY

The most apparent effect that roads have on amphibians and reptiles is direct mortality that corresponds with behavior patterns of different species that place them in harm's way. The timing and direction of movements from breeding or hibernation sites, daily activity cycles that coincide with traffic patterns, and the attraction of some species to roads, are species-specific phenomena that may increase on-road mortality risk. In addition to warm surfaces, roads provide concentrations of prey for scavengers and habitat for breeding amphibians (roadside borrow pits) or nesting female turtles (road shoulders).

Movement-associated Behavior

A variety of overland movements bring amphibians or reptiles into contact with roads, or with habitats influenced by road construction, traffic flow, or highway operation. The

intrapopulational and extrapopulational movements noted for individual turtles (Gibbons et al. 1990) provide a categorization scheme for identifying the purposes for which other amphibians and reptiles make overland movements that could result in encounters with roads (Table 1).

Behaviors such as movement speed and defensive behaviors (i.e., predator reactions) influence responses and susceptibility to road mortality and fragmentation. Slow-moving animals, or those that cross the road at a wide angle, increase their mortality risk (e.g., Langton and Burton 1997; Rudolph et al. 1998). Slow movements of amphibians (Hels and Buchwald 2001), turtles (Gibbs and Shriver 2002; Aresco 2005b), and snakes (Klauber 1931; Andrews and Gibbons 2005) while crossing roads have been documented. The speed of amphibians and turtles seems fairly consistent across species (but see Finkler et al. 2003 where gravid female spotted salamanders (*Ambystoma maculatum*) show reduced speed relative to males); however, crossing speeds of snakes vary significantly among species, suggesting that snakes may suffer a greater range of road mortality rates than other taxa (Andrews and Gibbons 2005). Variation in demographic characteristics (e.g., sex, age) or physical condition (e.g., gravid, satiated) has not been documented as being related to road crossing speed, although this variation would be expected with snakes since natural differences in speed exist between sexes (Plummer 1997) and are dependent on the time since the last meal was consumed (Garland 1983).

Little is published regarding crossing angles for herpetofauna. Research on snakes demonstrated that individuals almost always move perpendicularly across the road, taking the shortest route possible (Shine et al. 2004; Andrews and Gibbons 2005). The probability of road mortality would correlate directly with the amount of deviation from a perpendicular crossing trajectory as a higher deviation would result in a greater amount of time spent on the road. Furthermore, minimizing crossing distance would suggest that the road is an area that animals are simply passing through and not selecting as habitat.

Immobilization behaviors in response to oncoming or passing vehicles could also significantly influence crossing time and probability of mortality. Mazerolle et al. (2005) found that the strongest stimuli for immobilization behavior across six amphibian species were a combination of headlights and vibration. Andrews and Gibbons (2005) found a high rate of immobilization in response to a passing vehicle among three snake species, at levels that would greatly jeopardize some from crossing a busy highway. These responses would most logically be related to natural predator defenses, where some snakes exhibit flight as an initial defense

(black racer, *Coluber constrictor*) while others immobilize and rely on crypsis (canebrake rattlesnake, *Crotalus horridus*; Andrews and Gibbons 2005).

Daily Movement Patterns

The time when different species are active during the day or night can determine their susceptibility to direct mortality because of daily traffic patterns. Thus, the exclusively nocturnal scarlet snake (*Cemophora coccinea*; Nelson and Gibbons 1972) would be expected to have a lower probability of encountering a vehicle on roads with traffic intensity concentrated during the daytime than would eastern coachwhips (*Masticophis flagellum*), a species active only during the day (e.g., Gibbons and Dorcas 2005). Some species of snakes (e.g., corn snakes, *Elaphe guttata*) shift their times of greatest overland activity contingent on the season and temperature (Gibbons and Semlitsch 1987). Further, some reptile species exhibit crepuscular behaviors during parts of the year (e.g., Klauber 1931) that could result in a coincidence with rush-hour traffic. Regional classification of amphibians and reptiles in regard to their probabilities for overland activity during particular times of day relative to traffic density would be a worthwhile exercise in assessing the potential relative impact of selected roads on target species.

Migration

Migration is typically defined as persistent movement of an individual across longer distances in search of specific resources; these movements generally recur on a seasonal basis as part of an individual's life cycle (Dingle 1996). Amphibians and reptiles migrate in search of mates, breeding or nesting sites, prey, and refugia that tend to be concentrated in distinct habitats that are patchily distributed and seasonally available. Migratory movements may span a variety of habitats, for example black rat snakes (*Elaphe obsoleta*) traverse a mosaic of ecotonal field and forest habitats seasonally (e.g., Weatherhead and Charland 1985). Some species are philopatric, with migratory routes that are similar across successive years (e.g., amphibians, Blaustein et al. 1994; turtles, Buhlmann and Gibbons 2001; snakes, Burger and Zappalorti 1992), while movements of some species appear irregular and erratic (e.g., snakes, Fitch and Shirer 1971). According to Carr and Fahrig (2001), the survival of populations in fragmented habitats depends on the interaction between the spatial pattern of roads and the movement

characteristics of the organisms. Herpetofauna therefore depend on the maintenance of migration corridors, which may be compromised due to excessive on-road mortality or behavioral avoidance (Landreth 1973; Webb and Shine 1997). Depending on the mechanisms driving migratory patterns (e.g., genetic, behavioral), an individual's ability to readily adapt to a road that interferes with the animal's migratory route may be limited (Langton 1989). Deterministic movements by wildlife complicate the ecological provisions that must be retained when managing an area, a process by which an ecological understanding is essential (Gibbons and Semlitsch 1987).

Breeding and Nesting

Basic breeding activity patterns can be diagnostic of the likelihood of road encounters. For example, an individual can be terrestrial for the majority of its life, but moves long distances to wetlands for breeding (e.g., marbled salamanders, *Ambystoma opacum*) or remains terrestrial within a prescribed area (e.g., slimy salamanders, *Plethodon glutinosus*, Semlitsch 2003). Further, some amphibians make repetitive, within-season forays to breeding ponds before final migration to an overwintering site (Lamoureux et al. 2002), and many others migrate *en masse* between breeding ponds and terrestrial habitats (e.g., Holdgate 1989; Ashley and Robinson 1996; Semlitsch 2000). Some reptiles such as aquatic turtles that seek terrestrial habitat for nesting (Buhlmann and Gibbons 2001) and possibly for predator avoidance (Bennett et al. 1970) also traverse multiple habitat types. Most terrestrial reptiles do not have focal breeding sites and are less likely to be affected by the presence of roads in a region in regards to this particular aspect. However, seasonal aggregations have been documented in some oviparous snake species that are widely spaced for the remainder of the year (e.g., Parker and Brown 1980; Gannon and Secoy 1985).

In general, breeding activity patterns are an essential component to incorporate when investigating road effects, as reproductive interactions among sexes are the primary determinant of seasonality (e.g., Aldridge and Duvall 2002), social interactions (e.g., Gillingham 1987), and major movement patterns across the landscape. These factors in turn influence the likelihood of road encounters. For instance, pond-breeding female amphibians cross roads during migration to wetlands to deposit eggs. Further, evidence is mounting that female turtles are more susceptible to road mortality than males because of their attraction to roadsides for nesting sites

(e.g., Aresco 2005a; Steen et al. 2006). Whether lizards and snakes are attracted to roadsides for egg-laying purposes because of habitat alterations is unknown.

Movement to Hibernation Sites

Aside from migrational behavior associated with the seasonal timing of breeding and nesting, some herpetofauna, especially certain reptiles, have predictable overland movements associated with ingress and egress from denning habitat. When such movement patterns place wildlife in association with roads due to historical travel routes, mortality of individuals can be increased and population integrity jeopardized. Long-distance movements have been documented in many species of snakes, especially in colder regions in which long-term hibernation is a necessity and suitable hibernation sites are limited. In northern latitudes, some snakes make loop-like migrations between winter hibernacula and summer foraging habitats (e.g., 17.7 km, red-sided garter snakes, *Thamnophis sirtalis*, Gregory and Stewart 1975; 11 km, prairie rattlesnakes, *Crotalus viridis*, Duvall 1986), with distances and patterns that can vary with sex (dark green snakes, *Coluber viridiflavus*, Ciofi and Chelazzi 1991). Extensive documentation exists that some species of large snakes traverse great distances between summer feeding areas and hibernation dens (e.g., Imler 1945; Parker and Brown 1980; King and Duvall 1990; Fitch 1999). The mean overland distance moved by timber rattlesnakes (*Crotalus horridus*) during a year in the New Jersey Pine Barrens was more than 1 km (Reinert and Zappalorti 1988). Movements between feeding areas have been documented for the federally threatened copperbelly watersnake (*Nerodia erythrogaster*), which moved long distances terrestrially between wetlands during warm months, presumably in search of foraging opportunities (Hyslop 2001). Any situation that involves movement to and from hibernacula or foraging areas, could readily lead to fatal encounters for a species if roads are constructed between critical areas.

Dispersal

Virtually all species of herpetofauna engage in dispersal activities during some stage of their lives. The metamorphosing young of pond-breeding amphibians disperse from the wetland. Most hatchling turtles, lizards, and snakes disperse overland from the nest site, and the young of live-bearing species move from the birth site. Dispersal of some amphibians

encompasses long distances (more than 500m) from breeding ponds (Semlitsch and Bodie 2003) increasing their likelihood of traversing roads (see Bonnet et al. 1999 for snakes). In contrast, individuals that inhabit small home ranges and are limited in dispersal ability are subject to the isolation effects of fragmentation (Andrews 1990; Boarman and Sazaki 1996).

Defensive Behaviors

Amphibians and reptiles use a variety of mechanisms to defend themselves from predators. Although herpetofauna are adapted to avoid or deter many of their would-be predators under natural conditions, the creation of road systems can potentially interfere with normal behaviors. One of the most obvious road characteristics that can put some species at risk is exposure while traversing open space, regardless if traffic is present. A secondary problem is the tendency of some species to avoid the open space of a road (e.g., snakes, Andrews and Gibbons 2005), which could result in genetic isolation of populations. Roads may also directly or indirectly affect additional defensive behaviors, such as by increasing the susceptibility of predation in species that depend on camouflage to avoid detection. The replacement of natural plant communities with roadside plantings that differ in species composition (see Indirect Effects section) could increase exposure of some prey species to predators relative to natural conditions.

Foraging Behavior

A straightforward principle of feeding ecology is that if a barrier is placed between an animal and its food source, individuals cross the barrier if passable or attempt to circumvent if impassable. Many species of snakes make overland movements from hibernation sites to locations where prey are likely to be found (e.g., prairie rattlesnakes, King and Duvall 1990; timber rattlesnakes, Reinert 1992; cottonmouths, Glaudas et al. 2006). Additionally, several venomous species (e.g., eastern diamondback rattlesnakes, *Crotalus adamanteus*, Brock 1980; rattlesnakes, *Crotalus* spp., Kardong and Smith 2002) are known to follow mammalian prey for several meters following envenomation. Desert tortoises (*Gopherus agassizii*) in the Mojave Desert have been reported to travel overland to acquire dietary supplements of localized nutrients (Marlow and Tollestrup 1982), a behavior pattern that could be dramatically affected if a road were placed between their normal activity area and habitats with suitable soil nutrients.

Freshwater turtles living in an ephemeral wetland habitat will travel overland to another wetland if the ephemeral habitat becomes unsuitable due to diminished prey availability. Any of these situations can lead to negative impacts on certain populations by resulting in direct mortality on roads, or by separating some or all of a population from a feeding source. Another cause of mortality for reptiles related to feeding is the consumption of road-killed carrion (Berna and Gibbons 1991), resulting in their becoming roadkill victims themselves (see Indirect Effects section).

Communication and Social Behavior

Many of the direct and indirect effects of roads on amphibian and reptile behaviors associated with intraspecific communication and social behaviors have been noted above. Roads clearly have the potential to disrupt air-borne sound communication of anurans and migratory, breeding, or nesting routes of amphibians, snakes, and turtles. The ultimate impacts on herpetofaunal populations as a consequence of the species-specific susceptibilities are yet to be determined for most situations and most species.

DEMOGRAPHIC AND LIFE HISTORY TRAITS

The persistence of a species in fragmented landscapes is dependent on its life history and ecology. Thus, many anuran populations are dependent on recruitment and dispersal of juveniles (Sinsch 1992; Semlitsch 2000; Hels and Nachman 2002; Joly et al. 2003). Road mortality may be particularly detrimental to populations of species with low reproductive rates (Rosen and Lowe 1994; Ruby et al. 1994; Fowle 1996; Kline and Swann 1998; Gibbs and Shriver 2002). Additionally, habitat generalists may be more adaptable to altered conditions created by roads and urbanization than specialist species (geckos, Sarre et al. 1995; skinks, Prosser et al. 2006; snakes, Kjooss and Litvaitis 2001). Lastly, our ability to detect and measure road impacts is reliant on the success of sampling techniques. Due to the covert nature of many herpetofaunal species, sampling methods can be particularly challenging (Lovich and Gibbons 1997).

Susceptibilities of herpetofauna to roads may vary within populations due to behavior patterns that vary by age or sex. Adult behavior can not always be used to accurately interpret juvenile behavior, due to different physiological needs (e.g., water retention), predator

composition (e.g., Rothermel and Semlitsch 2002) and ecological requirements (e.g., greater canopy and habitat cover, Gibbs 1998a; deMaynadier and Hunter 1999). For example, hatchlings of many species of freshwater turtles travel overland between nests and aquatic habitat, whereas juveniles are less likely to leave the aquatic habitat than are adults.

Sex Ratios

In many species of amphibians and reptiles, one sex may be more susceptible to road mortality or indirect impacts of roads due to differential behavior between the sexes. For example, female Italian crested newts (*Triturus cristatus*) emigrated longer distances from water than males (Schabetsberger et al. 2004). Further, the sexes may experience differential vulnerabilities that could influence risk of road mortality. For instance, experiments with five species of Australian scincid lizards demonstrated that running speeds of gravid females were reduced by 20-30% and basking behaviors were increased (Shine 1980). Roth (2005a) suggested that habitat loss adjacent to riparian areas would have the greatest impact on gravid female cottonmouths because they moved the farthest from the core area most frequently, even though males had the largest home range sizes (Roth 2005b). Habitat use varies with age class, sex, and season for many species of herpetofauna (e.g., snakes, Reinert and Kodrich 1982; Madsen 1984). Dalrymple et al. (1991) urged the need to incorporate both sex and age into models of seasonal activity patterns, necessary components of road impact assessments. The effects of sex-biased road mortality on sex ratios will be discussed further in the Population Demographics section.

Populations of some reptile species may actually be predisposed to producing aberrant sex ratios as a consequence of artificial environmental conditions associated with roads. Environmental sex determination has been demonstrated in American alligators (*Alligator mississippiensis*, Ferguson and Joanen 1982), with male alligators produced at higher temperatures and females at lower ones. Nesting within road shoulders by alligators could result in an excess of males in a localized area due to elevated temperatures. Most species of turtles that have been examined exhibit environmental sex determination (e.g., Bull and Vogt 1979; Mrosovsky and Yntema 1980; Ewert and Nelson 1991), where nest temperature during the first third of incubation determines the sex of developing embryos. Extensive variability has been reported, but 30°C is generally regarded as the pivotal temperature, above which hatchlings

emerge from the nest as females and below which they are males, the reverse of that observed for alligators. The ranges of temperature on either side of 30°C in which both sexes are still produced vary interspecifically and possibly intraspecifically. In some species, females are produced at both the highest and lowest viable temperatures, with males being produced at intermediate temperatures (Ewert and Nelson 1991).

The basic trait of environmental sex determination coupled with the fact that many species of turtles apparently nest selectively on road shoulders and roadsides when suitable nesting sites are available (e.g., Aresco 2005a; Steen et al. 2006), suggests the possibility of roads influencing sex ratios. If shoulders and roadsides are suitable for nesting, sex ratio modifications could prevail, with an excess of female turtles being produced because of high temperatures compared to surrounding nesting areas shielded from the sun by vegetation. However, road shoulders could possibly have lower than normal environmental temperatures under some circumstances due to wind exposure, resulting in a sex ratio favoring males.

Longevity

Many species of amphibians and reptiles exhibit extended longevity under natural conditions (Gibbons 1987; Gibbons et al. 2006). Although being long-lived does not increase the annual probability of an individual being killed on a highway, it can be indicative of species that have evolved under circumstances in which older animals experience low levels of mortality attributed to predators or disease under natural conditions. In some species, long-lived females have the highest survivorship and are the major contributors to population sustainability (e.g., Congdon et al. 2001; Litzgus 2006). Species that frequently cross roads succumb to direct mortality from traffic. Roads and traffic are comparable to a new predator for which an amphibian or reptile species has evolved no natural defenses and has no innate adaptations to increase survivorship. As a result, populations may become unstable due to the additive mortality experienced by older individuals.

SPATIAL HETEROGENEITY

As road density increases, the probability that individuals reliant on landscape complementation (i.e., spatial arrangement of necessary habitat types) will be killed or injured by traffic while in search of resources increases (Fahrig and Grez 1996). Species that depend on

a non-fragmented landscape to complete their life cycles (e.g., Dunning et al. 1992; Pope et al. 2000) will be in greatest jeopardy. These organisms are considered vulnerable to habitat fragmentation because their subpopulations periodically go extinct locally and must be re-established through dispersal from neighboring sources (Lehtinen et al. 1999). Not only is there a gradient of vulnerability across species, some species are more area-sensitive than others (Hager 1998). Habitat fragmentation is doubly concerning because it not only reduces the quality of habitat, but immediately reduces the quantity (Fahrig 1999).

Landscape permeability and maintenance of movement corridors are critical to allow for natural fluctuations in metapopulation dynamics (Pulliam 1988) of amphibians and reptiles (Gibbs 1998a; Marsh and Trenham 2001), which ultimately influence extinction and recolonization rates (Merriam 1991; Laan and Verboom 1990). Many herpetofaunal species require not only the terrestrial periphery of wetlands, but corridor linkages with other isolated water bodies (Gibbons 2003; Roe et al. 2003). The degree of isolation is determined by considering distances between habitat patches and any features that hinder movement between them (Vos and Chardon 1998). Sjögren (1991) suggested that metapopulation dynamics of amphibian populations are necessitated by the historical, discontinuous distribution of wetlands across the landscape. Interpopulation proximity and connectivity were identified as important factors for the persistence of a northern metapopulation of pool frogs (*Rana lessonae*, Sjögren 1994). The degree of connectivity across the landscape is species-specific, varying with dispersal ability and the number of dispersing individuals (e.g., Laan and Verboom 1990). Several studies of small or isolated habitat patches have documented the absence of anuran species, including pool frogs (Sjögren 1991, 1994), common frogs (*Rana temporaria*, Loman 1988), common treefrogs (*Hyla arborea*, Vos and Stumpel 1996), and moor frogs (*Rana arvalis*, Vos and Chardon 1998).

INTERACTIONS WITH HUMANS

Many species of herpetofauna are not heralded by certain members of society, a response that is contrary to many ancient cultures (some presently) that embraced amphibians and reptiles with reverent symbolism. In particular, snakes are widely maligned, yet create an insatiable source of curiosity and awe (e.g., Wilson 2003). Rodent-eating snakes provide a particularly useful ecological service in consuming animals that are social and health nuisances

near human settlements (Parmenter et al. 1993). Many amphibians and reptiles often retreat or experience population decline in the presence of humans (see references throughout this report). Others exhibit behavioral alterations, such as reduced movement or altered patterns, for which the life-history consequences are not biologically understood (e.g., Parent and Weatherhead 2000).

Additionally, many herpetofaunal species are furtive animals and are therefore rarely encountered. This lack of steady interaction between herpetofauna and humans has led to a populace that is largely uneducated about the true nature and behavior of this group of animals (Gibbons and Buhlmann 2001), an ignorance which can lead to fear. Snakes ranked as the top phobia of Americans, a trend that was greater in women than men and decreased overall with increasing education levels (Mittermeier et al. 1992).

Swerving to miss animals on roads is the second greatest cause of single car accidents in the U.S. (Sherman 1995); however some drivers will intentionally run over certain species. While this behavior is particularly prevalent with snakes, intentional killing on roads has been noted with turtles as well (Boarman et al. 1997). Deliberate killing of snakes is noted throughout the literature and known to be a common activity in many regions of the world (e.g., Klauber 1931; Langley et al. 1989; Bush et al. 1991; Rubio 1998). Many species of snakes present a relatively large target as they crawl across roadways, which may affect the frequency of intentional killing (Whitaker and Shine 2000). Langley et al. (1989) conducted a survey of college students and found that both males and females chose to intentionally run over a snake more than any other animal. Aside from a common distaste for herpetofauna, drivers are largely uneducated regarding wildlife behavior on roads and how they respond to approaching vehicles (e.g., squirrels zigzagging, cats beelining); locals in New Hampshire have suggested incorporating wildlife behavior elements into driver-education programs (Sherman 1995).

Roads increase the degree of human-wildlife interactions as they facilitate an increased use of surrounding habitats by humans, the hunting and collection of amphibians and reptiles, and future development of an area. Roads provide easy access to the movement corridors of amphibians and reptiles, placing local populations under pressure from human predation and collection (Bennett 1991; Krivda 1993; Ballard 1994; McDougal 2000). Animal presence in urban areas surrounding roads enables human collection (Dodd et al. 1989) and could contribute to the further decline of already endangered species (eastern indigo snakes;

Drymarchon couperi, Whitecar 1973; Kuntz 1977). There are also secondary interactions that can result in wildlife death, such as the disposal of litter along highways and in areas with increased human activity. A two-year survey conducted in Virginia along 4.34 km of highways and interstates counted 10,681 discarded bottles, 427 of which had trapped a total of 795 vertebrates, including 28 lizards and plethodontid salamanders (Benedict and Billeter 2004). An even more threatening example is the mortality incurred by domestic mammalian pets and by feral animals. Feral cats that are established on western Milos are predators of Milos vipers (*Macrovipera schweizeri*), as evidenced by the loss of two telemetered individuals (Nilson et al. 1999). While habitat loss was the major cause for blue-tongued lizard (*Tiliqua scincoides*) injury in highly urbanized areas, domestic pets were the primary threat in the suburbs (Koenig et al. 2002). Further, adults were most susceptible to mortality by vehicles and dogs during the mating season (springtime), while domestic cats mostly preyed on juveniles. Lastly, habitat loss and road impacts related to human behavior can occur from increased fire frequency around roads, mostly as a result of unextinguished cigarettes.

URBANIZATION AND FRAGMENTATION

Urbanization accompanied by unmanaged human expansion is the greatest threat to wildlife persistence. This occurrence encompasses many of the major threats to animal populations, primarily habitat loss, spread of alien species, overexploitation, and disease (Wilcove et al. 1998). Habitat loss and fragmentation are often considered the most pervasive and serious threats to amphibians and reptiles (e.g., Mittermeier et al. 1992) and the catalyst for the federal listing of many species (Wilcove et al. 1998). Urbanization occurs at multiple spatial scales from the opening of a store, construction of a residential neighborhood or development of a city. However all of these are enabled through the establishment of roads. Assessing the susceptibility of wildlife to impacts from urbanization is complex because natural trophic dynamics are altered due to shifts in resources and species composition (Faeth et al. 2005) and the appropriate scale for investigation varies with taxa (Mazerolle and Villard 1999).

The importance of managing urbanization and fragmentation is emphasized by the emergence of research findings stating the importance of landscape composition, contiguous habitat, and the critical nature of the surrounding area (e.g., Guerry and Hunter 2002; Gibbons 2003; Roe et al. 2004), including the provision of intact habitat buffer (Semlitsch and Bodie

2003) for species persistence. Knutson et al. (1999) found a significant negative correlation between amphibian abundance and richness and the presence of urban land. Physical instability in streams in Atlanta, GA, resulting from urbanization, had a negative impact on salamander population densities, the degree of which was inversely proportional to the amount of urbanization (Orser and Shure 1972). Nest-site selection by loggerhead sea turtles (*Caretta caretta*) was positively correlated with distance to the nearest human settlement (Kikukawa et al. 1999).

Lastly, the stability and persistence of source-sink dynamics requires permeability of the surrounding landscapes to enable local recolonization following extinction (Pulliam 1989). However, if no corridor is available, a local extinction will remain permanent as the population is disconnected from its source, which likely contributes to resistance between patches (Bennett 1991), thereby catalyzing population isolation. These dynamics are essential to many amphibian populations (Marsh and Trenham 2001), yet are often disregarded during landscape development and road placement.

There are, however, several amphibian and reptile species that will readily reside in human-disturbed areas (e.g., Neill 1950), and are specifically tolerant of human presence along roads (e.g., Shine and Mason 2001). In a comparison of residential development and an undeveloped park, Delis et al. (1996) found that while sensitive species are not present in more developed areas, amphibian species that opportunistically breed (e.g., *Rana* spp.) are able to persist in residential areas. Furthermore, tiger salamanders (*Ambystoma tigrinum*) have been observed breeding in particularly disturbed habitats including wetlands decimated by grazing and water treatment plants in Yellowstone National Park (DMJ unpubl. data). Abandoned houses, trash piles, and disturbed areas are known to be visited and sometimes inhabited by certain snake species (e.g., Zappalorti and Burger 1985; Ernst and Ernst 2003). We question the ultimate sustainability of these occurrences due to the seemingly inevitable fate of wildlife frequently encountering humans and urbanization. Sometimes species appear to occur in healthy numbers in suburban areas, but are no longer evident over time and following increased urbanization. Minton (1968) found reductions in herpetofaunal species presence and an apparent loss of breeding activity in a suburban area over a 20-year period. Regardless, the persistence of species that are not tolerant of urbanization could be limited, especially those residing in regions (e.g., Florida, eastern kingsnake, *Lampropeltis getula*, Krysko and Smith

2005) or habitat types (e.g., coastal sandhills, eastern indigo snake, Lawler 1977) that are economically prime for development.

DIRECT EFFECTS

“Now I do come from a part of the country where the people say that the only thing in the middle of the road is a yellow line or roadkill”
– Blanche Lincoln

Researchers have conducted surveys along roads in an effort to quantify the most conspicuous effect that roads impose on wildlife--mortality inflicted by vehicles. Direct effects involve injury or mortality that occurs during road construction or subsequent contact with vehicles associated with increased urban development. Direct mortality from roads is prevalent throughout the world on public and private lands. Further, although urban areas present obvious concerns for roadkills, road mortality has been considered the greatest non-natural source of vertebrate death in protected areas (e.g., parks and reserves, Bernardino and Dalrymple 1992; Kline and Swann 1998). As our road network continues to expand, so does the death toll with estimates as high as one million vertebrate fatalities along America's roadways each day (Lalo 1987; White and Ernst 2003).

Historically, published reports of roadkills were often based on a single trip and rarely distinguished observations by species. Further, some of the earlier papers are incidental documentation on pleasure or business-related road trips where data collection was motivated by concern of the drivers over the frequency of roadkill (e.g., Stoner 1925). Over time, scientists fine-tuned questions to gain insight into the interactions between roads and wildlife. To date, the literature is saturated with investigations focused on charismatic megafauna and birds, but the question remains, what role do roads play in the worldwide decline of amphibian and reptile populations? Reviews that summarize research in the emerging field of road ecology glaze over these taxa at best. Many studies have been designed to document all vertebrate mortalities across a given survey area and include the proportion of herpetofauna observed (Fig. 3). However, over the decades the number of studies investigating the impacts of traffic, particularly direct mortality, on these taxa has increased (Fig. 4). In Table 2 we provide a summary of published road studies that report herpetofaunal fatalities. For more detail regarding specifics of these studies please see Jochimsen et al. (2004).

Direct mortality of herpetofauna has been documented since the beginning of the 20th century, but the effects of roadkill were not observed until decades later (e.g., amphibians, Puky 2004; snakes, Fitch 1999). Studies investigating road effects specifically on amphibians have been conducted in Europe perhaps longer than in any other region, and mitigation efforts have been in place since the 1960s (Puky 2004, 2006). A review of five road studies conducted in central Europe reported that amphibians were observed more frequently than specimens of four other vertebrate taxa, comprising 70.4 to 88.1 percent of all observations (Puky 2004). Kuzmin et al. (1996) synthesized all data concerning the amphibians inhabiting the province of Moscow and include a summary of the conservation issues affecting these populations, which include habitat destruction, and fragmentation due to roads.

While on-road mortality is generally the most significant of the direct effects, mortality associated with construction activities may also have severe consequences for amphibians and reptiles present within the impending path of development. For example, Goodman and colleagues (1994) reported the entrapment of radiated tortoises (*Geochelone radiata*) that had fallen down a steep embankment adjacent to an unfinished road in Madagascar. These individuals died from exposure to sun and heavy rainfall, or were collected by humans. In Yellowstone National Park, recently metamorphosed western toads (*Bufo boreas*) were inadvertently buried during blading of the shoulder areas along the Grand Loop Highway north of Old Faithful (Charles R. Peterson pers. comm.). The late summer blasting of a rocky outcrop in eastern Idaho for road expansion killed terrestrial garter snakes (*Thamnophis elegans*) known to use the site for hibernation; subsequent surveys have not detected individuals in the remaining habitat (Charles R. Peterson pers. comm.). The loss of certain habitat features, such as rocky areas, due to construction activities could also alter the prey base that snake species depend on for survival (e.g. eastern kingsnakes, Smith and Dodd 2003). Given that construction activities often have unforeseen consequences, it is advisable for a biologist to perform environmental assessments of the road sites before, during, and after construction.

One of the greatest challenges in addressing direct effects on herpetofauna is that because of human safety issues, prioritization is given to studies regarding large mammalian megafauna. However, in southeastern areas where roads transect water bodies, American alligators can be found crossing roads. Such wildlife-vehicle interactions can present a threat to wildlife and humans. Traffic deaths have been suggested as the major known source of

mortality for some large, endangered species, including the American crocodile (*Crocodylus acutus*, Kushlan 1988 and Harris and Gallagher 1989); automobile collisions accounted for 46% of human-related mortality of this species in southern Florida (Gaby 1987). Crocodilians also present a human safety concern for drivers as evidenced by the death of a woman when her car flipped after a collision with an alligator crossing Highway (HWY) 17 in Jasper County, South Carolina (Associated Press, 11 June 2005). Although this prioritization is a logical one, neglect of smaller wildlife might result in a missed opportunity to deal with road mortality before rates are irreparable.

With the exception of areas in which herpetologists have collected data, wildlife collisions with “harmless” species are not generally reported as they do not often present a direct human safety threat or substantial automobile damage. However, we note that roadkill is distracting, resulting in deviant driver behavior. This attitude is particularly true with snakes, which are frequently a target of intentional killing where drivers will actually swerve to run over animals (e.g., Langley et al. 1989). Roadkill even presents bizarre concerns as apparent by the vulture that collided with the tank of the space shuttle Discovery in Cape Canaveral, FL while scavenging on road-killed carcasses (Associated Press, 27 April 2006). These situations concerning the deaths of wildlife and human alike are readily avoidable in most instances by proactive planning of road designs.

Many factors influence roadkill rates. We will briefly present some of those factors below, and Table 2 elaborates on correlative findings specific to study. In this section, we will mention the importance of organismal ecology, road characteristics, bordering habitat, and weather conditions as interacting factors of influence not only for herpetofauna (e.g., Puky 2004), but other taxa as well (e.g., Clevenger et al. 2003). We then expand on the use of road driving as a survey technique and data modeling to assess ultimate impacts.

ORGANISMAL ECOLOGY

Life history parameters influence not only severity of road impacts in general (e.g., Dodd et al. 1989) as discussed in the Susceptibilities section, but also the overall likelihood of observing an individual on the road as related to biotic and abiotic conditions. For amphibians, road mortality may be proportionally high during pulses of movement related to fluctuations in water level (e.g., Smith and Dodd 2003), breeding (e.g., Hodson 1966; Fahrig et al. 1995;

Ashley and Robinson 1996), and dispersal (McClure 1951; Palis 1994), behaviors that vary across age and sex. Road mortality is likely substantially higher for some species of anurans relative to most salamanders due to higher reproductive output and tendency to breed in roadside habitats. In addition, anurans possess a delicate body structure that may make them more vulnerable to the high pressure wave created by a passing vehicle, which can create enough force to cause the animal to expel its innards without experiencing a direct hit from a vehicle (Holden 2002). Reptile examples include movements related to fluctuations in water level (Bernardino and Dalrymple 1992; Aresco 2005b; Smith and Dodd 2003), adult males searching for mates (Bonnet et al. 1999; Whitaker and Shine 2000; Jochimsen 2006b), and nesting migrations of adult females in the spring (Fowle 1996; Bonnet et al. 1999; Haxton 2000; Baldwin et al. 2004).

The detectability of some animals might be increased by high mortality and long carcass persistence, whereas other characteristics might result in underestimation. For instance, slow-moving turtles, especially species that retreat into their shells when vehicles pass are highly likely to be killed while crossing roads. However, testudines are long-lived species that likely experience irreparable population impacts when adult females are killed (Congdon et al. 1993) when crossing roads, and therefore, likely suffer from road mortality disproportionately to most other herpetofaunal species. On the other hand, mortality counts of lizards could easily be considered underestimations. The lack of evidence for high mortality of lizards could be a detection issue due to small size and rapid deterioration of road-killed specimens of many species (e.g., Kline and Swann 1998). However, lizards could actually experience lower mortality rates due to their ability to cross roads faster than other reptiles (Vijayakumar et al. 2001; but see Kline et al. 2001 for estimates predicting higher mortality rates in lizards than snakes). Also, most species of lizards do not migrate seasonally and exhibit high site-fidelity within small home ranges, potentially limiting their encounters with roads (Rutherford and Gregory 2003).

ROAD CHARACTERISTICS

Road placement is the quintessential feature that determines the diversity and severity of road impacts on the surrounding wildlife and habitat. Roads placed in the vicinity of water bodies, particularly wetlands and ponds, may be associated with high levels of road mortality

(e.g., Ashley and Robinson 1996; Fowle 1996; Forman and Alexander 1998; Smith and Dodd 2003). Road placement may alter home range size and dimensions, as well as habitat use and selection. Boarman and Sazaki (1996) found that individuals whose ranges were bisected by roads were more likely to use road edges or cross roads for foraging and mating activities, thereby increasing their chance of being killed. Additionally, on a landscape level, the pattern and spatial distribution of roads can determine fragmentation levels and therefore the extent of population-level impacts (e.g., turtles, Gibbs and Shriver 2002). Further, road distribution not only influences species occurrence and persistence, but also species richness (tiger salamanders, Porej et al. 2004).

Road density is measured as the total length of roads per unit area and can serve as a useful index for addressing the ecological impacts of roads and vehicles on landscape connectivity and wildlife movement (Forman and Hersperger 1996). Increased road density inevitably results in a decrease in patch size and available habitat which results in increased probability of road encounter and number of road-killed individuals, ultimately reducing population sizes. Several studies have determined effects of road density on populations and species richness (Dickman 1987; Halley et al. 1996; Vos and Stumpel 1996; Findlay and Houlahan 1997; Vos and Chardon 1998; Knutson et al. 1999; Lehtinen et al. 1999; Findlay and Bourdages 2000); these findings will be discussed more directly in the Effects on Higher Levels of Ecological Organization section.

The distribution of road densities across the landscape affects the degree of habitat loss. The higher the road density and the more dispersed the distribution, the greater the habitat loss. Rowland et al. (2000) concluded that evenly spaced roads had the most extensive impact on surrounding habitat, while clustered road configurations left larger blocks of unaffected habitat. Further, this study demonstrated that it is possible to have an area with relatively high road density, but habitat loss equivalent to an area with lower road density depending on the spatial distribution of roads. Similarly, in a modeling assessment by Jaeger and colleagues (2005a), population persistence was higher if roads were spatially clustered as opposed to evenly distributed across the landscape. However, they further found that if the degree of animal avoidance was low, it was better to maintain sufficient core habitat away from the road than to keep the number of patches low (Jaeger et al. 2006).

Road mortality can also increase when surges of animal movement coincide with increased traffic volume (e.g., Joly et al. 2003; Table 2). More vagile species are more vulnerable to increases in traffic densities, as evidenced by negative impacts on northern leopard frog (*Rana pipiens*) population density up to 1.5 km from the road (Carr and Fahrig 2001). Dalrymple and Reichenbach (1984) noted a considerable rise in the road mortality of snakes, including endangered plains garter snakes (*Thamnophis radix*), when migrations to over-wintering hibernacula coincided with peak levels of hunting activity in a wildlife area in Ohio. Seasonal variation of habitat use within a population of massasauga rattlesnakes (*Sistrurus catenatus*), an endangered species of rattlesnake, on Squaw Creek Wildlife Refuge in Missouri resulted in an overlap of peak snake movements and human visitation to the refuge, resulting in elevated mortality levels during spring and autumn migrations (Seigel 1986). Additionally, Bernardino and Dalrymple (1992) found that 56% of annual road mortalities of snakes in Everglades National Park could be attributed to high visitation rates to the park coinciding with increased movement of snakes. However, several studies suggest that nocturnal species experience reduced susceptibility to road mortality due to lower traffic levels at night (Dodd et al. 1989; Enge and Wood 2002; Jochimsen 2006a; Andrews and Gibbons in press).

Traffic levels can reduce permeability of the road, essentially creating a barrier to movement by inflicting high rates of mortality. Franz and Scudder (1977) noted that 55% of snakes crossing HWY 441 across Paynes Prairie (n=132) were killed in the first lane and only 21 snakes reached the far lane of the two-lane highway, where they were ultimately run over. In a one-year survey along U.S. 441 at Paynes Prairie, Smith and Dodd (2003) observed only 26 animals alive on the road (AOR) surface but observed almost 3000 dead amphibians and reptiles (Table 2), and concluded virtually all crossing attempts by wildlife would be unsuccessful. Of the 26 AOR animals, 11 were basking within the right-of-way, 3 crossed successfully, 7 were injured or roadkilled, and 5 turned around and retreated in the original direction. Both of these studies from Paynes Prairie observed few individuals within the grassy median that separates the north- and south-bound lanes of the highway, further supporting a low success rate of crossing. Aresco (2004, 2005b) found that U.S. 27 creates an impenetrable barrier for turtles along the 1.2 km section bisecting Lake Jackson in Tallahassee, Florida. This highway has traffic volumes of 21,500 vehicles/day and in addition to the 612 turtles discovered dead on the road (DOR), 8,209 individuals were captured along drift fences that restricted them

from entering the highway. Using a model from Hels and Buchwald (2001), Aresco (2005b) estimated the likelihood of mortality was 0.98; this estimate is potentially conservative, as there has been no evidence of turtles reaching the median.

Some studies have found that even low traffic volumes may be sufficient to cause high levels of amphibian mortality. On a road in the Netherlands near a breeding pond for common toads (*Bufo bufo*), a flow of 10 vehicles per hour resulted in 30% mortality of migrating females and the author projected that a flow of 60 vehicles per hour would incur 90% mortality (van Gelder 1973). Due to a high level of variation among species for mortality rates in response to traffic levels, mortality rates of some species can increase, decrease, or remain constant depending on the species. Mazerolle (2004) was able to detect interspecific variation in mortality rates at traffic flows as low as 5-26 vehicles per hour.

The relationship between traffic volume and mortality of reptiles is unclear. The distance from the road that desert tortoise populations were reduced was positively correlated with traffic densities; at the highest level (5000 vehicles per day) reductions were apparent 4000 m from the road (von Seckendorff Hoff and Marlow 2002). Seigel (1986) found that the proportion of DOR massasauga rattlesnakes varied seasonally and were correlated with peak traffic patterns in the fall (Seigel 1986). However, some studies do not report a significant correlation between traffic volume and number of road-killed reptiles, which authors attribute to already reduced populations adjacent to the road (Nicholson 1978; Dodd et al. 1989; Enge and Wood 2002), discrepancies in the timing of traffic and survey data collection (Smith and Dodd 2003), or variance in species composition and densities along road sections (Enge and Wood 2002).

Low traffic volumes on rural roads can result in high reptile mortality (72%, Louisiana, Fitch 1949; 82%, Georgia, Herrington and Harrelson 1990). Enge and Wood (2002) noted that 93% of snakes were observed DOR on rural roads in Florida where traffic loads were less than 1,000 vehicles per day. Rural roads are the largest single classification of road types and therefore, the extent of their impact should not be underestimated. Aside from wildlife mortality, this road class also poses the largest threat to human safety, particularly in the southeastern U.S. where 30% of the nation's traffic fatalities occurred in 8 southeastern states between 1996 and 2000, 64% of which were on rural roads (Sander 2005). Further, 71% of Florida's fatalities occur on rural roads.

HABITAT CORRELATIONS

The highest rates of road mortality occur where roads disrupt the spatial connectivity of essential resources and habitats across the landscape. Many amphibians fall victim to roads in great numbers during mass migrations of breeding adults and emerging metamorphs from wetlands (e.g., Ashley and Robinson 1996; Smith and Dodd 2003; Table 2). Breeding adults may enhance their mortality risk by crossing roads twice annually if their migration corridor between upland areas and wetlands is bisected by a road (Jackson 1996). Average mortality rates for salamanders (red-spotted newts, *Notophthalmus viridescens*; spotted salamanders; red-backed salamanders, *Plethodon cinereus*) crossing a paved rural road in New York ranged from 50 to 100% (Wyman 1991). If mortality is sustained, population declines can be insinuated when numbers of migratory individuals are reduced in subsequent years (e.g., mole salamanders, *Ambystoma talpoideum*, Means 1999). Cooke (1995) documented road casualties of adult individuals near a breeding site in England for 21 years, but cautioned against the use of the data to represent numbers killed, and even more so against using such data as an indicator of population trends.

Numerous studies have reported correlations of road mortality with adjacent habitat and vegetative cover type in herpetofauna (e.g., Enge and Wood 2002; Jochimsen 2006a; Table 2) and other vertebrate taxa (e.g., Cristoffer 1991). These correlations may be associated with broader habitat classification (e.g., Sumler 1975) or habitat features, such as canopy cover and soil type (Titus 2006), or by the degree to which the bordering vegetation encroaches on the road (Klauber 1939; Fitch 1987). Further, composition shifts in the bordering plant community can lead to shifts in herpetofaunal composition (Ashley and Robinson 1996; Mendelson and Jennings 1992). This shift may also occur in response to the intrusion of invasive species and their influence on crossing corridors and aggregations of roadkill (Jochimsen 2006b).

ABIOTIC CORRELATIONS

While hydrological and temperature influences appear to be the most important determinants of herpetofaunal movement and therefore road mortality (Turner 1955; Carr 1974; Harris and Scheck 1991; for specific examples see Table 2), there are others that have been little explored that may be influential as well. For instance, the amount of natural nocturnal

lighting (i.e., moonlight; artificial influences are discussed in the Indirect Effects section) can inhibit an organism's willingness to move due to potential predator exposure. Movement rates in snakes have been shown to vary with moon phase in response to degree of light diffusion (Kevin Messenger unpubl. data). Copperheads (*Agkistrodon contortrix*) at Land Between the Lakes National Recreation Area in western Kentucky and Tennessee increased movement during full moons (illumination >88%) although the author discusses potential observer and data bias (Titus 2006). However, Titus (2006) also suggests that lighting could assist in foraging by serving as a secondary cue to heat-sensing pits.

ROADS AS TRANSECTS

Since the 1930s, herpetologists have driven U.S. roads to document occurrence and collect specimens (e.g., snakes, Klauber 1931; Scott 1938), and many herpetologists still consider road surveys valuable for monitoring amphibian and reptile occurrence despite obvious biases with this method (e.g., Case 1978; Enge and Wood 2002; Steen and Smith 2006). Data that are collected incidentally (e.g., Klauber 1932; Scott 1938) may not be representative of activity since surveys are conducted in accordance with the human schedule as opposed to that of the target species. However, these data published in the first half of the 20th century have provided a framework for biologists to demonstrate that roads are not a new issue. It is widely accepted that road survey data are valuable, and that this method may prove most effective for the objective of a study. Road surveys are occasionally used to monitor species richness, distributions, and the status of populations (Pough 1966; Seigel et al. 2002; Weir and Mossman 2005; Lee 2005); however, we urge caution in the interpretation of these data to generate quantified population estimates or relative abundances, as these parameters can not be considered independent of the myriad impacts of roads on herpetofauna. For example, Jochimsen (2006a) found that numbers of individuals detected of different species varied dramatically between road surveys and drift fence arrays at known hibernacula. Therefore, we recommend that road cruising data are supplemented with additional methodologies when targeting these objectives.

Actual roadkill counts may be underestimated due to a variety of factors (Table 3). Counts can vary with speed limit (e.g., Cristoffer 1991) and traffic density (e.g., Mazerolle 2004). Several studies report high incidences of carcass removal by scavengers (Kline and

Swann 1998; Enge and Wood 2002; Smith and Dodd 2003; Antworth et al. 2005). Results from all-night surveys conducted in Saguaro National Park indicated that, on average, no more than 24% of the animals killed between sunset and early morning persisted on the road long enough to be observed during regular surveys later in the day (Kline and Swann 1998). Enge and Wood (2002) reported similar data from their pedestrian survey of snake communities in Florida, where 70.5% of the 207 snake carcasses on the road were gone by the following day, and less than 1% remained for 5 or more days.

The most thorough, long-term records of direct road mortality have been provided for snakes, with documentation of traffic fatalities since the 1930s (Fig. 5). Reports in which the majority of specimens are already dead are not uncommon (Fig. 6). Rates of snakes found (DOR) presented here range from 24-94%, and the median DOR proportion of these studies is 71.7%. However, rates can be lower when in protected areas where human use is less than that of public roads. For example, roads surrounding Squaw Creek National Wildlife Refuge in Missouri yielded DOR rates of 23.2% of massasauga rattlesnakes ($n=172$, Seigel and Pilgrim 2002). However, the authors still concluded that vehicular traffic was the most detrimental impact of refuge activities on this species.

Carcass removal rates may vary dramatically due to a variety of biotic and abiotic factors. Traffic density may influence the species composition of scavengers (KMA unpubl. data). Injured individuals may leave the road surface before dying (Dodd et al. 1989; Jochimsen 2006a), and carcasses may be displaced by passing vehicles (Enge and Wood 2002; Jochimsen 2006a), or obliterated during high traffic volumes (Clevenger et al. 2001; Hels and Buchwald 2001; Smith and Dodd 2003). Carcasses may be difficult to detect during surveys if abiotic conditions influence their persistence (KMA unpubl. data), or observers fail to notice incomplete remains (Klauber 1931; Boarman and Sazaki 1996; Mazerolle 2004). Survey design may bias detection, as small or greatly deteriorated specimens might not be observed from a moving vehicle, but be counted when transects are conducted on foot (Franz and Scudder 1977; Enge and Wood 2002; Smith and Dodd 2003). Slender, small snakes or darkly patterned species are more difficult to detect (e.g., Mendelson and Jennings 1992; Sullivan in press). The timing of surveys may also influence results based on how they coincide with periods of wildlife activity and maximum road mortality (e.g., Duever 1967). Finally, yearly variation of environmental factors may influence mortality estimates, so that surveys conducted in a

particular year may not provide an accurate representation of long-term trends (e.g., Ashley and Robinson 1996).

ASSESSING IMPACTS OF ROADKILL FROM SURVEY DATA

Due to the difficulty of collecting all of the data necessary to form direct conclusions regarding population-level impacts, or even extrapolating roadkill counts over a greater distance, modeling has become a useful exercise to assess larger impacts. Ehmann and Cogger (1985) estimated that 4.45 million anurans and 1.03 million reptiles get killed annually on roads throughout Australia by extrapolating data from four surveys of four different road segments (range, 2.5-25.1 km) across the total length of roads in Australia permeating the focal habitat. These are the largest approximations reported anywhere in the literature and are often cited within reviews concerning road effects. While there are obvious valid concerns arising from such extraordinary numbers, literal figures generated from this level of extrapolation are limited in use until more extensive research is performed. In another example, pedestrian surveys on rural roads in Florida estimated annual mortality at 12.8 snakes/km ($n=228$; 6 km; 2.8 yrs); extrapolated across the state of Florida (107,950 km in 1998), approximately 1.4 million snakes are killed annually on rural roads alone across the state (Enge and Wood 2002). Reed et al. (2004) estimated that 500,000 snakes die annually in the U.S., a number that is likely to be substantially higher if accurate counts across the country were available. The authors conclude that road mortality is not only substantial, but exceeds the damage incurred by other human activities, such as the pet trade.

The list of literature documenting road mortality of snakes spans over 60 years, yet the actual effects on snake populations have mainly been estimated using models or based on mean kill rates determined by survey efforts. In a three-year survey on New Mexico highways, the mortality rate of snakes was estimated at 0.007 snakes/km/per year, yielding annual estimates of roadkills at 10,489, 13,840 and 25,744 respectively (Campbell 1953, 1956). These figures were calculated by determining a mortality rate per mile via quantitative road-cruising and then adjusting those totals for the additional miles covered by other established public roads in New Mexico. Klauber (1972) estimated the total road deaths in San Diego County, California at 15,000 snakes per year based on his survey efforts in the 1930's and adjusted for increases in traffic levels. Researchers reported the traffic casualties of 20 species along a road transect in

the Sonoran desert ($n=264$, 44.1 km, 4 yrs, Rosen and Lowe 1994). Incorporating these data into a computational model, the authors presented an algebraic method for estimating highway mortality of snakes. Using this model, the estimated death toll for these snake species is close to 2,383 individuals (13.5/km/year) annually. Over a four-year period along this transect, the estimated impact of this highway mortality would result in a loss of all individuals within 65 m of the road edge. Smith and Dodd (2003) report the highest rate of snake mortality on roads of any published study (to our knowledge) at 1.854 individuals per km surveyed (623 dead snakes across 336 km) and the death toll for the 52-week survey period was 1,292 snakes. Based on these kill-rate data, the authors estimated that 2,164 snakes died from traffic-induced injuries between 1998 and 1999 across Paynes Prairie. We advise that such estimates should be interpreted with caution due to variation in snake and traffic densities, as well as seasonal and geographic differences, but report these values to emphasize the potential impact that road mortality may have on snake populations.

Modeling is also a useful exercise for investigating how mortality rates may vary across certain temporal or spatial scales. The estimated survival rate of toads crossing roads in Germany with traffic densities of 24-40 cars per hour varied from zero (Heine 1987) to 50% (Kuhn 1987). Hels and Buchwald (2001) calculated that the probability of an individual getting killed while crossing a road ranged from 0.34 to 0.98 across traffic volumes, depending on various attributes of a given species. Their model has been adapted to assess mortality probabilities for salamanders (Gibbs and Shriver 2005), turtles (Gibbs and Shriver 2002; Aresco 2005b) and snakes (Andrews and Gibbons 2005), but has yet to be applied to lizards. However, these estimates are based on individual deaths presented as proportions, so the extrapolations to true population levels are equivocal. Many species cross roads along corridors (e.g., because of the location of a wetland or hibernation site), making extrapolations from short segments of road potentially inaccurate because of over- or underestimates. However, with proper consideration of the level of variance that can be expected for a particular region, such extrapolations can provide useful preliminary assessments of mortality ranges that can be expected for a highway complex when surveys cannot be completed in every location.

In summary, ample evidence exists that road mortality of herpetofauna results in significant loss of individuals and leads to concerns for the sustainability of populations in some

situations. As the research on road impacts has been disproportionately focused on mammals and birds, we are still learning about some of the more straightforward direct effects of roads on herpetofauna. However, roads are unequivocally a major source of mortality of many amphibians and reptiles in many areas, raising serious concerns for some populations. The extrapolation of road mortality numbers across broad geographic regions and time can be useful both biologically and politically, but such projections must be used with discretion when applied to scientific conservation or management efforts.

INDIRECT EFFECTS

“When one tugs at a single thing in nature, he finds it attached to the rest of the world.”
-John Muir

Roads are designed to serve as travel corridors for humans, usually without regard for the ecological integrity necessary for wildlife. Therefore, problems may arise when wildlife use road systems for their own movement or other activities. Unlike natural corridors, roads frequently cross both topographic and environmental contours, thereby fragmenting a range of different habitat types (Bennett 1991) and affecting wildlife groups that possess a diversity of ecological and life history strategies. Road construction creates a zone of intense human activity that subsequently alters habitat and wildlife behavior (Bennett 1991). Once the area is accessible to humans, perpetual habitat destruction and human expansion often follows.

The manifold effects of roads extend far beyond encounters between wildlife and vehicles. Roads affect wildlife indirectly, through landscape fragmentation and alteration of physical conditions in the vicinity of roads (Andrews 1990; Forman et al. 2003). Additionally, multiple effects extend across a range of spatial scales beyond the road edge (e.g., Jaeger 2000). Here, we refer to these secondary ecological consequences as indirect effects. When discussing indirect road effects on herpetofauna, the information base becomes sparse because these effects are more pervasive and more difficult to quantify than direct effects, and documenting indirect effects due to roads often requires extensive and long-term monitoring. Secondly, research has been disproportionately focused on mammals and birds, and therefore, we are still learning about some of the most basic effects of roads on herpetofauna so the complex nature of secondary effects leaves many unasked questions.

EDGE EFFECTS

A habitat edge is simply a transition zone between original habitat and altered habitat (Mitchell and Klemens 2000) and is often of compromised quality. The transformation of physical conditions on and adjacent to roads eliminates areas of continuous habitat while simultaneously creating long-lasting edge effects (Forman and Alexander 1998). Roads have been documented as having greater edge effects than clearcuts in Wyoming forests (Tinker et al. 1998), a trend that was further exaggerated through even distribution of the road network across the landscape. Forman and Alexander (1998) coined the term “road-effect zone,” which includes the road and the area extending beyond the road surface that experiences alteration of ecological effects. The zone has dynamic boundaries dependent on both biotic (e.g., habitat quality and soil structure) and abiotic (e.g., wind, precipitation) fluctuations that vary seasonally or annually. The combined effects (thermal, hydrological, chemical, sediments, noise, species invasion, fire, and increased human access) of this “road-effect zone” were quantified in two studies (Netherlands, Reijnen et al. 1995; U.S., Forman & Deblinger 2000); effects extended more than 100 meters from the road in the surrounding habitat. Forman (2000) subsequently estimated that about 20% of the U.S. land area is affected ecologically by the infrastructure network. Further analyses determined that 16% of the total land area within the lower 48 states of the U.S. is within 100 m of any road type, 22% within 150 m, and 73% within 810 m (Riitters and Wickham 2003). Edge effects from roads can be 2.5-3.5 greater than those emanating from clearcuts (Reed et al. 1996), resulting in fragmentation even in remote areas. Further, edge effects within protected areas, such as National Forests, could extend to over 40% of the area for some species due to high road densities (Semlitsch et al. 2006). While edge effects and disturbance distances from roads have been sparsely addressed for herpetofauna, studies focused on other organisms have observed impacts permeating out from the road at surprising radii (birds, 500-600 m rural roads, 1600-1800 m highways, van der Zande et al. 1980).

The penetration of road impacts into the surrounding landscape will vary with regards to location, time, and especially the organism in question. Many herpetofaunal species may decrease directly or indirectly in response to a reduction of prey that are themselves influenced by the reduced habitat quality associated with roads. For example, a decrease in invertebrate

abundance was correlated with reduced litter depth up to 100 m from the road (e.g., Haskell 2000). Presumably, these habitats would not be ideal for reproductive behaviors of species that are not naturally “edge” species due to abiotic alterations, (e.g. temperature and light gradients). Regardless, all animals residing in or using this zone are subjected to a higher risk of on-road mortality or death caused by other off-road factors.

Clearly, some species would benefit from roadside edge habitat under certain circumstances yet experience increased risks in others. Edge effects altered plant species composition up to a maximum of 200 m beyond the road surface (Angold 1997), and presumably would be even greater in instances of mobile, wide-ranging vertebrates. Alternatively, species that thrive in disturbed environments may experience road effects across a comparable area, but effects can be positive in that they support or encourage growth and reproduction. Therefore, researchers should use caution when measuring effect distances as variation occurs across and within each component of the system (e.g., trophic position, Faeth et al. 2005).

Due to this variable and convoluted nature of biological responses to the plethora of indirect effects, the inherent difficulty in studying the broader scale effects of roads on ecological systems must be recognized for progress in this area of research. Identification of umbrella species, in particular long-distance movers such as eastern indigo snakes that are sensitive to edge effects, could assist in assessments that would protect multiple species from the effects of landscape fragmentation (Breininger et al. 2004). Forman (2005) performs patch-corridor analyses to develop the best location for a road. He suggests that in general, road effects are low adjacent to narrow corridors and lowest around small patches. Further, he proposes that an ecologically-optimum road network includes: a few busy roads rather than many lightly used roads, a few large roadless areas, and permeable roads between the roadless areas for species connectivity. While challenging, this area of study can not be avoided as it is essential that we understand the whole system to adequately assess the impact of even a single road. However, due to time and funding limitations, we encourage research scientists to professionally and efficiently prioritize research topics, organisms, and locations.

USE OF THE ROAD ZONE FOR HABITAT

Foraging Opportunities

Edge habitat can result in an increased density of disturbance-tolerant species which may then consequently attract predators. Adams and Geis (2002) documented an increase in small mammal abundances within the road right-of-way. Getz and colleagues (1978) observed small mammals using road corridors for dispersal and residence. Avian edge nesters were at a higher relative abundance (Ortega and Capen 2002) in habitats adjacent to roadsides. A higher density of snake species were observed in the ecotonal area along a road transect in California, possibly due to an increase in prey diversity and density (Sullivan 1981b). Slow worms (*Anguis fragilis*) were commonly found in roadside habitats where invertebrate prey was bountiful (Wells et al. 1996). Slow worms use the road shoulder so extensively that a population disappeared after a widening project reduced shoulder width and increased slope (Henle 2005). Small mammal species residing along road borders in Australia were the most common prey items in road-killed carpet pythons (*Morelia spilota*; Freeman and Bruce in press). Mass numbers of western toad tadpoles were observed in deep ruts on a forest road in Idaho, along with two terrestrial garter snakes that were actively foraging on the young anurans (DMJ pers. obs.). Dodd et al. (2004) observed alligators attracted to roadside pools that had formed at the opening of culverts (i.e., Ecopassages) that could have possibly served to increase foraging opportunities. Finally, some toad species have been observed foraging for insects under streetlights (e.g., Neill 1950).

Roads also provide simplified foraging opportunities for predators due to increased exposure of animals crossing the road (e.g., attempted predation by red-tailed hawk (*Buteo jamaicensis*) of a black rat snake crossing a highway, Vandermast 1999). Alternatively, dead animals attract scavengers. Although the opportunity for these observations is rare, there are several incidences reported in the literature. Guarisco (1985) observed an adult bullfrog (*Rana catesbeiana*) scavenging on a road-killed plains leopard frog (*Rana blairi*). Jackson and Ostertag (1999) recorded a gopher tortoise (*Gopherus polyphemus*) scavenging on a road-killed great-horned owl (*Bubo virginianus*). Jensen (1999) witnessed an eastern box turtle (*Terrapene carolina*) scavenging on a road-killed copperhead. Morey (2005) noted a juvenile western diamondback (*Crotalus atrox*) foraging on a subadult Couch's spadefoot toad (*Scaphiopus couchii*). On multiple occasions, fresh water snakes (*Tropidonophis mairii*) were observed feeding upon road-killed frogs (*Litoria* spp.) along road segments with high concentrations of amphibian crossings in Australia (Bedford 1991a). Bedford (1991b) further observed a road-

killed mulga snake (*Pseudechis australis*) that had consumed a flood plain goanna (*Varanus panoptes*); the mulga snake was believed to be foraging on the road-killed goanna when struck by a vehicle. Lastly, a cottonmouth was repeatedly observed in attempts to scavenge a dead red-bellied watersnake (*Nerodia erythrogaster*) on a road shoulder (Berna and Gibbons 1991).

There are also many examples of correlations between species presence and roadside features. Anurans appear to use ditches temporarily when moving long-distances between local populations (Reh and Seitz 1990, Pope et al. 2000). Roadkill aggregations of amphibians and turtles occurred alongside water-filled ditches that were created as borrow pits during highway construction (Main and Allen 2002). Across Paynes Prairie, Franz and Scudder (1977) observed the highest number of snakes along road sections bordered by permanent water. Anderson (1965) noted the propensity of aquatic snake species presence in roadside ditches (watersnakes, *Nerodia*, ribbon snakes, *Thamnophis*). There has been documentation throughout the century that roadside verges in Britain harbor reptiles (lizards, Leighton 1903 and Smith 1969; lizards and snakes, Langton 1991). Clusters of dead Organ Pipe shovel-nosed snakes (*Chionactis palarostris*) were observed along road edges planted with thickets that may have served as an attractant (Rosen and Lowe 1994). Gopher snake (*Pituophis catenifer*) mortality was positively correlated with cover of an invasive grass species (Jochimsen 2006a, 2006b) in Idaho. Assessments of indirect road impacts associated with predator-prey relationships must be conducted in the context of individual species and their ecological requirements.

Thermoregulatory Activities

Studies have documented individuals using the road zone for thermoregulatory purposes, which suggests that roads may serve as an attractant to certain species. Australian lizards (land mullet, *Egernia major*) were noted to selectively use clearings adjacent to roads for thermoregulation (Klingeböck et al. 2000). These lizards were typically abundant along forest edges and the average distance from the center of a lizard's activity area to the nearest road was 17 meters ($\sigma = 2.2$ m). Open patches, such as those created by roads and tree harvesting, benefit large-bodied lizards of the Amazon (e.g., ameiva, *Ameiva ameiva*) by increasing foraging efficiency and providing access to warm basking sites (Vitt et al. 1998; Sartorius et al. 1999). However, both studies conclude that such disturbed areas support high

densities of these large lizard predators which could result in cascading effects on the local prey assemblages.

Many of the reports of reptiles using roads for thermoregulation involve snakes (e.g., Klauber 1939, Brattstrom 1965, Moore 1978, Sullivan 1981a, Bernardino and Dalrymple 1992, Ashley and Robinson 1996). Published documentation of reptile thermoregulatory behaviors first stemmed from the western U.S. (e.g., Klauber 1931) where desert species are adapted for open habitats and the road zone is more comparable with their natural habitat (Andrews and Gibbons 2005). McClure (1951) noted that snake mortality in Nebraska peaked in May and October during cooler temperatures when individuals were frequently observed basking on road surfaces. During road surveys in Idaho, snakes were observed motionless on the road with obvious prey items in their gut (DMJ unpubl. data). For instance, a western rattlesnake (*Crotalus oreganus*) remained stretched on the road verge for over an hour despite high traffic volumes, and on the same evening a gopher snake was discovered coiled on the road surface. Thermoregulatory behavior has often been assumed, but not necessarily observed or critically interpreted, in situations where intact habitat occurs directly alongside the road shoulder, on roads with low traffic densities, or at times of day when traffic levels are reduced and the road has cooled but is still warm (KMA pers. obs.). However, observations of snakes lying motionless on roads, common grounds for an interpretation of thermoregulation, can also be explained in terms of a defensive behavior (immobility) exhibited by some snake species while on the road (Andrews and Gibbons 2005). The authors speculate that some snake species perceive the road as a threatening (i.e., foreign) environment. This response could thereby reduce the frequency with which the road would pose as an attractant for thermoregulatory activity, particularly in the southeastern U.S. where quality basking sites are presumably more prevalent. Further research is needed to explore directly the degree to which lizards and snakes are attracted to roads for thermoregulatory purposes and important variables (e.g., species, season, abiotic conditions) in the selection of roads as basking habitat.

Reproductive Behaviors

Roads and the peripheral areas they impact can also serve as an attractant for non-adaptive reproductive activities among some species of amphibians and reptiles, thereby creating a population sink. Amphibians, particularly anurans, will use roadside ditches for

breeding. Generally, pools and roadside ditches are only temporary and may dry before metamorphosis of young, so that successful egg and larval development may be rare (Richter 1997). Depressions along forest roads fill with rainwater in spots of blocked stream flow or tire ruts, creating habitat that amphibians may use for hydration or breeding (e.g., Reh and Seitz 1990; Trauth et al. 1989; Pauley 2005). However, this habitat is not suitable, as mortality will occur following any subsequent vehicles passage (DMJ pers. obs.).

The road zone can also serve as an attractant for reproductive behaviors of reptiles. Roadside nesting by turtles results in reduced survivorship of both adult females and hatchlings on the road itself, and can give rise to skewed sex ratios within nests because of the associated high temperatures (see Effects on Higher Levels section). Hódar et al. (2000) reported that common chameleons (*Chamaeleo chamaeleon*) in southern Spain selectively used habitats adjacent to roads and orchards for nesting habitat, where reproductive activity coincided with increased traffic densities. Chameleons are highly susceptible to road mortality during this time period and also suffer from illegal collection along roadsides (Caletrio et al. 1996). While there is little data regarding roadside reproductive behaviors in snakes, Van Hyning (1931) documented eastern kingsnakes in Florida mating in a roadside ditch under loose sand and grass roots.

Dispersal Corridors

Some species use roads as dispersal corridors, which may ultimately have detrimental affects on amphibian and reptile populations. Seabrook and Dettmann (1996) concluded that roads and trail systems facilitated the range expansion of the invasive cane toad (*Bufo marinus*) across Australia, which has negatively influenced a variety of other amphibian and reptile species. Surveys revealed a significant increase in toad density along roads and vehicle tracks compared to transects within surrounding vegetation. Additionally, the majority of tracked individuals actively used roads as dispersal corridors (Seabrook and Dettman 1996) and are invading new areas at a rate of over 50 km a year potentially due to rapid adaptation for longer legs which enables increased dispersal rates (Phillips et al. 2006). Phillips et al. (2003) estimated that cane toads could pose a threat to as many as 30% of terrestrial Australian snake species. Additionally, fire ants (*Solenopsis invicta*) proliferate in roadside areas in the United States (Stiles and Jones 1998) and have been identified as problematic predators on oviparous

reptiles (e.g., Allen et al. 2001; Buhlmann and Coffman 2001; Parris et al. 2002), thereby reducing reproductive output and hatchling survivorship. Tuberville et al. (2000) documented the apparent decline of the southern hognose snake (*Heterodon simus*) across much of its range; although there is uncertainty regarding the mechanism of decline, both fire ant invasions and road mortality were suggested as potential contributors.

Roads also enable the spread of invasive plant species along roads and into surrounding habitats, sometimes displacing native vegetation (Tyser and Worley 1992, Parendes and Jones 2000, Tikka et al. 2001). However, Harrison and colleagues (2002) found that disturbance related to roads may support the propagation of invasives, but that roads did not necessarily serve as corridors for invasions into new landscapes. Pauchard and Alaback (2004) support this dispersal pattern along forest roads in Villarrica and Huerquehue National Parks in the Andean portion of south-central Chile, and note that invasion is influenced by elevation, land use trends, and the surrounding landscape matrix. Introduced species comprised 74% of the roadside flora in Hawaii, a trend that was not observed on adjacent substrates (Wester and Juvik 1983). When such invasions eliminate native flora and fauna, the quality and availability of habitat and prey may be compromised consequently depreciating health or survivorship of consumer species (e.g., Maerz et al. 2005) and may lead to additional movement, possibly increasing mortality risk (Jochimsen 2006a). Success of exotic vegetation increased with urbanization and the efficiency of trophic transfer decreased in upstate New York (Kleppel et al. 2004). Additionally, exotic plants within road corridors may alter mineralization processes and organic matter in soil, as observed along a pipeline (Zink et al. 1995), which could subsequently have repercussions on invertebrate communities and their vertebrate predators, including herpetofauna.

ENVIRONMENTAL ALTERATIONS

Hydrologic

Hydrological changes, such as alteration of flood regimes, debris, and runoff from roads, often occur beyond the immediate vicinity of road placement (Jones and Grant 1996, Jones et al. 2000). Adjacent wetlands may experience elevated discharge and fluctuations in water levels due to the impervious nature of roads, subsequently reducing suitable habitat for breeding, foraging, and amphibian development (Richter 1997). Runoff from roads likely alters

flow velocities and flood regimes (i.e., extent, depth, and frequency of flow), all of which can influence embryonic survival, breeding success, and species richness. For example, Richter and Azous (1995) found lower amphibian richness in wetlands experiencing water-level fluctuations of greater than 20 cm and flow velocities greater than 5.0 cm/sec. An additional negative consequence of abnormal flooding for most pond-breeding amphibians is the increased likelihood of fishless isolated wetlands interconnecting with wetlands containing predatory fish.

Increased sedimentation initially resulting from road construction and erosion is problematic for amphibians, however, data regarding the impacts of siltation on reptiles are lacking. Increased runoff in urbanized areas had a negative impact on stream populations of dusky salamanders (*Desmognathus fuscus*), resulting in a decline in population density (Orser and Shure 1972). The authors attributed this decline with excess runoff due to erosion of stream banks, increased amounts of particulate material suspended within the water column, and the scouring of stream channels. Low-gradient streams experience the greatest sedimentation impacts in western Oregon, resulting in decreased densities of Pacific giant salamanders (*Dicamptodon tenebrosus*) and southern Torrent salamanders (*Rhyacotriton variegatus*, Corn and Bury 1989). Similarly, densities of tailed frogs (*Ascaphus truei*), Pacific giant salamanders, and southern Torrent salamanders were lower in streams altered by road construction in Redwood National Park (Welsh and Ollivier 1998) due to increased sedimentation. In addition to direct reduction of amphibian densities, erosion may indirectly influence individuals through depression of invertebrate prey densities in streams experiencing sediment loading from roads (Richter 1997, Welsh and Ollivier 1998, Semlitsch 2000). Due to these sensitivities, it appears that stream amphibians are suitable indicators of ecosystem stress (Welsh and Ollivier 1998). Erosion stemming from road development and urbanization also destroys beach habitat (e.g., Kamel and Mrosovsky 2004), critically impairing nesting and hatching success rates for marine turtles.

Erosion effects on amphibians are especially prevalent in portions of the Pacific Northwest, U.S. where the highest density of logging roads are documented (Riitters and Wickham 2003). McCashion and Rice (1983) found that 24% of erosion from logging roads in California could be prevented with conventional engineering methods, and the remaining 76% could be attributed to site placement and conditions. Across 30,000 acres of timberland, 40% of the erosion was attributed to roads. Sediment load can vary with traffic density (Bilby et al.

1989), but even on low traffic density logging roads in southwestern Oregon, erosion rates were found to be 100 times worse than in undisturbed areas (Amaranthus et al. 1985). Lastly, drainage concentrations from ridgetop roads in the western U.S. can cause landsliding and integration of the channel and road networks (Montgomery 1994).

Toxins

Heavy metal contamination from tires, gasoline, motor oil and subsequent residues can result in serious localized pollution that may permeate into the surrounding landscape. Data directly investigating the impacts of road-associated pollution on herpetofauna are scarce; however, general documentation is available and suggests problems likely exist for herpetofauna and other wildlife. Pollutant compounds from vehicle emissions, de-icing products, road degradation, and mechanical deterioration of car parts were found in habitat situated up to 30 m from the road (Hautala et al. 1995). Lead levels in soil and vegetation decreased with increasing distance from roads, and concentrations were positively correlated with traffic density (Goldsmith et al. 1976; Warren and Birch 1987). Akbar et al. (2003) found similar correlations between concentration, road distance, and traffic volumes for lead in Pakistan. However, their assessment suggests that overall levels (lead, copper, manganese, and zinc) found in the vegetation and soils were not detrimentally high for the vegetation, but could potentially accumulate in roadside fauna that then enter the food chain. Lagerwerff and Specht (1970) found that concentration of toxins decreases with soil depth in addition to increasing distance from the road. Lead was found not only in soil and vegetation samples close to the road, but in the milk of cows grazing on roadside pastureland (Singh et al. 1997). In addition, lead, and elevated copper, cadmium and zinc levels were found to be negatively correlated with distance from the road (Jaradat and Momani 1999). Samples from 13 urban parks in Hong Kong had significantly higher levels of metal contamination than those from control areas distantly located from roads (Tam et al. 1987). Further, washing the leaf samples with water reduced contaminant levels, suggesting that main source is aerial deposition. Scanlon (1979) also documented high concentrations of heavy metals in earthworms and small mammals in proximity to roads. Concentrations were positively correlated with traffic density; therefore, urban areas consistently experienced highly elevated levels. Scanlon (1979) also observed that deposition was spatially influenced by wind patterns and direction. These data are difficult to

assess due to the variability in microhabitat conditions along road verges (Hansen and Jansen 1972) and because of the lack of information related to metal bioaccumulation in food chains.

Compounds associated with road construction, road maintenance, and vehicular by-products contribute to the deposition of pollutants on and around roads, which may alter reproduction and have long-term lethal effects on wildlife (Lodé 2000). Fill used during road construction in Great Smoky Mountain National Park leached toxic chemicals that entered streams via runoff (Kucken et al. 1994), thereby eliminating a significant proportion of the populations of two salamander species (black-bellied salamander, *Desmognathus quadramaculatus*; Blue Ridge two-lined salamander, *Eurycea wilderae*) and reducing the populations of an additional two by 50%. Lead concentrations in bullfrog and green frog (*Rana clamitans*) tadpoles living in roadside habitats were at sufficient levels to decrease growth and reproduction and were correlated with daily traffic volume (Birdsall et al. 1986). Rowe and colleagues (1998) reported that sediments containing high levels of arsenic, barium, cadmium, chromium, and selenium caused oral deformities in bullfrog tadpoles. Mahaney (1994) found that petroleum contamination inhibited tadpole growth in green treefrogs (*Hyla cinerea*) and prevented metamorphosis in treatments with high contamination. Physiological (i.e., respiratory) and behavioral alterations were observed with lizards (*Sceloporus undulatus*) and frogs (*Pseudacris cadaverina*) when exposed to ozone (Mautz and Dohm 2004). Anthropogenic acid precipitation resulting from automobile activity acted as an immune disruptor in adult frogs (northern leopard frogs, Vatnick et al. 2006). Buech and Gerdes attributed the death of hundreds of blue-spotted salamanders (*Ambystoma laterale*) along a forest service road to desiccation from exposure to calcium chloride, which is sprayed periodically for dust-control (deMaynadier and Hunter 1995). Additionally, roadside herbicide applications may compromise water quality (Wood 2001). Kohl and colleagues (1994) found that 2-33% of herbicides applied to road shoulders can leach out into runoff in the first storm following application. Leaching rates can attain levels between 10-73% of the applied herbicide; however, rates are compound-specific (Ramwell et al. 2002).

Chloride from de-icing salt runoff contaminates fresh waters peripheral to road systems (Environment Canada 2001; Kaushal et al. 2005; Karraker in press) and can alter the composition of the vegetation community (Scott and Davison 1985; Isabelle et al. 1987). De-icing salt can still be found in high concentrations ($\text{Na}^+ > 112 \text{ mg/L}$, $\text{Cl}^- > 54 \text{ mg/L}$) within 300

m from the application point (Richburg et al. 2001), but it is possible that general effects on aquatic communities could extend over 1 km into the surrounding habitat (Forman and Deblinger 2000). Exposure experiments with de-icing salt in roadside pools with larval wood frogs (*Rana sylvatica*) resulted in reduced survivorship, decreased time to metamorphosis, reduced weight and activity, and increased amounts of physical abnormalities with higher salt concentrations (Sanzo and Hecnar 2006). Embryonic survivorship of spotted salamanders in New Hampshire was significantly lower in roadside pools relative to those located in the forest (Turtle 2000), where highway runoff of sodium chloride (frequently used as a de-icing salt) had contaminated roadside pools.

Although less is known about physiological effects of road-associated pollutants on reptiles (but see Campbell and Campbell 2001 for a review on snakes), similar issues could exist with the uptake of pollutants directly from marine or terrestrial environments or from prey items (e.g., Storelli and Marcotrigiano 2003; Krysko and Smith 2005), where transferred concentrations vary between sexes and among body sizes (e.g., Rainwater et al. 2005). As Scanlon (1979) found higher levels in invertebrate-eating shrews than plant-eating rodents, food chain implications of road-related heavy-metal contamination need to be further explored for herpetofauna as many species consume invertebrate prey.

Noise

Vehicular traffic and road infrastructure also emit pollution in the form of vibration and noise, which may result in the modification of behavior and movement patterns of certain wildlife species (Bennett 1991). The effects of traffic noise and vibrations on vertebrates include hearing loss, increase in stress hormones, and interference of breeding communications (Dufour 1980; Forman and Alexander 1998). Exposure to loud noise (120 db) induced immobility in northern leopard frogs (Nash et. al 1970), a reaction that may inhibit the ability of animals to successfully find shelter or cross roads (Maxell and Hokit 1999). Noise from motorcycles and dune buggies (≥ 100 db) decreased receptiveness of lizards to acoustical cues, and exposures of 8 minutes in duration induced hearing loss (Bondello and Brattstrom 1979). The authors concluded that exposure to vehicle noise may indirectly increase mortality risk for herpetofauna reliant on acoustical cues to locate prey or avoid predators. Amphibians and reptiles suffered physiological and behavioral hearing loss and misinterpretation of

environmental acoustical signals when exposed to off-road vehicle noise (Brattstrom and Bondello 1983). Background noise often resulted in modification of calling behavior in male treefrogs which may impair the ability of females to discriminate among call types necessary to discern locations of calling males during breeding migrations (hourglass treefrogs, *Hyla ebraccata*, and yellow treefrogs, *Hyla microcephala*, Schwartz and Wells 1983; gray treefrogs, *Hyla versicolor*, Schwartz et al. 2001).

Further, these effects can have behavioral implications by disrupting cues necessary for orientation and navigation during migratory movements, especially for species that rely on such cues for sustaining ecological behaviors (e.g., breeding frogs and salamanders). Low-frequency vibrations on the ground surface mimicked rainfall and stimulated the emergence of Couch's spadefoot toads (*Scaphiopus couchii* Bondello and Brattstrom 1979; Dimmitt and Ruibal 1980). These toads reside in arid habitats, and only emerge from burrows to mate when thunderstorms provide appropriate temperature and moisture conditions. It is possible that traffic noise on paved roads may also trigger emergence, as we have observed dozens of Great Basin spadefoot toads (*Scaphiopus intermontanus*) roadkilled in southeastern Idaho in the absence of appropriate abiotic conditions (DMJ unpubl. data).

Light

Herpetofauna are susceptible to alterations in foraging, reproductive, and defensive behaviors in response to artificial lighting along roads and urban areas (e.g., anurans, Buchanan 2006; salamanders, Wise and Buchanan 2006). Exposure to artificial light can cause nocturnal frogs to suspend normal foraging and reproductive behavior and remain motionless long after the light has been removed (Buchanan 1993). Airplane and motorcycle noise reduced the calling frequency of some anuran species (painted chorus frogs, *Microhyla butleri*; black striped frogs, *Rana nigrovittata*; Malaysian narrowmouth toads, *Kaloula pulchra*) but increased the frequency of another (Taipeh frogs, *Rana taipehensis*, Sun and Narins 2004); the authors predict that the increase in Taipeh frog calls was a response to the decrease in call frequency of the former species. Although essentially nothing is known regarding the effects of noise and light pollution from roads on reptiles, disorientation due to artificial lighting obscuring the natural light of the horizon on developed beaches (e.g., Tuxbury and Salmon 2005) has proven to be a significant and well-documented hindrance of the ocean-finding ability of hatchling sea

turtles (e.g., McFarlane 1963) and nesting females (e.g., Witherington 1992). Much work needs to be done to assess the overall impacts of artificial lighting at night before informed recommendations can be made (Perry et al. in press).

Aside from the sources of point and non-point pollution listed above, amphibians and reptiles are likely to be negatively affected by numerous factors not yet documented such as physical or atmospheric pollution, predator-prey balance, and parasitism as has been noted for other forms of wildlife (e.g., Forman et al. 2003). Further, some indirect effects of roads have not yet even been considered with any wildlife species and will pose unknown challenges for investigators in the future to determine their ultimate impacts on herpetofauna.

OFF-ROAD ACTIVITY

This issue is of particular concern due to the increase in off-road vehicle production and the degree of recreational use. In fact, both the USDA Forest Service and National Park Service are reviewing regulations in efforts to improve land management. Between 1982 and 1986, the number of all-terrain vehicles (ATVs) sold in the U.S. tripled to more than 2.5 million (Davis et al. 1999). Accurate estimates regarding the number of vehicles that travel off road are difficult to attain because in addition to registered off-road vehicles (ORVs), street-licensed vehicles and unregistered drivers also participate in this recreational activity. Data are lacking and are generally based on indirect measurements such as fuel reports from state governments (Forman et al. 2003). An Oak Ridge National Laboratory study suggests that privately owned pickups and sport-utility vehicles traveled 36.2 billion km and motorcycles traveled 3.1 billion km off-road in the U.S. in 1997 alone (Davis et al. 1999). Research suggests that ecological impacts are comparable across vehicle type and are correlated with intensity of use and sensitivity of the environment (Stokowski and LaPointe 2000). For a comprehensive review covering the environmental and social effects of ATVs and ORVs see Stokowski and LaPointe (2000).

Although less studied, ORV activity poses a conservation threat to herpetofauna, mainly through habitat alteration including soil erosion, sedimentation of streams, devegetation, and decrease in soil moisture. Maxell and Hokit (1999) elaborate on how human recreation off roads influence herpetofauna through summaries of research conducted in the western U.S. (www.montanatws.org). For example, population declines of desert tortoises have been

attributed to off-road activity (Bury 1980). Furthermore, potential prey decreased in abundance in response to increased ORV use. Primack (1980) reported that sand compaction associated with ORV use led to nesting difficulties for turtles in coastal ecosystems, and that some individuals were disoriented by tire tracks. Iverson et al. (1981) suggest that impacts from ORVs are numerous and sustained such that even low-use trails might be problematic. They performed field experiments and found that off-road activity increased the quantity and frequency of water runoff and erosion as a result of decreased soil porosity, effectiveness of surface stabilizers, and hydraulic resistance to overland flow. Bury and Luckenbach (2002) found that ORV activity in the western Mojave Desert resulted in reduced habitat quality for desert tortoises, as areas unused by ORVs had 3.9 times the plant cover, 3.9 times the desert tortoises, and 4 times the active tortoise burrows. Busack and Bury (1974) detected a negative correlation between the abundance of lizard species within 1 hectare plots and the degree of vegetation damage due to ORVs; the density of individuals also decreased by 85% within areas of concentrated use compared to control plots (Bury et al. 1977). Off-road activity directly impacted flat-tailed horned lizard (*Phrynosoma mcallii*) habitat (Lovich and Bainbridge 1999) and exhibited indirect effects in behavior modification (Wone and Beauchamp 1995; Beauchamp et al. 1998). Additionally, flat-tailed horned lizards demonstrated immediate response to ORV activity with erratic movement patterns (Nicolai and Lovich 2000).

However, the creation and maintenance of recreational trails may provide habitat for some species. Two studies in Owyhee County, Idaho reported that the density of most reptile species increased with proximity to motorized vehicle trails (Munger and Ames 2001; Munger et al. 2003). The trails clear surrounding cheat grass (*Bromus tectorum*) which the authors suggest enables swifter movements of reptiles through the road zone. It is noteworthy that the authors only examined low-use trails; substantial increases in trail use would likely result in the mortality of individuals attempting to follow the corridor.

Aside from off-road vehicular impacts, off-road activity can consist of management practices of the surrounding landscape that can also influence movement patterns of animals. Both natural (e.g., fire) and man-made (e.g., clearcuts, invasive species) disturbances can force reptiles to retreat to more suitable habitat, which results in a movement burst that can increase road crossing in search of habitat patches (Bush et al. 1991; Jochimsen 2006a). Bush and colleagues (1991) also note that fires create more of an impact in areas where the surrounding

landscape has been cleared, eliminating suitable retreat habitat during the burn. Roadside mowing can have negative impacts on surrounding snake populations (massasauga rattlesnakes, Seigel 1986; plains garter snakes, Dalrymple and Reichenbach 1984) and in general by perpetually creating disturbance (Varland and Schaefer 1998). Mowing not only incurs direct mortality of individuals, but reduces cover availability, soil moisture, and prey densities, often rendering the habitat unsuitable for certain species (Kjoss and Litvaitis 2001). Impacts would likely be minimized if mowing schedules were organized to coincide with periods of inactivity for the animals.

SPATIAL EFFECTS

A budding arena of investigation regarding road effects on herpetofauna is the study of impacts on spatial movements and behaviors. Roads that fragment natural habitats may alter patch size, dimensions, and landscape configuration (i.e., spatial arrangement of habitats) which in turn affects wildlife dispersal patterns (Fahrig and Merriam 1994). Barrier effects can occur when 1) animals are killed on the road in unsustainable numbers such that sufficient interchange of individuals does not take place; 2) the surrounding habitat quality is reduced such that animals cannot persist; or 3) animals behaviorally avoid the road, contributing to isolation and habitat fragmentation. Vehicles can also force wildlife to adapt their behavior either by posing an impenetrable barrier, in which animals selectively avoid the road due to awareness to traffic as suggested by Klauber (1931) and other influences on crossing behavior (Andrews and Gibbons 2005).

Roads serve as a barrier to movement by the mechanism of selective (i.e., genetic or behavioral) road avoidance. Behavioral avoidance has been documented in wildlife groups ranging from invertebrates (e.g., snails, Baur and Baur 1990; bumblebees, Bhattacharya et al. 2003; beetles, Keller et al. 2005) to birds (e.g., Laurance et al. 2004) to mammals (e.g., mice, Mader 1984; wolves, Thurber et al. 1994), but documentation of these occurrences with herpetofauna is novel. Models show that differing catalysts for avoidance accentuate differing degrees of vulnerability at the population level (Jaeger et al. 2005a), thereby, indicating a need for species-level considerations. In more extreme situations, the road forms a complete barrier as seen in Europe where a restored pond was not recolonized by anurans or salamanders over a

period of more than 12 years, despite the fact that populations existed within 150 m of the other side of the road (Henle 2005).

The degree of permeability, hence the severity of the barrier effect, is specific to the type of movement being made. For example, movement data collected in Maine on eight species of amphibians reflect that the highest proportion of movements across roads were natal dispersals (22.1%) rather than either migratory movements (17.0%) or home-range movements (9.2%; deMaynadier and Hunter 2000). While anuran movements and habitat use generally seemed unaffected by wider (i.e., 12 m) logging roads with heavy use (300 vehicles/day), salamander (i.e., mole salamanders, *Ambystoma* spp.; red-backed salamanders, *Plethodon serratus*; red-spotted newts), species abundance was 2.3 times higher at forest control sites than at roadside sites (deMaynadier and Hunter 2000).

Roads can hinder amphibian movement (e.g., Gibbs 1998b) and reduction in permeability can create a partial barrier even on low-use forest roads (e.g., Marsh et al. 2005). Gibbs (1998b) compared drift-fence captures of frogs and salamanders along the forest edge with captures in the forest interior to determine relative permeability of forest edges to amphibian movement. Forest edges associated with roads were less permeable than forest edges associated with open habitat, suggesting that some woodland amphibians will cross substantial areas of open land during breeding migrations, if physical barriers such as a road do not inhibit their movement. Radio-tracked tiger salamanders moved in all directions within surrounding forest habitat, but avoided open habitats including paved roads, commercial development, and fields during terrestrial emigrations from breeding ponds (Madison and Farrand 1998).

Road avoidance by reptiles is also an increasingly common finding. Roads have been shown to restrict the movement patterns of desert tortoise populations (Boarman and Sazaki 1996). Blue-tongued lizards were able to persist in suburban settings via their ability to use artificial cover and feed on garden species, but were found to actively avoid roads (Koenig et al. 2001). Lastly, although data revealed that land mullets selectively used edge-habitat adjacent to roads, radio-tracked individuals avoided crossing roads (Klingensböck et al. 2000).

Road avoidance by snakes was suggested by Klauber (1931) and is increasingly being noted in the literature in the forms of incidental observations (timber rattlesnake, Fitch 1999, Sealy 2002, and Laidig and Golden 2004), single-species assessments (massasauga rattlesnakes, Weatherhead and Prior 1992 and Bruce Kingsbury pers. comm.; red-sided garter snakes,

Thamnophis parietalis, Shine et al. 2004; tiger rattlesnakes, *Crotalus tigris*, Goode and Wall 2002; eastern hognose snakes, *Heterodon platirhinos*, Plummer and Mills 2006) and interspecific comparisons (nine species, Andrews and Gibbons 2005). Road avoidance could be attributed to many factors (Andrews and Gibbons 2005), such as vehicular traffic, changes in microhabitat (e.g., oil residue and scent-trailing implications), and the open space that increases vulnerability to predators (e.g., Klauber 1931; Fitch 1999; Enge and Wood 2002; Andrews 2004) and is associated with human use (e.g., Sealy 2002). Massasauga rattlesnake occurrence was strongly correlated with wetlands and coniferous forests and individuals seldom used roads or trails (only 2% of relocations, Weatherhead and Prior 1992). More specifically, Bruce Kingsbury (pers. comm.) found that paved roads and road shoulders are almost completely impermeable to massasauga rattlesnake movement, while gravel roads and mowed paths are not. Radiotelemetry data on eastern indigo snakes indicated that snakes did not cross paved roads, although they would readily cross dirt roads and trails (Hyslop et al. 2006). Hyslop and colleagues also noted that all snake activity (n=32) occurred within boundaries of paved roads, although six individuals were within 100 m of paved roads. Further, telemetry data from indigo snakes inhabiting Ross Prairie Reserve in Florida suggest that roads function as a home range boundary (Daniel J. Smith pers. comm.).

Andrews and Gibbons (2005, 2006) performed experiments that revealed significant levels of variation among species in road avoidance rates. A correlation was found between the propensity to cross roads and body length, where smaller snakes had a higher road avoidance rate. The authors suggested that this finding is likely due to natural behaviors of smaller snakes to avoid open spaces (but see Kevin Messenger (unpubl. data) who regularly finds southeastern crowned snakes (*Tantilla coronata*) crossing roads). Enge and Wood (2002) also speculate that small secretive species that often occur in high numbers within habitats adjacent to roads may be reluctant to emerge onto the road surface (see also Klauber 1931; Dodd et al. 1989; Fitch 1999). Seigel and Pilgrim (2002) observed shifts in the composition of snakes crossing roads after a flood where few adult massasauga rattlesnakes crossed roads; the remaining individuals that crossed were disproportionately comprised of neonates. Data collected in the area surrounding the road did not reflect this skew, possibly implying road avoidance.

Further, some animals attempt to cross, but deter and retreat; these individuals or species are prone to both mortality and road fragmentation since they enter the road, but do not

ultimately cross (ringneck snakes, *Diadophis punctatus*, Andrews and Gibbons 2005). Road deterrence has also been observed with watersnakes (*Nerodia* spp.) at Paynes Prairie (Franz and Scudder 1977). In a mass unidirectional movement catalyzed by drought conditions in Alachua County, Florida, banded watersnakes (*Nerodia fasciata*) were observed retreating to the original side of entry after disturbance from a passing vehicle, but would then attempt to cross again (Holman and Hill 1961). To our knowledge, published studies on other herpetofaunal taxa examining road deterrence and other incomplete crossing behaviors are not available.

Genetically-inherited avoidance or learned avoidance of roads has not been directly documented. However, if a genetic or learned component for response to roads and traffic exists within species, natural selection can be expected to occur for individuals that are biased towards behaviors that increase survival. For instance, in areas of greater intact habitat, organisms that avoid the road would be at a selective advantage (i.e., reducing the chance of mortality) increasing the chance of breeding successfully. Alternatively, in fragmented landscapes, individuals that risk crossing roads might be effective breeders. Increasing awareness of the prevalence of behavioral avoidance of roads within and among amphibian and reptile species suggests a topic of interest from both ecological and evolutionary perspectives. This occurrence has been observed with Florida scrub-jays (*Aphelocoma coerulescens*) which showed a decreased mortality rate over time, but higher levels of mortality among immigrants who were inexperienced at living along the road (Mumme et al. 2000). An alternate explanation was that selective mortality was taking place due to demographic heterogeneity within the population. Ultimately, the roadside environment only served as a sink as inexperienced fledglings were killed on roads and the population was maintained by immigrants only.

In summary, indirect impacts from roads on herpetofauna vary considerably within and among amphibian and reptile taxonomic groups. Many indirect effects of roads are poorly understood and some have yet to be considered, posing unknown challenges for investigators to determine their ultimate impacts on wildlife. Potential discoveries of the indirect effects of roads on herpetofaunal biology promise a wealth of opportunities to conduct meaningful ecological research applicable to conservation on a global scale.

EFFECTS ON THE HIGHER LEVELS OF ECOLOGICAL ORGANIZATION

“It is the whole range of biodiversity that we must care for – the whole thing – rather than just one or two stars.”
 -David Attenborough

The difficulty in assessing road impacts at the population and community levels of biological organization is a consequence of the overall sparseness of available data. Although we present only what has been documented regarding effects at the population- and community-levels, potentially all road impacts on individuals, for which extensive data are available in some areas, may inevitably result in impacts at higher ecological levels if sustained.

POPULATION-LEVEL IMPACTS

Habitat fragmentation has been documented to affect population dynamics and distributional patterns of amphibians (e.g., Marsh and Trenham 2001) and reptiles (e.g., Robinson et al. 1992). Specifically, roads may have an impact on population size and the degree of isolation through mortality (i.e., direct removal of individuals), edge effects on roadsides that attract or restrict individuals' movements, the fragmentation of continuous habitat, and modification of behaviors that make animals less likely to cross the road successfully. While these factors have all been discussed throughout this report, most studies have been unable to apply their findings to the population-level beyond speculative conclusion. Forman and Alexander (1998) concluded that vehicles are prolific killers of terrestrial vertebrates, but with the exception of a small number of rare species, roadkills have minimal effect on overall population size (mostly based on avian and mammalian data). However, our review of the literature reveals documentation of amphibian and reptile population declines as a result of direct road mortality and isolation.

The negative repercussions of road impacts on herpetofaunal populations are often underestimated (Vos and Chardon 1998). One challenge is that the direct and indirect effects of roads on populations become apparent at different rates. Initial habitat loss and on-road mortality may have a more pronounced and immediate effect that readily translates to population declines, while the consequences of effects such as reduced connectivity, demographic effects, suppressed gene flow, and lower reproductive success would more likely not be realized for several generations (Findlay and Bourdages 2000; Forman et al. 2003). For example, breeding in a population of Columbia spotted frogs (*Rana luteiventris*) at a roadside

pond in Yellowstone National Park did not cease until almost two decades after the relocation of a highway that isolated the breeding pond and summer foraging area from a stream used for hibernation (Patla and Peterson 1999).

Secondly, natural fluctuations in amphibian and reptile population dynamics require the perspective of broad temporal and spatial scales to study road effects adequately. For instance, variation in natural abiotic factors regulates populations of larval and adult amphibians (Wilbur 1980). Therefore, breeding populations of frogs and salamanders fluctuate by as much as 1-2 orders of magnitude among years (Pechmann et al. 1991; Blaustein et al. 1994), with pond-breeding amphibians experiencing the highest degree of variation in population size (Green 2003). Thus, documenting that a population decline was caused by road phenomena rather than by natural causes can sometimes be difficult.

Lastly, as roads are the enablers for further habitat conversion and landscape development, detrimental effects on populations also occur secondarily (Riitters and Wickham 2003) and indefinitely. Urbanization is the most drastic form of subsequent development, but even biologically conservative landscape changes such as silviculture practices can have negative impacts. In Florida, silviculture was implicated in a population decline of flatwoods salamanders (*Ambystoma cingulatum*), where the largest known breeding migration of this species was reported (Means et al. 1996). The reported silvicultural impacts on salamander populations would not have been achieved without the building of roads to permit successful tree farming.

Species persistence in fragmented landscapes is dependent on ecological strategy. For example, habitat generalists may be able to adapt better to altered conditions created by roads than are specialists (geckos, Sarre et al. 1995; snakes, Kjooss and Litvaitis 2001). Further, the impact of road mortality is particularly detrimental on animal populations of long-lived species that exhibit low annual recruitment, delayed reproduction, and high adult survivorship, strategies exhibited by many turtles. The persistence of many anuran populations is dependent on juvenile recruitment and survivorship (Sinsch 1992; Semlitsch 2000; Hels and Nachman 2002; Joly et al. 2003). Hels and Nachman (2002) modeled the probability of subpopulation persistence of spadefoot toads (*Pelobates fuscus*) in a fragmented landscape in Denmark and found that persistence probability was most sensitive to the rate of juvenile survivorship.

Traffic density has been indicated as influencing population persistence in anurans. The abundance of roadside anuran populations in Ottawa, Canada was negatively correlated with traffic volume (Fahrig et al. 1995). Vos and Chardon (1998) also found a negative correlation between population persistence and road and traffic densities with moor frogs. Conversely, a road-cruising survey conducted over eight years in Kouchibouguac National Park, Canada did not detect a decreasing trend in amphibian abundance despite high levels of road mortality, which could be a factor of local population resiliency, moderate traffic volumes, or sampling limitations (Mazerolle 2004). Regardless, the author cautions that the effects of roads with low traffic volumes should not be underestimated.

Salamander populations have also exhibited decreased abundances as a result of roads. Further, there is evidence that unpaved forest roads may have detrimental population-level effects (Gucinski et al. 2001). In the southern Appalachians of Virginia, red-backed salamanders exhibited decreased abundances for 20-80 m into the forest habitat adjacent to roads (Marsh and Beckman 2004). However, the authors did not detect a response to the forest roads from the sympatric and congeneric slimy salamanders (*Plethodon glutinosus*, *Plethodon cylindraceus*). Also, Semlitsch and colleagues (2006) noted decreased abundances of woodland salamanders (*Plethodon* spp.) near roads and further found that roadside individuals tended to be large. The authors suggest a 35 m road-effect zone exists on either side of narrow, low use forest roads.

Due to the long-lived nature of turtles, road effects would presumably have a delayed effect at the population level and have not yet been adequately documented with field data. Road mortality is well documented for eastern box turtles (McClure 1951; Dodd et al. 1989), a species whose populations may not be able to sustain annual loss of adults (Doroff and Keith 1990). The development of residential areas and a four-lane highway in Virginia resulted in continual road mortality in an isolated population of chicken turtles (*Deirochelys reticularia*; Mitchell 1994; Buhlmann 1995). Boarman and Sazaki (1996, 2006) conducted transect surveys to measure signs of desert tortoise activity as an indicator of population density and noted reduced activity within 400-800 m from the edge of California Highway 58. Activity reduction in this species was further noted to be affected by traffic level (von Seckendorff Hoff and Marlow 2002). Similarly, according to population estimates, densities of western painted turtles (*Chrysemys picta*) were depressed within close distances of the highway (Fowle 1996). A

landscape model by Gibbs and Shriver (2002) indicated that population-level vulnerability to roads is influenced by the dispersal and migratory patterns resulting from differing ecological strategies and habitat association, with terrestrial and semi-terrestrial land turtles (*Terrapene*) being more susceptible to road mortality than most pond turtles (*Chelydra*, *Chrysemys*). The authors further estimate that roads result in annual mortality rates of more than 5% of individuals in populations of terrestrial and large-bodied turtles. Cumulative rates of mortality for these species should not exceed 2-3% to achieve healthy population growth and maintenance (Doroff and Keith 1990; Brooks et al. 1991, Congdon et al. 1993, 1994).

Declines have also been documented in several snake species. Expansion of the San Diego-Tijuana highway in the early 20th century resulted in an apparent decline of snakes in the surrounding area as exhibited by a marked decrease in roadkill numbers over four years (Klauber 1939). Rudolph et al. (1998) noted that the distribution of timber rattlesnakes was negatively correlated with road density in eastern Texas. Trapping results revealed that population sizes of timber rattlesnakes and Louisiana pine snakes (*Pituophis ruthveni*) were reduced by approximately 50% up to a distance of 450 m from roads with moderate traffic volume and trapping arrays suggest that abundance is limited up to a kilometer from the road (Rudolph et al. 1999). A two-year (1999-2000) monitoring study on massasauga rattlesnakes in Illinois revealed an estimated population size between 65 and 72 individuals (Chris Phillips pers. comm.). Vehicular traffic accounted for 60% of the 28 known cases of mortality that occurred during August, a rate of mortality that is likely to further contribute to the endangered status of this species. Roe and colleagues (2006), using a model by Hels and Buchwald (2001), detected a higher probability (14-20% of annual population mortality) of road mortality for the wide-ranging and imperiled copperbelly watersnake than the more sedentary northern watersnake (*Nerodia sipedon*, 3-5% mortality), further portraying how impacts must incorporate the ecological strategies of the species of concern.

However, some studies have not detected any shifts in snake abundance due to roads. In an investigation of how wetland distances from roads influence northern watersnake abundance, no significant effect was found, which the authors attributed to a lower vagility as this species does not depend on forest area as much as other watersnake species that rely on moving between wetlands (Attum et al. 2006). Lastly, Sullivan (2000) detected similar abundances of snakes along a 19-km transect of road surveyed in the 1970s and 1990s, with the exception of

gopher snakes, despite an increase in traffic levels, off-road vehicle use, grazing, and human predation.

Demographic Effects on Populations

Many amphibians and reptiles exhibit intraspecific variation in ecological requirements and strategies between sexes (e.g., Johnson 2003; Koenig et al. 2001; Morreale et al. 1984; Reinert and Zappalorti 1988), across life history stages (e.g., deMaynadier and Hunter 1999; Jochimsen 2006b), and among seasons (e.g., Carpenter and Delzell 1951; Gibbons and Semlitsch 1987; Dalrymple et al. 1991). Different responses to impacts from urbanization and road development lead to skewed population structure in amphibians and reptiles via altered sex ratios and composition of age classes. Intraspecific variation in road impacts can often be linked to spatial and temporal attributes of movement, which can most often be correlated with the mating system. For instance, males of polygynous species are often more risk prone as they are responsible for courting and defending multiple females within a territory, as seen with West Indian rock iguanas (*Cyclura lewisi*) on Grand Cayman Island (Goodman et al. 2005).

Differential direct mortality of the sexes on roads undoubtedly occurs also within amphibians. For instance, male-biased road mortality constituted 1.4 – 2.0% of the estimated population of breeding long-toed salamanders (*Ambystoma macrodactylum*) which the authors suggested was a possible contributor to a female-biased (3:1) sex ratio (Fukumoto and Herrero 1998). From a biological perspective, natural differences in behaviors exist that would presumably result in differential road effects. For instance, the crawling speed of gravid females of some species is slower than that of males (spotted salamanders, Finkler et al. 2003).

An increasing amount of data are emerging that present substantial removal of adult female turtles due to tendencies to nest in road shoulders, in some instances leading to male-biased populations surrounding roads. Female diamondback terrapins (*Malaclemys terrapin*) using the road shoulder for nesting habitat in New Jersey experienced a rate of road mortality that exceeded the rate of replacement, and resulted in substantial decreases in the numbers of mature females encountered (Wood and Herlands 1997). Road mortality that was disproportionately higher for female diamondback terrapins was also observed by Szerlag and McRobert (2006a, 2006b). Aresco (2005a) documented male-biased populations that were coincident with rates of road mortality that were biased towards nesting females for three

species of freshwater turtles (Florida cooters, *Pseudemys floridana*; common musk turtles, *Sternotherus odoratus*; yellow-bellied sliders, *Trachemys scripta*) at Lake Jackson in Florida. Marchand and Litvaitis (2004) documented a positive correlation between the proportion of male painted turtles and road density in New Hampshire, which they attributed to female-biased road mortality. Steen and Gibbs (2004) documented a correlation between male-biased sex ratios (painted turtles, common snapping turtles, *Chelydra serpentina*) and high road densities in New York, although they observed no influence on morphology or abundance. In a nation-wide comparison of data collected from turtles on-roads versus off-roads, a female bias (61%) was consistently observed on-roads relative to off-road data (41%; Steen et al. 2006). Although correlations with abundance have not been found in these studies (Steen and Gibbs 2004; Marchand and Litvaitis 2004), documentation of a female bias in road mortality suggests future population instability and reduced reproduction. Further, Gibbs and Steen (2005) performed a meta-analysis on 36 species of U.S. turtles and found that population sex ratios have become increasingly male-biased over time, a trend that was correlated with an increase in road coverage area. Although nesting female eastern box turtles in suburban areas in South Carolina were observed crossing roads at a higher frequency than males, no change in population sex ratios was confirmed and the population continued to persist (Brisbin et al. in press). Female oblong turtles (*Chelodina oblonga*) in the suburbs of Perth, Australia, experienced differential mortality rates while crossing roads in attempts to nest in residential gardens (Guyot and Kuchling 1998). Although skewed sex ratios were not documented in the latter two populations, disproportionate losses among the sexes as a consequence of sex-biased mortality rates could be unsustainable despite the ability of the species to persist initially in human-dominated environments.

Conversely, with snakes, a higher proportion of males are killed on roads, which could have a destabilizing effect on local populations, although the trends are not as consistent as observed with turtles. Data on six species of French snakes (whip snake, *Coluber viridiflavus*; Aesculapian snake, *Elaphe longissima*; viperine snake, *Natrix maura*; grass snake, *N. natrix*; aspic viper, *Vipera aspis*; adder, *Vipera berus*) correlates road mortality frequencies with periods of movement, which vary among sexes, but found an overall higher propensity for males, which move longer distances, to be killed (Bonnet et al. 1999). Road mortality in male timber rattlesnakes in North Carolina is suggested as a significant cause in population decline

and the mechanism for a female-biased skew in the sex ratio (Sealy 2002). This pattern with timber rattlesnakes was also observed on roads in eastern Texas (Rudolph and Burgdorf 1997).

The presence and degree of sex-biased road mortality varies across species and regions. For example, Sherbrooke (2002) found an overall male bias in road captures of Texas horned lizard (*Phrynosoma cornutum*), although Moeller and colleagues (2005) detected a higher average number of females on roads. In an analysis of 15 species of snakes in South Carolina, seven species exhibited significant male-biased mortality whereas eight species showed no significant difference in mortality rates among sexes (Andrews and Gibbons in press). On a road transect survey through Everglades National Park in Florida, males were more common in four species, females were more common in four, and one species exhibited no differences in road-capture frequencies among the sexes (Dalrymple et al. 1991). Further, Titus (2006) observed overall uniform capture rates of male and female copperheads, although temporal variation in movement patterns was observed across the sexes.

Movement patterns vary among age classes as well as between the sexes and could presumably result in variation in road mortality rates, although the phenomenon has been poorly documented in both amphibians and reptiles. Existing information on age-biased road mortality trends in reptiles is heavily biased towards snakes. In Idaho, adult male gopher snakes were more susceptible to road mortality during spring emergence from hibernacula, while dispersing subadults accounted for 74% of autumn mortality (Jochimsen 2006b). Bonnet and colleagues (1999) found a higher likelihood of neonatal road mortality during post-hatching dispersal (*Coluber* and *Natrix*). Pulses of juveniles and young-of-year were observed in the autumn in four species (Dalrymple et al. 1991). Enge and Wood (2002) found concentrations of neonate mortality in late summer and early autumn. Brito and Álvares (2004) observed a pulse of road-killed immature vipers (*Vipera latastei* and *Vipera seoanei*) in the spring, which they attributed to increased dispersal rates following hibernation, although they noted a higher overall mortality rate for adults. Lastly, more adult copperheads were observed on roads in western Kentucky than juveniles (Titus 2006).

In conclusion, little is understood regarding demographic effects of roads on amphibians, while data are clearly demonstrating global trends for reptiles. The consequences of sex and age structure modifications within populations and the ultimate alteration of demographic patterns as a result are unknown at this time. However, sex ratios of reptiles and

probably amphibians can clearly be altered due to the presence of roads, and influences on age structures are likely. Seasonality appears to be the primary determinant of differential impacts among sexes and age classes as temporal patterns are a critical mechanism driving movement peaks. The variation in sex and age biases in road captures needs greater exploration for the necessary translation to population-level demographic impacts from roads.

Genetic Effects on Populations

Amphibian and reptile taxa often have restricted or disjunct distributions and small population sizes. Further, many species rely on dispersal and migration to maintain population connectivity, increasing vulnerability to local extinction due to landscape change (e.g., Marsh and Trenham 2001) and a decreased ability to recolonize (Rodriguez et al. 1996). Barrier effects created by roads hamper gene flow, reducing genetic diversity and increasing inbreeding rates, an effect that is particularly dramatic in smaller populations (e.g., Lande 1988). Even if individuals are observed crossing roads, genetic differentiation may occur if these individuals do not reproduce (mammals, Riley et al. 2006; Strasburg 2006). Therefore, we suggest that the monitoring of mitigation success should consider both movement and genetic connectivity.

However, despite the significance of these potential effects, few studies have empirically documented genetic effects due to roads on herpetofauna. In Germany, habitat division by highways reduced both average heterozygosity and genetic polymorphism of common frog populations, which appeared to be highly inbred as a result (Reh 1989; Reh and Seitz 1990). Further, genetic exchange occurred in the absence of roads between populations separated by 3-7 km of grassland or up to 40 km of ditches, but roads reduced gene flow in populations that were less than 4 km apart (Reh 1989). Reduced heterozygosity was also observed in agile frogs (*Rana dalmatina*) in ponds near highways in western France (Lesbarrères et al. 2003). Further, roads in urban environments reduced genetic diversity and abundance in common toad populations in Britain (Scribner et al. 2001).

Gene flow also appears to be significantly constrained by the presence of urban areas and roads. In common frogs in Britain, population subdivision values were more than double among urban sites compared to rural sites (Hitchings and Beebee 1997) and urban sites demonstrated lower genetic diversity and higher inbreeding in comparison with rural areas (Hitchings and Beebee 1998). Based on a study that used microsatellites, Rowe et al. (2000)

suggested that the presence of urban areas resulted in greater genetic differentiation in natterjack toads (*Bufo calamita*) than would be expected by separation occurring simply from distance. Vos et al. (2001) used microsatellites to investigate effects of roads on gene flow in moor frogs and also found that road presence increased the genetic differentiation between populations, although extreme subdivision among the populations was not detected. The interpretation of these data is problematic as anthropogenic effects may be confounded by historical patterns of population subdivision and therefore, it may be difficult to determine the exact contribution of road effects on genetic structure (e.g., Cunningham and Moritz 1998; Vos et al. 2001). Furthermore, if a barrier has only recently existed, then it may take several generations before genetic differentiation is detected. In this case, direct monitoring through radiotelemetry or mark-recapture may be more valuable. However, in the instance of the study by Vos and colleagues (2001), fragmentation of the study area had existed for more than 60 years and microsatellites are generally sensitive genetic markers. For example, data from microsatellite markers from a population of voles showed genetic differentiation around a 50-year-old highway (Gerlach and Musolf 2000). A combination of techniques could be advantageous for assessments across broader biological, temporal, and spatial scales. In Australia, van der Ree and colleagues (2006) employed microsatellites, while using natural history data from radiotelemetry and trapping techniques to complement the genetic data. Such information will assist in parameterizing quantitative models that can predict effects on population viability from reduced dispersal from landscape barriers, such as roads (van der Ree et al. 2006).

Although virtually all genetic studies of road impacts on herpetofauna heretofore have focused on amphibians, reptiles likely sustain comparable genetic impacts from roads. Life history traits such as long life spans, low reproductive rates, and delayed maturity of many reptile species increase the difficulty in discerning the role that roads and urban fragmentation have on genetic isolation. Nonetheless, modern genetic approaches offer great potential for providing insight into how roads affect populations of both amphibians and reptiles. This increase in technological ability will allow for more accurate genetic investigations of populations surrounding roads, thereby permitting impact assessments within populations as applicable to an evolutionary time scale. Additionally, the emergence of landscape genetics has merged the arenas of population genetics and landscape ecology (Manel et al. 2003). This

approach aims to assess population substructure at fine taxonomic levels across varying geographic scales, which can be achieved by detecting genetic discontinuities (i.e., distinct genetic change within a geographic zone) as they are correlated with environmental features, including barriers such as mountains, temperature gradients, or roads.

COMMUNITY-LEVEL IMPACTS

Herpetofaunal species richness has been correlated with landscape-level variables, such as spatial configuration of habitats (including the presence of core and buffer habitats) and road density (Dickman 1987; Findlay and Houlahan 1997; Halley et al. 1996; Vos and Stumpel 1996; Knutson et al. 1999; Lehtinen et al. 1999). It follows that patch characteristics and the surrounding landscape composition can be predictors of species presence and abundance (Mazerolle and Villard 1999). Species assemblages are therefore affected in fragmented habitats when landscape connectivity is reduced.

Data on community-level impacts on herpetofauna are lacking in general, especially with reptiles. Herpetofaunal biodiversity was positively correlated with forest cover and wetland area, but was negatively correlated with paved road density in a study in southeastern Ontario (Findlay and Houlahan 1997). Amphibian species richness is particularly sensitive to fragmentation due to individual movements among ponds, where assemblage composition has been linked to the distance to the nearest neighboring pond and amphibian dispersal ability (Vos and Stumpel 1996; Halley et al. 1996). In a model based on survey data, tiger salamander occurrence and overall species richness was negatively correlated with paved road density within 1 km of a wetland (Porej et al. 2004).

The amount of urban land cover in general has consistently been shown to influence species assemblages, which often correlates with increased road density and wetland isolation, a finding that supports the species-area hypothesis (MacArthur and Wilson 1967). Species richness of amphibians and reptiles in habitat patches bordered by roads or other artificial boundaries in the city of Oxford showed a positive correlation with patch size and negative correlation with distance from permanent water source (Dickman 1987). Kjos and Litvaitis (2001) sampled early-successional habitats bordered by idle agricultural lands, edges of industrial sites, powerline corridors and highways and found that species richness and abundance of snakes increased with increasing patch size, although the proportion of large-

bodied individuals on small patches was greater. Minton (1968) performed a survey of herpetofauna in a suburban area of Indianapolis, Indiana. Results indicated that land clearing, ground cover removal, aquatic habitat modification, isolation by roads that reduced access to breeding and hibernacula, and direct killing by man in developed areas all have negative impacts on species composition. While some species of herpetofauna can persist in urban areas, it is likely contingent upon prey base persistence and the retention of breeding and overwintering locations. All of these biologically important features are affected negatively for most species as a result of the construction and use of roads, as they become barriers to access and also result in sustained road mortality.

Species shifts have been attributed to changes in vegetation type and cover along roadsides. For instance, the presence of two new species (corn snakes; rough green snakes, *Ophedrys aestivus*) at Paynes Prairie, Florida along Highway 441 and a three-fold increase in the number of Florida cottonmouths are suggested to have occurred in response to habitat changes adjacent to the road edge (Franz and Scudder 1977; Smith and Dodd 2003). Shifts in the abundance of snake species in the desert grasslands of Arizona and New Mexico were attributed to succession of vegetation communities along bordering highways (Mendelson and Jennings 1992). Enge and Wood (2002) performed a comparison of Florida snake communities in xeric upland habitats using drift fences located in both intact and disturbed sandhill and xeric habitats. Forty-six percent of southern hognose snakes were found on road segments bordered by disturbed habitats, although such segments covered only 21% of the survey route. Despite documentation of 18 species in the survey, drift fence data referenced from protected areas showed that rough green snakes, southern hognose snakes, and Florida brown snakes (*Storeria dekayi*) were seldom captured in drift fences although they were frequently observed during road surveys and comprised 43% of the observed road mortality, suggesting a concentration of these species along roadsides. Lastly, construction of an impoundment and dyke in Ontario increased water depth and circulation altered plant communities, causing subsequent shifts in the amphibian and reptiles species noted along the bordering causeway (Ashley and Robinson 1996).

Analyses of road impacts on herpetofauna at ecological scales higher than the individual or species are inherently difficult because larger, more significant impacts on populations and communities are not instantaneous. As with populations, cumulative effects that roads may

have on local wildlife communities may take decades to become apparent. Due to natural fluctuations across spatial and temporal scales, effective analyses require long-term research. This factor further complicates our assessment as many of the existing studies were only monitored over a short period of time and were not repeated. However, Findlay and Bourdages (2000) found that species richness in wetlands corresponded with historical road density estimates from 30 to 40 years prior to the survey, rather than recent densities. In a 25-year assessment of amphibian and reptile populations at the John F. Kennedy Space Center in Florida, all species present during the 1970s surveys were detected again during the 1990s with the exception of the eastern hognose snake (Seigel et al. 2002). However, road survey data detected shifts in species composition in addition to an overall decline in snake abundance, particularly in cottonmouths and Florida green watersnakes (*Nerodia floridana*). Suggested factors were habitat loss, fragmentation, and cumulative road mortality.

Ecological modeling offers an outlet to predict long-term effects from data analysis of short-term surveys. However, the full extent of road impacts will be realized only through data collection at population and community levels. Unfortunately, long-term research is usually complicated by the availability of time and funding. Further, this limited resource availability discourages ideal experimental designs for more complex scales and long-term data collection. The challenge in measuring the range of road effects across temporal scales should be noted for biologically valid data extrapolations.

SOLUTIONS

“What is the use of running when we are not on the right road?” –German proverb

The continued expansion of our road network contributes to landscape fragmentation, which is recognized as one of the major threats to biodiversity (Forman 1995). Consequently, scientists, conservation advocates, and agencies are driven to design various pre- or post-construction measures to prevent, mitigate, or compensate for road impacts on surrounding habitats and wildlife (Forman et al. 2003). This section will discuss a variety of options available to minimize road impacts on herpetofauna and summarize research related to the effectiveness of these efforts and factors that define project success.

POST-CONSTRUCTION MITIGATION

Internationally, road systems were designed and constructed primarily in the “pre-ecological era,” prior to the understanding that superimposing this infrastructure would disrupt ecological systems of horizontal flows and biological diversity (Forman 1998). Hence the majority of solutions are applied post-construction. Here, we define mitigation as the process by which a solution is devised for an existing road that attempts to reduce road mortality or assist in re-establishing connectivity. The majority of mitigation projects have focused on larger mammalian fauna, but over the past two decades the drive to develop methods to mitigate road effects on amphibians and reptiles has increased. The synthesis by Jochimsen et al. (2004) provides a composite summary of the various mitigation structures based on descriptions provided by Jackson (1996), Forman et al. (2003), and the USFS website - Wildlife Crossings Toolkit (www.wildlifecrossings.info).

Road closure and signage are some of the least expensive mitigation techniques, although not necessarily the most convenient, effective, or biologically valuable. While road closure is often pondered as an option to reduce impacts, it is usually only feasible in remote areas with limited public access, such as protected forests and refuges (e.g., Arroyo toads, *Bufo californicus*, Eastwood and Winter 2006). Road closure has proven effective in some areas, particularly when the closure only occurs during parts of the year in association with predictable migrations (Seigel 1986; Podlucky 1989; Ballard 1994). However, closing roads can often poses driver inconvenience, which can ultimately result in antagonism for wildlife-protection measures with roads.

Road signage has likely been most effective in raising local awareness of wildlife-road interactions. However, it does not necessarily reduce mortality as many drivers disregard signs and fail to reduce speeds, consequently running over animals (e.g., red-sided garter snakes, *Thamnophis sirtalis*, CARCNET, www.carcnet.ca). Studies suggest that signage has been ineffective in ten states in the U.S. and two places in Canada (TranSafety, Inc. 1997).

The installation of culverts (i.e., underpasses, ecopassages) in conjunction with barrier fences is commonly used to increase road permeability and reduce on-road mortality. Underpasses placed with guide fencing have become the most common mitigation structure as overpasses are not ideal for amphibians and reptiles due to avoidance of exposed areas (but see

Teufert et al. 2005). The use of the culvert and fencing design with herpetofauna was initiated in Europe at the Toad Tunnel Conference in Germany in 1989 that addressed topics including mortality of amphibians, tunnel design, and structural characteristics that influenced animal passage (Langton 1989). The general functions of these structures are to provide safe passage for an animal across the road and to enhance connectivity between fragmented habitats (Forman et al. 2003). Similar culvert designs have also been applied to railways (Pelletier et al. 2006). Further, several European countries have successfully used pipes and directive rails (Germany), fine-meshed fencing (France and Netherlands), and concrete trenches (Switzerland) to direct amphibians to culverts rather than using expensive concrete barrier walls (Bank et al. 2002). In addition, the potential for non-wildlife-engineered passages to be adapted for wildlife use is often overlooked (Forman et al. 2003). Such structures may provide important linkages across landscapes for various species (Rodríguez et al. 1996), and recent studies have evaluated this potential (e.g., Aresco 2005b; Mata et al. 2005; Ascensão and Mira 2006). However, fences and culverts may be limited in the objective of reestablishing connectivity with animals that exhibit high road avoidance (Jaeger and Fahrig 2004).

Innovative approaches are evolving in regards to mitigation design. For instance, while many projects monitor road mortality alone to determine culvert placement, a project in Poland supplemented field data by conducting interviews with local park officials to identify precise locations of amphibian choruses and breeding ponds (Brodziewska 2006). Massachusetts Department of Transportation (DOT) performed a two-year pre-construction survey for a new highway alignment and determined that it would impact three turtle species (wood turtles, *Clemmys insculpta*; spotted turtles, *Clemmys guttata*; eastern box turtles, Kaye et al. 2006). They then adapted a culvert design that was subsequently shown to be initially effective through radiotelemetry and thread bobbin trailing.

Despite the initiatives to address road and wildlife conflicts over the past three decades, knowledge regarding the ultimate effectiveness of mitigation efforts is generally lacking (Mata et al. 2005). Furthermore, evaluation studies tend to focus on mammal passage and are not very rigorous by design. The majority of studies simply compare pre-versus post-construction measurements of road mortality and typically concentrate on one species. Few develop and test hypotheses, or list predetermined criteria that provide a basis from which to assess passage performance (Forman et al. 2003). Evaluations of passage effectiveness in terms of connecting

landscapes and natural processes are often based solely on total count measurements of individuals observed crossing. Forman et al. (2003) emphasize that future studies need to place observations in a population context (abundance and distributions in the vicinity) across broad time scales (frequency of crossing).

In addition to diminution of road casualties, for a project to be deemed truly successful it must also restore ecological processes. Goals of a successful mitigation project include (Forman et al. 2003): (1) reduction of roadkill rates post-mitigation efforts; (2) maintenance of habitat connectivity; (3) persistence of gene flow among populations; (4) affirmation that biological requirements are met; (5) allowance for dispersal and recolonization; (6) maintenance of metapopulation processes and ecosystem function. Encouragingly, a general survey summarizing the status of North American mitigation regimes found increases in the number of species considered in projects, monitoring time of structures, and the number and diversity of participants solicited in the process (Cramer and Bissonette 2006). In Table 4 we summarize case studies (organized alphabetically) that attempt to address these criteria in assessment of various mitigation efforts. Several of these projects were published within peer-reviewed journals, or symposia proceedings, while others were discovered within on-line databases or websites.

Furthermore, research reveals that multiple variables ranging from fine-scale microhabitat conditions to broad-scale landscape context can affect structure efficacy (Table 5). Several recent studies have been designed to compare structure efficacy by examining use across structure type and design (Mata et al. 2005; Ascensão and Mira 2006). We stress that species may differ in their preferences and each case needs to be evaluated on an individual basis as best as possible (e.g., Lesbarrères et al. 2004; Wright in press).

Once in place, crossing structures must be monitored and evaluated to determine their conservation value and ecological performance (e.g., Clevenger 2005). Regular monitoring is necessary to ensure accessibility to passage entrances (e.g., Puky 2004) and identify maintenance needs (e.g., Jackson and Griffin 2000). In fact, some highway projects have delegated funds for long-term management into budgets during the planning phases of development (Cuperus et al. 1999). Vegetation may need to be maintained, in order to prevent trespass over the fence for some species, particularly hylid frogs or others with climbing ability (Ryser and Grossenbacher 1989; Dodd et al. 2004), although, some species will be capable of

trespass regardless of maintenance (Aresco 2005b). Further, erosion should be controlled and monitored as it readily occurs along the base of the fence resulting in areas where animals can trespass (Roof and Wooding 1996). van der Grift (2005) states that monitoring studies provide evidence that passages are frequently used by a variety of wildlife species, but only if regularly inspected and maintained. He also recommends that in order to judge the success of mitigation measures, future monitoring studies must assess their long-term influence on population viability.

Additionally, predator aggregations may form at culvert openings, an instance that could potentially result in mortality levels comparable or greater to that experienced with road mortality. This effect may not be exhibited within the first year following culvert construction as it results from learned behavior of the predators, and therefore requires longer-term monitoring for detection. This occurrence may eventually lead to prey avoidance of the culverts (e.g., Little et al. 2002), in which instance the culverts become ineffective at restoring landscape connectivity. Further, prey may temporally shift activity patterns as a predator avoidance strategy (Little et al. 2002). Little et al. (2002) present observational evidence of these two occurrences and urge for more research into these responses. Finally, human access to mitigation structures and areas should be restricted to reduce site disturbance and illegal collection, in addition to protect human safety along road shoulders (Dodd et al. 2004; Aresco 2005b).

PROACTIVE PLANNING

Post-construction mitigation measures serve only as a second option as they do little to minimize, remove, or avoid the majority of indirect effects of roads, and because retrofitting is more costly, both fiscally and environmentally. Integrated planning is regarded as one important area in which we need to make significant advances in order to design sustainable transport systems (e.g., Clevenger 2005). Geographic Information Systems (GIS) can help identify potential problem areas prior to the blueprint stage of road planning (Clevenger et al. 2002; White and Ernst 2003) thereby avoiding construction in ecologically sensitive places. Selection of mapping datasets is an important consideration in addressing ecological impact due to scale issues and variation in the level of inclusion of minor roads across datasets (e.g., Hawbaker and Radeloff 2004). Landscape-level planning will better enable the retention of

ecological function amidst development. Forman and Collinge (1997) define spatial planning, as “a pattern of ecosystem or land uses that will conserve the bulk of, and the most important attributes of, biodiversity and natural processes in any region, landscape or major portion thereof,” and suggest it as an important approach when 10-40% of the natural vegetation has been removed.

Animals that exhibit spatial patterns of road mortality enable the identification of crossing hotspots and predictive modeling options that can direct mitigation designs (e.g., Ramp et al. 2005). Combining GIS map layers of wildlife habitat and design blueprints can identify overlap between road design plans and sensitive habitats or species (Clevenger et al. 2002) allowing for the consideration of alternative routes that would reduce roadkill and increase connectivity. Further, as all members of the wildlife community can not be fully assessed in the planning and impact assessment phases, target species must be selected. Forman (1995) suggests a selection of two species: the largest animal that may be using the passages, and the one that is most sensitive to road barrier effects. Jaeger et al. (2005b) proposes that the modeling of critical thresholds above which a population is prone to extinction can assist in setting environmental standards to reduce fragmentation. However, in many instances, the ecological data necessary to achieve confident modeling results are not available. Further, long-term planning would ideally incorporate not only current designs but future anthropogenic change as projected by localized population and development growth estimates.

Dialogues and activities between professional and citizen sectors are arising with increasing frequency. Training sessions on biological and engineering techniques have been organized (e.g., Jacobson and Brennan 2006), some of which are focused specifically on amphibians and reptiles (e.g., Michael N. Marchand pers. comm.). In the Netherlands, the problem of habitat fragmentation due to transport corridors is being addressed by a *Long-Term Defragmentation Programme* (van der Grift 2005) where population viability modeling and local knowledge serve to prioritize mitigation measures (i.e., locations where wildlife passages are most urgently required). On a smaller scale, North Carolina DOT and NC State Parks joined biologists to discuss the impact of a planned road through Gorges State Park on a timber rattlesnake rookery and a high density of eastern box turtles. The agencies agreed to move the road over 100 m immediately away from the critical habitat and install culverts and guider fences (John Sealy pers. comm.). In Vermont, the eastern racer (*Coluber constrictor*) was

thought to be extirpated but was recently discovered along Interstate 91, an event that has catalyzed collaborative radiotracking and mark-recapture programs between VTrans, FHWA, Vermont Department of Fish and Wildlife, and the Vermont Department of Forest and Parks (Slesar and Andrews 2006).

Consideration of wildlife ecology and movement corridors during the process of road planning ultimately reduces construction costs by avoiding costs associated with mitigative structures, which may total millions of dollars. Developing ecological initiatives in planning stage is critical; however, this timing is challenging as awareness of projects often emerges once construction has been initiated, which is beyond the period when designs can be adjusted. Many European countries have established national policies that require formal ecological evaluations of potential projects (Seiler and Eriksson 1997). Transportation and environmental agencies in Switzerland have initiated a defragmentation program that involves the identification and restoration of areas where road infrastructure bisects critical wildlife habitat (Trocmé 2006). In the U.S., Florida has been a leader in proactive planning through the development of an interagency “Efficient Transportation Decision Making Process” (ETDM; White and Ernst 2003). Ultimately, the success of mitigating the effects of roads on wildlife and habitats will depend on effective communication and cooperation between government agencies, engineers, local citizen communities, non-profit organizations, and scientists.

Transportation designs should be based on the needs of the local human populace and wildlife for a plan that targets the desirable and ecologically-sustainable level of urbanization; therefore, much of the decision process should be designed and enforced at the local level (e.g., FHWA 2004). A steering committee of eight federal agencies, including FHWA, U.S. Army Corp of Engineers, U.S. Fish and Wildlife Service, NOAA National Marine Fisheries, Bureau of Land Management, National Park Service, and U.S. Forest Service, produced a report to assist in transportation designs at the ecosystem level (Eco-Logical: An Ecosystem Approach to Developing Infrastructure Projects; http://www.environment.fhwa.dot.gov/ecological/eco_index.asp). Citizen initiation in dealing with road issues has increased (e.g., Nelson et al. 2006), likely due to an increased awareness regarding ecological problems associated with roads and the availability of alternatives.

CONCLUSIONS

“The idea of wilderness needs no defense. It only needs more defenders.” –Edward Abbey

Ecologists, engineers, government officials, and the general public are increasingly aware that roads create ecological disturbance and destruction to wildlife at multiple levels. The approach in the U.S. has been to alleviate traffic problems by building new roads, an action that is rarely effective, often generating new traffic instead of dispersing existing volumes (e.g., Pfliegerer and Dieterich 1995). Until 2005, when the Bush administration overturned the Roadless Areas Ruling (enacted in 2001 by President Clinton), national forests were protected from further road development and retained fairly intact roadless areas, an important aspect that maintains regional connectivity (Strittholt and Dellasala 2001). Consequently, no U.S. areas outside of established wilderness are protected on a federal level from this expanding infrastructure. As in North America, herpetofauna throughout the world have the potential to be negatively influenced by roads as a consequence of urbanization, either directly from on-road mortality or indirectly through ecological impacts, particularly increased human accessibility to both protected and public landscapes.

Knowledge pertaining to road effects on herpetofauna no longer consists only of on-road mortality. The range, quantity and, potentially, the severity, of indirect impacts of roads and urban development on amphibians and reptiles far exceed those incurred from direct mortality of wildlife. Huge gaps exist in our knowledge of secondary environmental effects on wildlife. Further, designing controlled and replicated experiments in urban and suburban settings is challenging, due to the complex spatial mosaic and political divisions of ownership and occupancy (Felson and Pickett 2005). We encourage scientists to accept the challenge and proceed with the understanding of the complexity of road impacts and the seemingly immeasurable amount of variation inherent in diagnosing the problem and developing the solution.

Post-construction mitigation measures are being developed globally. Since the construction of the first amphibian tunnels in 1969 near Zurich, Switzerland (Puky 2004), many structures have become viable alternative approaches for reducing direct effects of roads for some amphibian and reptile species (Jochimsen et al. 2004). However, the minimization of indirect effects, such as pollution, cannot be accomplished with mitigation structures.

Additionally, few studies adequately monitor the effectiveness of road-crossing structures in restoring connectivity (but see Clevenger and McGuire 2001; Dodd et al. 2004), which is most often the purpose of construction.

Sanderson and colleagues (2002) warn if the shift to more sustainable development regimes does not occur soon, our option will switch from preservation to restoration resulting in solutions that are more costly, time consuming, and are more difficult as evidenced by development trends in Europe. Long-term and large scale effects are often omitted from environmental impact assessments prior to, during, or after the road construction process (e.g., Angermeier et al. 2004). The scope of environmental impact assessments is often skewed for several reasons. First, species loss is usually only considered as “take” in the road construction phase and is not addressed as an issue due to subsequent direct and secondary effects in post-construction eras (Angermeier et al. 2004). Secondly, state implementations of the National Environmental Protection Act (NEPA) have interpreted the instruction to document road impacts as “road construction impacts” and do not assess effects occurring after construction is completed (Angermeier et al. 2004), the phase when the highest number, most severe, and least understood impacts occur. In light of the many indirect effects that have been identified, and many more that remain to be documented, proactive transportation planning, public education, and communication among professional sectors of society are the most effective way to minimize and mitigate road impacts and the *only* effective mechanism for avoidance.

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TABLES AND FIGURES

TABLE 1. Categories of movement by individuals and factors that must be assessed when considering movement phenomena. Adapted from Table 16.2 in Gibbons (1990), Smithsonian Institution Press (with permission).

Category	Purpose	Primary benefits potentially gained by moving
Intrapopulational (short-range)	Feeding Basking	Growth: lipid storage Increased mobility due to body temperature increase; reduction of external parasites; enhanced digestion
	Courtship and mating (adults only) Hiding, dormancy	Reproductive success Escape from predators of environmental extremes
Extrapopulational (long-range)	Seasonal Seeking food resources Nesting (adult females) Mate seeking (adult males) Migration (hibernation; estivation) Travel from nest by juveniles Departure from unsuitable habitat	Growth; lipid storage Direct increase in fitness Direct increase in fitness Survival Initiation of growth Survival
<i>Note:</i> Movement for each purpose needs to be placed in the contexts of daily seasonal timing.		

TABLE 2. Published road studies documenting herpetofaunal road mortality along with major findings of study. * denotes that species were specified beyond suborder listings. “Opportunistic” indicates that data were collected incidentally in a non-standardized format.

Study	Location	Taxa	Number of Road-killed Individuals	Number of Species	Total Km Traveled	Transect Distance (km)	Survey Type and Duration	Major Findings
Aresco 2005b	Lake Jackson, Florida	HERPETOFAUNA	1,121	31				This highway serves an impassable barrier to turtles and projects the highest roadkill proportion of turtles at 100%; Female and juvenile turtles were disproportionately killed due to roadside nesting behaviors; Female turtles were more susceptible to road mortality during non-drought years; Turtle movement (and mortality rates) corresponded with the water level in the lake; Aquatic species had the highest mortality rates.
		Amphibians						
		<i>Anurans</i>	358*	9				
		Reptiles						
		<i>Crocodylians</i>	7*	1	?	1.3	2-4 times daily	
		<i>Squamates</i>						
		Snakes	143*	12				
Ashley and Robinson 1996	Lake Erie, Ontario	Lizards	1*	1				Amphibian and reptile mortality varied seasonally according to life history phenology with unimodal peaks for most species; Amphibian mortality was associated with roadside vegetation, while turtle mortality was associated with open water; 85.4% of amphibian roadkills were young of the year leopard frogs.
		<i>Testudines</i>	612*	8				
		VERTEBRATES	32,502	100				
		MAMMALS	302*	21				
		BIRDS	1302*	62				
		HERPETOFAUNA	30, 898*	17				
		Amphibians			2,549	3.56	Standardized; 3 times per week; 4 years	
Beck 1938	Paynes Prairie, Florida	<i>Anurans</i>	30,034*	7				Describes habitat relationships of species observed on roads.
		Reptiles						
		<i>Squamates</i>						
		Snakes	148*	5				
		<i>Testudines</i>	716*	5				
					?	NA	Opportunistic; 6 trips	
		Snakes	588	1				

Study	Location	Taxa	Number of Road-killed Individuals	Number of Species	Total Km Traveled	Transect Distance (km)	Survey Type and Duration	Major Findings
Bernardino and Dalrymple 1992	Everglades National Park, Florida				1,288	11.5	Standardized; 25 months	Relationship between mortality and seasonal fluctuation of water levels; Significant correlation between traffic volume and mortality.
		Snakes	856*	16				
Boarman and Sazaki 1996; William Boarman unpubl. data	California	VERTEBRATES	1078	24	?	28.8	Standardized; 3 years	Desert tortoise activity was significantly reduced in habitats within 0.8 km from the highway; Significantly more subadult carcasses were encountered on roads than by chance.
		MAMMALS	375	9				
		BIRDS	14	7				
		Snakes	39*	1				
		<i>Testudines</i>	35*	1				
Brito and Álvares 2004	Northern Portugal				?	NA	Opportunistic; 8 years	Adult males comprised the majority of roadkill observations; Mortality varied seasonally across sex and age classes and was associated with movement patterns.
		Snakes	91*	2				
Bugbee 1945	Western Kansas				416	NA	Opportunistic; 1 day	Some snakes not detected because they crawl off the road and die; More snakes were observed dead on gravel than dirt roads.
		Snakes	57	8+				
Campbell 1953, 1956	New Mexico				68,008	variable	Opportunistic; 3 years	Road mortality was associated with climatic conditions such as precipitation; Mortality was bimodal with peaks in spring and late summer; The author provides estimates for road mortality across the entirety of New Mexico.
		Snakes	305	5				

Study	Location	Taxa	Number of Road-killed Individuals	Number of Species	Total Km Traveled	Transect Distance (km)	Survey Type and Duration	Major Findings
Carpenter and Delzell 1951	Michigan	<i>Anurans</i>	1162*	8	12.96	1.44	9 standardized evening surveys; 2 years	Ratios of species observations differed between road and field surveys; Author suggests that male spring peepers (<i>Pseudacris crucifer</i>) migrate <i>en masse</i> , which resulted in a mortality pulse of 506 individuals on one evening; Mortality peaks varied across species and corresponded with spring migrations and breeding movements; More than 75% of all individuals observed were discovered dead.
		<i>Urodeles</i>	2*	2				
Clevenger et al. 2001; Clevenger et al. 2003	Southwestern Alberta	VERTEBRATES	858				Standardized; 554 days	All salamanders were encountered in 9 days and concentrated along a 1.05 km section of the survey route; Mortality events were correlated with heavy rainfall and warm weather; Movements across the road were primarily in one direction.
		MAMMALS	313*	14				
		BIRDS	316*	36	65,253	248.1		
		Amphibians						
		<i>Anurans</i>	45*	1				
		<i>Urodeles</i>	185*	1				
Dickerson 1939	Eastern and Southwestern US	VERTEBRATES	819				Opportunistic; 62 travel days; 3 years	Number of roadkills was three times greater west of the Mississippi than east of it; Mortality associated with roadside habitat and distance to cover; Peaks in roadkills associated with climatic conditions and varied seasonally; Snake mortality greater on paved roads compared to gravel.
		MAMMALS	617*					
		BIRDS	151*					
		HERPETOFAUNA	48					
		Amphibians			120,000	NA		
		<i>Anurans</i>	21					
		Reptiles						
		<i>Squamates</i>						
		Snakes	17					
		<i>Testudines</i>	10					

Study	Location	Taxa	Number of Road-killed Individuals	Number of Species	Total Km Traveled	Transect Distance (km)	Survey Type and Duration	Major Findings
Dodd et al. 1989	Northwestern Alabama	Snakes	239*	19	19,041	variable	Opportunistic; 5 months	Road observations were significantly correlated with the total distance traveled, the amount of rainfall, and season; There was no correlation between traffic volume and number of DOR individuals.
		Lizards	16					
		<i>Testudines</i>	160*	>1				
Duellman 1954	Michigan	HERPETOFAUNA			~17.5	3.5	Opportunistic; 30 hours	Author suggests mortality pulse was triggered by autumn rains; Salamander movement appeared random.
		Amphibians						
		<i>Anurans</i>	?*	5				
		<i>Urodeles</i>	275*	2				
		Reptiles						
		<i>Squamates</i>						
		Snakes	1 *	1				
Enge and Wood 2002	Florida				6132	6	Standardized; 1022 days	93% of individuals observed were DOR; Relative abundance of species differed between road transects and trapping arrays; Correlation between mortality and ruderal habitat; Neonates comprised 80% of all road-killed individuals from September-December.
		Snakes	213*	18				
Ervin et al. 2001	Southern California				?	?	14 months; 254 surveys	Mortality rates were correlated with rainfall, road type, and traffic volume.
		Amphibians	490					

Study	Location	Taxa	Number of Road-killed Individuals	Number of Species	Total Km Traveled	Transect Distance (km)	Survey Type and Duration	Major Findings
Fahrig et al. 1995	Ontario				506	140	Standardized; 6 evenings	Road observations were negatively correlated with traffic intensity; The proportion of dead individuals was positively correlated with traffic intensity; Anuran density in roadside ponds was negatively correlated with traffic intensity.
		<i>Anurans</i>	1,856	2				
Fitch 1949	Western Louisiana	<i>Squamates</i>	92	17	8480	~128	Opportunistic; 54 surveys; 4 months	18 species known to occur in study area were not observed during road surveys; Author lists habitat associations with species road records.
		Snakes	85*	16				
		Lizards	7*	1				
Fowle 1996	Western Montana				302.4	7.2	Standardized; 3 times/week	Adult males comprised 43% of road casualties; Seasonal patterns of mortality varied by sex and age.
		<i>Testudines</i>	205*	1				
Franz and Scudder 1977	Paynes Prairie, Florida				6638	6	Opportunistic; 58 months	Roadkill aggregations were associated with standing water in roadside ditches; Over 90% of the individuals encountered were DOR; Casualties varied seasonally across species.
		Snakes	1770*	12				
Haxton 2000	Central Ontario				?	NA	Opportunistic; 60 surveys; 3 years	Mortality peaked during the nesting season; Females comprised the majority of observations; Concentrations of carcasses were documented on highways adjacent to or bisecting wetlands.
		<i>Testudines</i>	86	1				

Study	Location	Taxa	Number of Road-killed Individuals	Number of Species	Total Km Traveled	Transect Distance (km)	Survey Type and Duration	Major Findings
Hellman and Telford 1956	Paynes Prairie, Florida	<i>Anurans</i>	Many	1	3.2	3.2	Opportunistic; 1 evening	93% of the individuals observed DOR were mudsnakes (<i>Farancia abacura</i>); This mortality event occurred during heavy rainfall associated with a hurricane.
		Snakes	239+*	5				
Hodson 1966	Britain	VERTEBRATES	577	16	?	3.2	At least once daily for 3 years	The greatest number of frog mortalities was documented during March and April.
		MAMMALS	168*	14				
		Amphibians	409*	1				
		Reptiles	2*	1				
Jochimsen 2006a	Idaho				12,261	183	Standardized; 67 surveys; 2 years	Gopher snakes comprised 76% of DOR specimens; 93% of all specimens were DOR; Peaks in mortality varied by sex and age class and were associated with movement; Roadkill aggregations were associated with landscape features; Adult males comprised the majority of observations.
		Snakes	272*	4				
Jochimsen 2006a	Idaho				746	10	Standardized; 12 surveys; 4 months	Very few snakes cross roads successfully, even at low traffic volumes; Five vehicles over a 3-hr period killed 56% of the individuals attempting to cross roads.
		Snakes	59*	3				
Klauber 1939	San Diego County, CA	Snakes	1562*	37	83,845	variable	Opportunistic	Includes description of seasonal and climatic factors that may influence snake occurrence on roads; Author provides habitat descriptions associated with road observations; Mortality levels were correlated with traffic density.
		Lizards	~273*	1				

Study	Location	Taxa	Number of Road-killed Individuals	Number of Species	Total Km Traveled	Transect Distance (km)	Survey Type and Duration	Major Findings
Kline and Swann 1998	Saguaro National Park	VERTEBRATES	2,030					
		MAMMALS	736					
		BIRDS	320		?	Variable	Opportunistic, weekly standardized, and 4 short transects (for toads); 3 years	Mortality rates peaked during the summer months; Mortality was episodic for amphibians and associated with rain events; Road casualties were higher along paved roads compared to dirt.
		HERPETOFAUNA						
		Amphibians	427					
		Reptiles	374					
Krivda 1993	Manitoba				48	NA	Opportunistic; 1 day	Mortality was attributed to placement of the road between nesting and denning area.
		Snakes	42*	1				
Lodé 2000	Western France	VERTEBRATES	2,266	96				
		MAMMALS	979*	27				
		BIRDS	600*	56				
		HERPETOFAUNA						
		Amphibians			2250.6	68.2	Once weekly; 33 weeks	Seasonal variation in mortality; Species abundance in the study area differed from roadkill composition; Exponential curvilinear relationship between traffic and roadkills; Relationship between road mortality and road embankment; Mortality was significantly lower along road sections with fauna passages.
		<i>Anurans</i>	466*	5				
		<i>Urodeles</i>	196*	4				
		Reptiles						
Main and Allen 2002	Southwest Florida	<i>Squamates</i>	25*	4				
		VERTEBRATES	1,035					
		MAMMALS	559	16	11,088	48	Standardized; 231 surveys	Road mortality was not correlated with traffic speed or volume but varied by land use; Mortality of herpetofauna varied seasonally in response to precipitation, and availability of standing water in roadside ditches.
		BIRDS	114					
		HERPETOFAUNA	155					

Study	Location	Taxa	Number of Road-killed Individuals	Number of Species	Total Km Traveled	Transect Distance (km)	Survey Type and Duration	Major Findings
Mazerolle 2004	Kouchibouguac National Park, Canada	<i>Anurans</i>	3185*	6	740	20	Standardized; 37 surveys; 8 years	A greater percentage of anurans were discovered DOR compared to urodeles; Pulses of mortality varied across species; The author did not detect a population decline of amphibians over the 8 years, despite high numbers of traffic casualties; Correlations of mortality with traffic intensity varied by species.
		<i>Urodeles</i>	254*	4				
McClure 1951	Nebraska	VERTEBRATES	6723	> 100	120,024	NA	Opportunistic; 3 years	Toads and gopher snakes comprised the highest percentage of road-killed individuals; Mortalities were correlated with season; Highest losses were documented along paved roads and adjacent to cultivated soils.
		MAMMALS	2723*	29				
		BIRDS	1580*	56				
		HERPETOFAUNA						
		Amphibians	1181					
		<i>Anurans</i>	1082	>3				
		<i>Urodeles</i>	99*	1				
		Reptiles	1224					
		<i>Squamates</i>						
		Snakes	868*	6				
Mendelson and Jennings 1992	Arizona and New Mexico				6261	112	Standardized; 106 trips	Species abundance has shifted over the past 30 years, most likely due to habitat changes in the region.
		Snakes	174*	23				
Palis 1994	Florida				?	0.3	Opportunistic; 1 evening	Individuals were all recent metamorphs emigrating from an adjacent pond; 43% of individuals were DOR.
		<i>Anurans</i>	55	1				

Study	Location	Taxa	Number of Road-killed Individuals	Number of Species	Total Km Traveled	Transect Distance (km)	Survey Type and Duration	Major Findings
Palis 1994	Florida				?	0.3	Opportunistic; 1 evening	Individuals were all recent metamorphs emigrating from an adjacent pond; 43% of individuals were DOR.
		<i>Anurans</i>	55	1				
		VERTEBRATES	79	8+				
		MAMMALS	40*	5				
Pinowski 2005	Venezuela	Reptiles	39					
		<i>Crocodilians</i>	19		2860	572	Standardized; 5 surveys	Road mortality was greatest within forest habitat adjacent to a river; The majority of fatalities occurred following the rainy season; The majority of caiman (<i>Caiman crocodilus</i>) carcasses were juveniles.
		<i>Squamates</i>						
		Snakes	17					
		Lizards	3					
Rodda 1990	Venezuela				15,000	NA	1,000 km / month; 1 year	Males comprised 78% of the road mortalities; Females were primarily killed during the nesting season, while deaths of males peaked during the mating season.
		Lizards	65	1				
Rosen and Lowe 1994	Organ Pipe National Monument, Arizona				15,527	44.1	Standardized; 4 years	3 species accounted for 40.5% of total casualties; Seasonal peaks in mortality and high mortality rates coincided with monsoons; Computational model estimates snake mortality at 13.5 / km / year for the study area.
		Snakes	264*	20				
		VERTEBRATES	1239*					
		HERPETOFAUNA						
		Amphibians						
		<i>Anurans</i>	~400*	>2				
Scott 1938	Iowa	<i>Urodeles</i>	1*	1	4,711	NA	Opportunistic; 1.5 years	Average of 0.429 animals killed/mi of rural paved highway; Author reports a direct correlation of roadkills with weather and roadside cover; Carcasses remained identifiable for an average of 4 days.
		Reptiles		8				
		<i>Squamates</i>						
		Snakes	35*	5				
		<i>Testudines</i>	24*	3				

Study	Location	Taxa	Number of Road-killed Individuals	Number of Species	Total Km Traveled	Transect Distance (km)	Survey Type and Duration	Major Findings
Shine and Mason 2004	Central Manitoba				?	?	Opportunistic; September	Road-killed snakes were smaller on average than individuals captured at dens; Adult females experienced the lowest risk of road mortality; Road mortality was more conspicuous during fall migrations back to hibernacula rather than during spring egress; Road mortality was concentrated near water bodies.
		Snakes	129*	1				
		VERTEBRATES	3,366	78				
		MAMMALS	72*	7				
		BIRDS	265*					
		<i>Anurans</i>	1333*	5				
Smith and Dodd 2003	Paynes Prairie, Florida	Reptiles	1696*	25	336	3.2	Standardized; 3 times / week for 52 weeks	Majority of vertebrate roadkills were anurans and snakes; Seasonal patterns of road mortality varied across taxa; Observations of snakes and anurans were related to local weather conditions; No correlation between traffic volume and road mortality rate; This study reports the highest mortality rate of snakes at 1.854 individuals / km surveyed.
		<i>Crocodylians</i>	29*	1				
		<i>Squamates</i>						
		Snakes	1292*	15				
		Lizards	1	1				
		<i>Testudines</i>	374*	9				
Sullivan 2000	San Joaquin Valley, California				4,198	18	Standardized; 51 surveys	54% of the snakes were discovered DOR; Juveniles comprised the majority of road records; The number of snakes encountered on roads was higher during surveys conducted in the 1990's compared to the 1970's.
		Snakes	236*	10				
Sullivan 1981b	San Joaquin Valley, California				4,424	18	Standardized; 80 surveys	59% of the snakes were discovered DOR.
		Snakes	153*	11				

Study	Location	Taxa	Number of Road-killed Individuals	Number of Species	Total Km Traveled	Transect Distance (km)	Survey Type and Duration	Major Findings
Tucker 1995	West Central Illinois				3,402	54	Standardized; 63 surveys over 21 days	76% of the individuals were observed on 5 days (associated with flood event); 95% of all individuals were discovered DOR; Mortality was correlated with daily high and low temperatures and river stage; A time lag of movement in response to weather conditions was detected; PCA indicated that temperature is the best overall predictor of snake movements.
		Snakes	108	12				
van Gelder 1973	Netherlands				126	1.5	Standardized; 84 evenings	Low traffic densities were associated with high levels of road mortality (10 cars/hr killed 30% of the individuals encountered during the survey).
		<i>Anurans</i>	122*	1				
		HERPETOFAUNA	384*	30				
		Amphibians	311*	6				
		<i>Anurans</i>	284*	4				
		<i>Caecilians</i>	27*	2				
Vijayakumar et al. 2001	India	Reptiles	73*	24	170.7	Four segments totaling 9.5	Standardized; Daily over one month	Lizards that live beneath forest litter comprised 45% of the road-killed specimens; Amphibian observations were correlated with rainfall; Road-killed amphibians were associated with coffee plantations, while reptiles were associated with forests.
		<i>Squamates</i>						
		Snakes	53*	14				
		Lizards	12*	6				

Study	Location	Taxa	Number of Road-killed Individuals	Number of Species	Total Km Traveled	Transect Distance (km)	Survey Type and Duration	Major Findings
Wilkins and Schmidly 1980	Southeastern Texas	VERTEBRATES	286					Seasonal trend in mortality, with roadkills of all vertebrate taxa peaking in spring; No variation of herpetofauna mortality with traffic volume.
		MAMMALS	187*					
		BIRDS	49*					
		HERPETOFAUNA	50					
		Amphibians						
		<i>Anurans</i>	16		1,768	47.2	25 to 50 times	
		<i>Urodeles</i>						
		Reptiles	34					
		<i>Squamates</i>						
Wood and Herlands 1997	Southern New Jersey	Snakes	7*					Authors predict an inevitable population crash, due to high levels of mortality experienced by females and hatchlings; Female turtles use road shoulder as nesting habitat; Road placement is important - high mortality may occur when sensitive habitats are bisected; Authors organized public awareness events.
		<i>Testudines</i>	27*					
					?	27	6 years	
		<i>Testudines</i>	4,020	1				

TABLE 3. Factors and corresponding citations that provide supporting documentation of how a particular variable can potentially influence the frequency and abundance of road-killed amphibians and reptiles.

FACTOR	REFERENCE
Road placement (roadkill aggregation)	Jochimsen 2006b
	Titus 2006
	Langen et al. in press
Speed limit	Cristoffer 1991
Obliteration of carcasses	Clevenger et al. 2001
	Hels and Buchwald 2001
	Smith and Dodd 2003
Traffic Density	Fahrig et al. 1995
	Mazerolle 2004
Abiotic conditions	KMA unpubl. data
Scavengers	Kline and Swann 1998
	Smith and Dodd 2003
	Antworth et al. 2005
Observer error	Klauber 1931
	Boarman and Sazaki 1996
	Mazerolle 2004
Sampling technique	Enge and Wood 2002
	Langen et al. in press
Injured individuals leave road	Dodd et al. 1989
	Jochimsen 2006a
Survey timing	Duever 1967
	Kevin Messenger unpubl. data
Passing vehicles displace carcasses	Jochimsen 2006a
Environmental variation	Ashley and Robinson 1996

TABLE 4. Summary and evaluation of post-construction mitigation projects that target amphibians and reptiles. In instances where project descriptions are not published, websites are included. Non-target species are denoted by italicized text. Statistically significant results are indicated by asterisks.

Study or Website	Location	Taxa	Description of Mitigation Project	Evaluation Technique	Road Mortality Reduced	Connectivity Restored
www.carcnet.ca; Shine Mason 2001	Canada	red-sided garter snake	Installation of 2 reptile tunnels (polymer concrete) with slotted grates and fencing (1994); Expansion of fencing and 4 additional pipes (1995)	Direct monitoring of tunnel use; Observational experiments	Yes	Yes
Amphibian Culverts in Albany County (www.wildlifecrossings.info)	New York	Anurans Urodeles	Installation of 2 concrete amphibian tunnels with box openings and wooden barrier walls (1999)	Road surveys	Yes	Yes
Pipe Culvert at Davis (www.wildlifecrossings.info)	California	western toad	1 amphibian tunnel installed during constructional disturbance of a drainage pond	No rigorous efforts	?	No
Shawnee National Forest (www.wildlifecrossings.info)	Illinois	timber rattlesnake <i>black rat snake</i> <i>eastern box turtle</i> <i>ground skink</i> <i>marbled salamander</i>	3 slotted culverts with hardware cloth fencing	Surveys	?	Inconclusive

Study	Location	Taxa	Description of Mitigation Project	Evaluation Technique	Road Mortality Reduced	Connectivity Restored
Aresco 2005b	Florida	<i>Anurans (10 species); Urodeles (2 species); Crocodilians; Lizards (6 species); Snakes (15 species); Testudines (10 species)</i>	700 m of vinyl fencing connected to a metal drainage culvert (3.5 m in diameter x 46.6 m long) that connects 2 lakes fragmented by U.S. Highway 27	Road surveys pre- and post-construction of the fencing (2 - 4 times daily over ~4 years); Mark-recapture of testudines; Observational surveys of tracks within culvert; Calculated probability of road mortality during attempted crossing for testudines	Testudines = Yes* Others = Reduced overall, but most were able to climb the temporary fence	Yes
Ascensão and Mira 2006	Portugal	<i>Lizards Snakes</i>	This study assessed the extent to which vertebrates used existing drainage culverts along 2 road sections (46 km total length) for passage beneath roads.	Crossing rates were estimated using marble dust placed within culvert entrances over 816 sampling days.	?	Somewhat; Herpetofauna comprised 4.4% of successful crossings
Boarman and Sazaki 1996; Boarman et al. 1998; Boarman and Sazaki 2006	California	desert tortoise <i>Lizards Snakes</i>	Caltrans installed 24-km of barrier fencing along both sides of State Highway 58. In addition, 24 culverts and 3 bridges designed to transport runoff were connected to fencing via funnels (1992).	Comparison of roadkill records along fenced and unfenced sections of highway (3 yrs); Sand traps placed at culvert entrances; Installation of ARS at culvert entrances; Marked tortoises with PIT tags; Population surveys within a 1.9 km plot (every 4 yrs).	Yes*	Yes

Study	Location	Taxa	Description of Mitigation Project	Evaluation Technique	Road Mortality Reduced	Connectivity Restored
Dodd et. al 2004	Florida	Anurans Crocodilians Snakes Testudines	Florida DOT constructed an Ecopassage that included the installation of a concrete wall with overhanging lip to connect 8 existing concrete box culverts , and 4 new cylindrical culverts (1996).	Roadkill surveys (pedestrian) pre- (1 yr) and post-construction (1 yr); Placement of 4 to 10 funnel traps within each culvert (7,580 trap nights); Sand track station in 1 culvert; Infrared cameras and monitors in 2 culverts. Track station and cameras were monitored 5 days/wk.	Yes	Yes
Foster and Humphrey 1995; Land and Lotz 1996	Florida	<i>Crocodilians</i>	Following the upgrading of State Road 84 (Alligator Alley) to Interstate 75, 24 wildlife underpasses with fencing were installed along a 64-km stretch of highway to minimize impacts on Florida panthers.	Installed game counters and cameras in 4 passages	Yes	Yes
Guyot and Clobert 1997	France	Hermann's tortoise	Physical removal of individuals pre-construction of new highway; Installation of 1 reptile tunnel and 2 culverts with fencing	Road surveys (4 yrs post-construction); Mark-recapture	Yes	Yes

Study	Location	Taxa	Description of Mitigation Project	Evaluation Technique	Road Mortality Reduced	Connectivity Restored
Hoffman 2003	Vermont	leopard frogs and <i>other wetland species</i>	Installation of silt fences (1000 ft in length)	Road surveys conducted on a weekly basis for 4 months along fenced and unfenced sections of highway	Yes	No
Jackson and Tyning 1989	Massachusetts	spotted salamanders	2 amphibian tunnels , with slotted openings, and fencing (1987)	Mark-recapture of individuals that encountered fencing	Yes	Yes
Jenkins 1996	Texas	Houston toads	Modification of existing drainage culverts through the addition of steel guiding walls	Road surveys	Only in the vicinity of project placement, with roadkill aggregations at the barrier endpoints	No
Mata et al. 2005	Spain	<i>Anurans</i> <i>Snakes</i> <i>Lizards</i>	This study assessed the extent to which vertebrates used 82 passages including drainage culverts (circular - 1.8 m in diameter), fauna tunnels (box - 2 x 2 m), underpasses and overpasses that were incorporated into the construction of a motorway (1998).	Marble dust track beds surveyed for 3 months to identify species using passages, and camera traps installed in 47 structures to estimate relative proportions of species using passages	?	Yes

Study or Website	Location	Taxa	Description of Mitigation Project	Evaluation Technique	Road Mortality Reduced	Connectivity Restored
Norman et al. 1998	New South Wales	<i>Anurans</i> <i>Lizards (3 species)</i> <i>Snakes</i>	This study monitored the use of 3 existing underpasses to make recommendations for the proposed construction of 16 new underpasses.	10 months of monitoring with photographic equipment, sand track beds, and road surveys	?	Yes
Samanns and Zacharias 2003	New York	spotted turtles Jefferson salamander	Mitigation plan to compensate for road construction includes 3 box culverts (4 ft x 4 ft) in conjunction with concrete fencing (avg. 50 m in length) and 2 wildlife cons pans/culverts (12 ft x 7 ft).	Surveys using coverboards placed within culverts; Pitfall traps; Track beds	To be determined	To be determined

TABLE 5. Summary of factors that influence effectiveness of mitigation structures for amphibians and reptiles that would ideally be taken into consideration when targeting post-construction mitigation plans. Table adapted from Jochimsen et al. (2004).

Structure Characteristics	Effect	Taxonomic Groups Tested	References
Ambient light	Maintenance of natural light via grates will assist in guiding animals through passages and provides places to bask. Duration of crossing time for amphibians through tunnels decreased with the addition of artificial lighting. Shafts or holes included in the design create optimal conditions.	Amphibians: frogs, toads, and salamanders Reptiles: lizards and snakes	Brehm 1989 Jackson 1996 Jackson 1999 Puky 2004
Construction material	Design and materials should be durable and require minimal maintenance; smooth concrete works well.	Amphibians	Eriksson et al. 2000 Smith and Dodd 2003
Dimensions - length	Microhabitat conditions in shorter tunnels may be less variable thereby reducing mortality risk for ectotherms, and increasing likelihood of successful passage. In a comparative study, crossing rates of reptiles were greater in culverts shorter in length. Research also suggests that amphibians prefer the shortest path possible.	Amphibians Reptiles: lizards and snakes	Ascensão and Mira 2006 Jackson 1996 Puky 2004
Dimensions - openness within structure	Two-directional tunnels with large cross-sections represent a most suitable solution. Amphibians accepted a tunnel of 0.2 m in diameter and 0.4 m in total height. A greater proportion of toads used large tunnels (diameter 1 m; length 15mm). Snakes and lizards demonstrated a higher crossing rate in culverts and underpasses 2 m wide. Increased width (> 1 m in diameter) may appeal to a wider variety of species. Viaducts and large overpasses may provide greater connectivity and maintain natural surroundings. More expansive passages may accommodate a greater number of species.	Amphibians: spadefoot, common toad, common frog, moor frog, edible frog, crested newt, smooth newt Reptiles: lizard and snake	Brehm 1989 Dexel 1989 Jackson 1999 Jackson and Griffin 2000 Rodríguez et al. 1996 Veenbaas and Brandjes 1999 Yanes et al. 1995
Hydrology	Design features at tunnel entrances should divert runoff to prevent flooding. Modifications such as shelving, floating docks, or bank areas within culverts will provide dry retreat sites during periods of high water and may expand likelihood of passage use to a greater range of species. Passages should be constructed above the water table to prevent flooding. Presence of flowing water may deter some amphibian species.	Amphibians: toads and spotted salamanders Reptiles: snakes	Eriksson et al. 2000 Jackson 1999 Jackson and Tynning 1989 Jackson and Griffin 2000 Jenkins 1996 Puky 2004 Rosell et al. 1997 Veenbaas and Brandjes 1999

Structure Characteristics	Effect	Taxonomic Groups Tested	References
Landscape context	Wetlands near culvert entrance may enhance connectivity and enhance habitat value. However, some studies documented an increase in predator concentration. Placement within vicinity of a range of habitat types is likely to increase the diversity of species using the passage. Should be considered to meet biological requirements of target species, because preferences vary. Crossing rates of reptiles were higher in culverts distantly located from urban areas, yet in one study, this only had a minimal effect.	Amphibians Reptiles: lizards and snakes	Ascensão and Mira 2006 Bekker 1998 Dodd et al. 2004 Eriksson et al. 2000 Little et al. 2002 Mata et al. 2004 Norman et al. 1998 Puky 2004 Vos and Chardon 1994
Moisture	Effects of moisture on olfactory cues within passages need to be investigated. Maintenance of damp conditions within tunnels, via slots or grates is important. Abiotic conditions beneath large open passages such as bridges and viaducts may be too dry for amphibians.	Amphibians: anurans and urodeles	Brehm 1989 Jackson 1996 Jackson 1999
Noise	Vehicular noise may cause amphibians to hesitate, but does not substantially interrupt migration. The effect on reptiles is not understood.	Amphibians: frogs and toads	Langton 1989
Placement	Many studies suggest placement is the key to mitigation success. The axis of the passage should be aligned towards breeding areas with placement in reference to traditional routes. Proximity of passages to breeding habitat is important. Structure usage is determined by location with respect to habitat. Maintaining the integrity of habitat adjacent to passage is critical. Reptiles preferred culverts with openings near the pavement edge. Distance between passages is a key characteristic in determining success and should be considered from a biological viewpoint in regards to migration radii of target species.	Amphibians: spadefoot, common toad, common frog, moor frog, edible frog, crested newt, smooth newt, Reptiles: lizard and snake	Ascensão and Mira 2006 Brehm 1989 Foster and Humphrey 1995 Jenkins 1996 Podloucky 1989 Puky 2004 Rodríguez et al. 1996 Roof and Wooding 1996 Rosell et al. 1997
Substrate	Retaining or replicating natural stream conditions within culverts may increase use by animals that use streams as migration corridors. Appropriate substrate (flat rocks) can provide cover. Use of dry substrate should be avoided. Anurans preferred tunnels lined with soil as opposed to bare surface. Researchers recommend that thin layers of detritus and leafy substrate be undisturbed to maintain scent trails. Deep layers of silt may build up over time and need to be removed.	Amphibians: anurans and urodeles	www.wildlifecrossings.info Dodd et al. 2004 Eriksson et al. 2000 Jackson 1996 Lesbarrères et al. 2004 Yanes et al. 1995

Structure Characteristics	Effect	Taxonomic Groups Tested	References
Temperature	Temperature disparities within small passages may cause hesitation. Larger underpasses and grating may increase airflow and maintain ambient conditions.	Amphibians Reptiles: snakes	CARCET website Brehm 1989 Jackson 1999 Langton 1989
Type of opening	Open-bottom arches and box culverts are preferred designs to maintain natural substrates. In one study, reptiles crossed more frequently through circular openings, while amphibians preferred square. However, in another study both amphibians and reptiles selectively used circular and adapted culverts. Vertical entry shafts should be avoided due to high mortality rates documented for amphibians	Amphibians Reptiles	Dexel 1989 Jackson 1996 Jackson 1999 Eriksson et al. 2000 Mata et al. 2005 Rosell et al. 1997
Vegetative cover	The presence of vegetative cover surrounding a passage entrance is favored by some species and may play at least a minor role in selection. Plantings parallel to the road will obscure view, offer refuge, and guide animals to passage opening.	Amphibians Reptiles: lizards and snakes	Eriksson et al. 2000 Mata et al. 2004 Rodríguez et al. 1996
Fencing	Increases passage efficacy. Most efficient during immigration to breeding ponds than emigration. Limited use with animals that exhibit high road avoidance. Fencing installed at angles < 65 degrees can be trespassed by amphibians - optimal height 45-60 cm buried to a depth of 10 cm. Overhanging lip may deter individuals from trespass; however some species may still be successful (hylid frogs). Aggregations of road casualties may be present at barrier endpoints, which may be prevented by extending fence ends out perpendicularly. Joints that connect fencing to passage should be sealed to prevent injury. Flexible material should not be used for construction materials, as it facilitates injury or trespass and requires increased maintenance. Monitoring needed to identify gaps (resulting from erosion, digging mammals, or washouts), and overhanging vegetation. Predation risk may be increased.	Amphibians: anurans and urodeles Reptiles: testudines and snakes	Aresco 2005b Arntzen et al. 1995 Boarman and Sazaki 1996 Brehm 1989 Dodd et al. 2004 Eriksson et al. 2000 Jaeger and Fahrig 2004 Guyot and Clobert 1997 Jenkins 1996 Puky 2004 Roof and Wooding 1996 Ryser and Grossenbacher 1989 Stuart et al. 2001

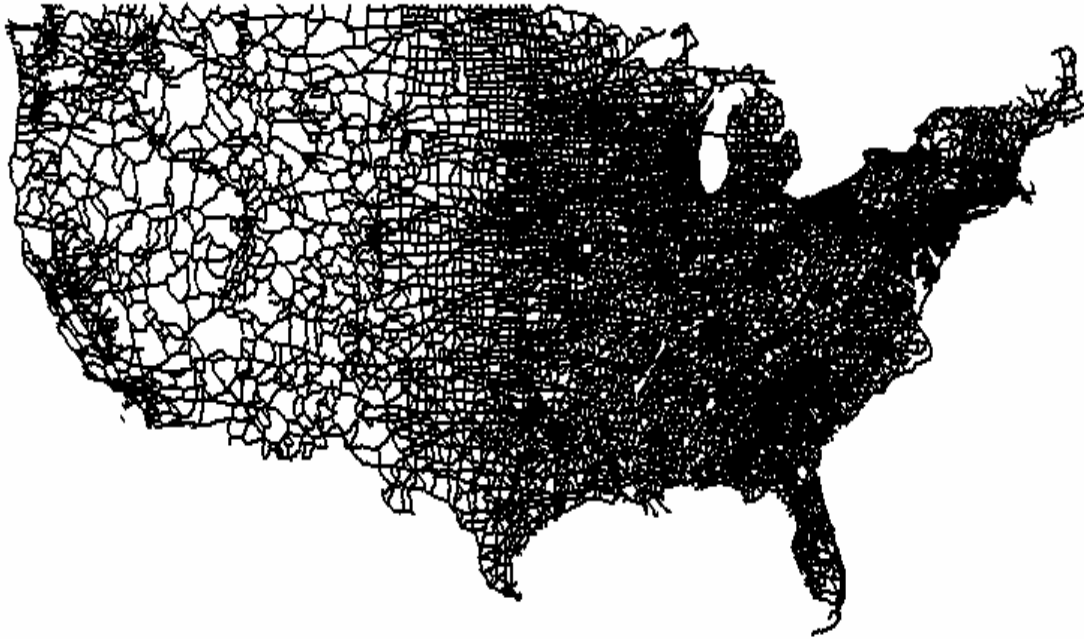


FIG. 1. Major roads and trails in the United States from data available as a Geological Information Systems (GIS) shapefile at www.geocomm.com created with ESRI ARC/INFO (version 7.0.4) published by the U.S. Geological Survey, Reston, Virginia, 1997. This shapefile was originally digitized by the National Mapping Division based on the sectional maps contained in "The National Atlas of the United States of America" published by the USGS in 1970, with updates based on the National Highway Planning Network database published by Federal Highway Administration. Contact person: Bruce Wright, U.S. Geological Survey, 521 National Center, Reston, VA, 20192.

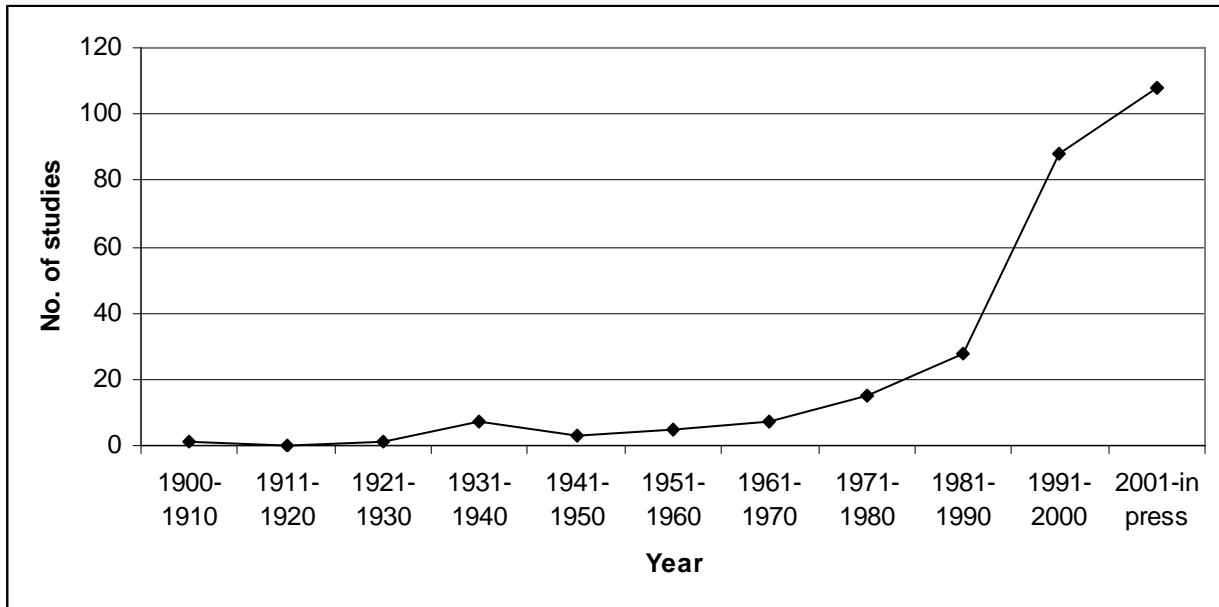


FIG. 2. The number of published studies represented within this document that involve herpetofauna and road issues displayed in 10-year increments. Literature includes publications specifically on herpetofauna and road issues, vertebrate studies on roads that include herpetofauna, and herpetofaunal research that includes roads. Note that the final decade (2001-2010) includes only 6 years, yet greatly surpasses the publication rate on roads in previous decades.

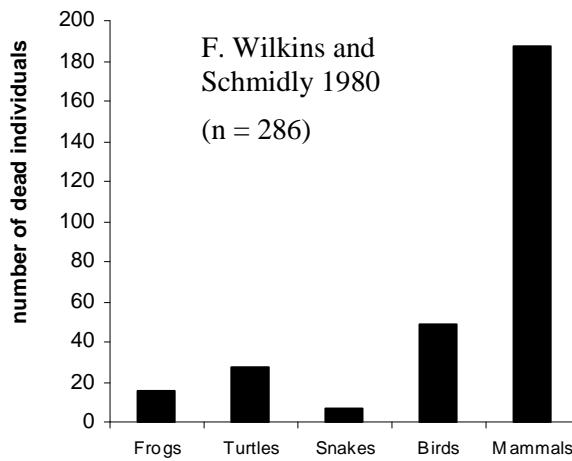
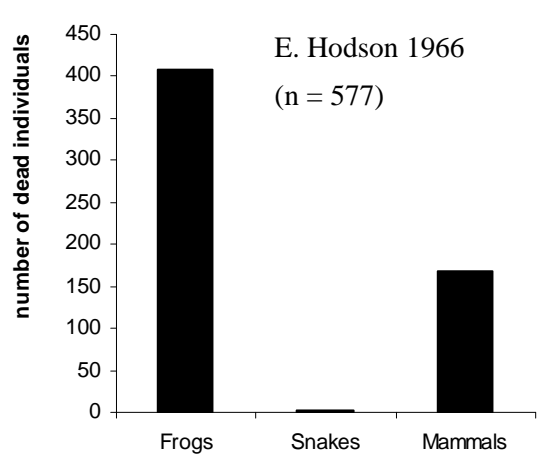
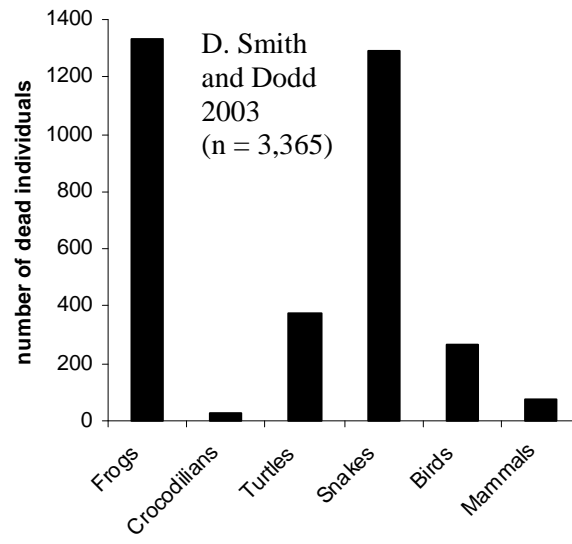
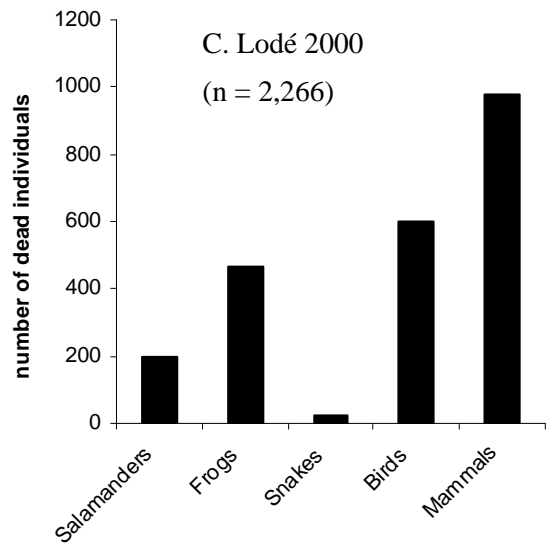
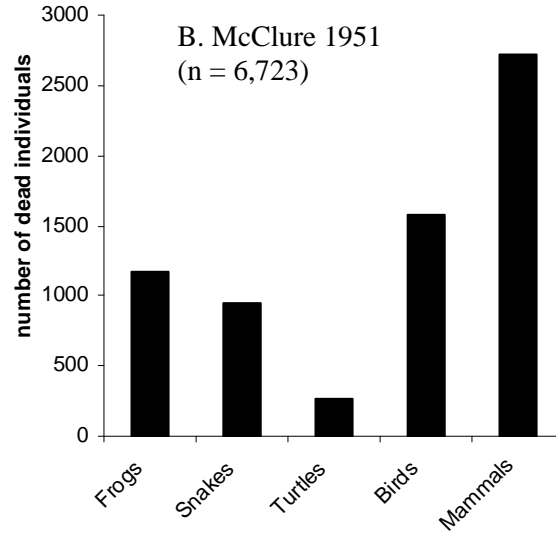
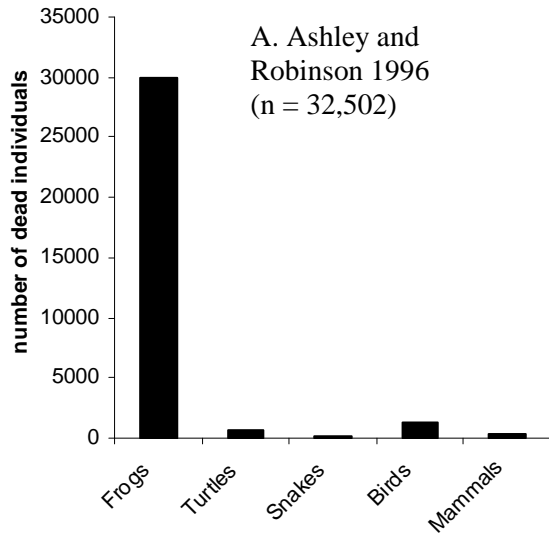


FIG. 3. Comparison of road mortality among different vertebrate groups. Each graph represents a separate study (n= total number across all groups). (A) 3.6 km survey route in Long Point, Ontario (2,549 total km traveled). (B) incidental driving in Nebraska (123,200 total km traveled). (C) 68.2 km survey route in western France (2,250.6 total km traveled). (D) 3.2 km survey route in Paynes Prairie, Florida (336 total km traveled). (E) 3.2 km survey route in Corby, England (2,336 total km traveled). (F) 47.2 km survey route in southeastern Texas (1,768 total km traveled).

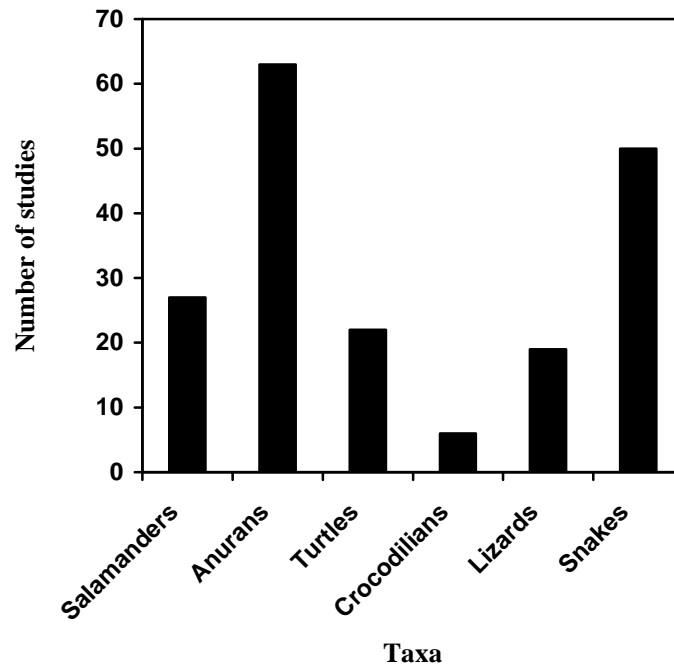


FIG. 4. The approximate number of studies (by taxa) documenting direct road mortality of amphibians and reptiles. Figure taken from Jochimsen et al. (2004).

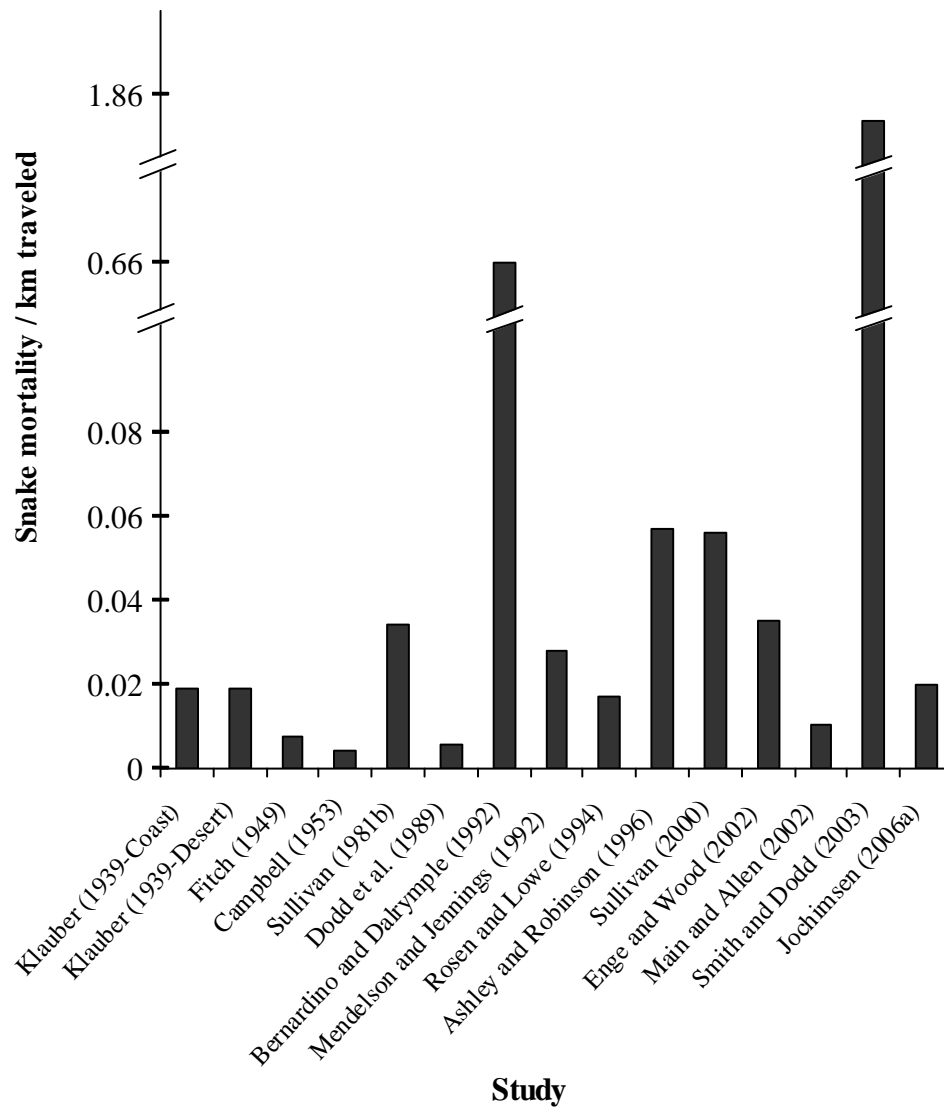


FIG. 5. Relationship between numbers of snakes found dead on the road (DOR) and distance traveled from 14 separate surveys taken at different times and locations in the United States. References for each survey are given on x-axis. Figure taken from Jochimsen (2006a).

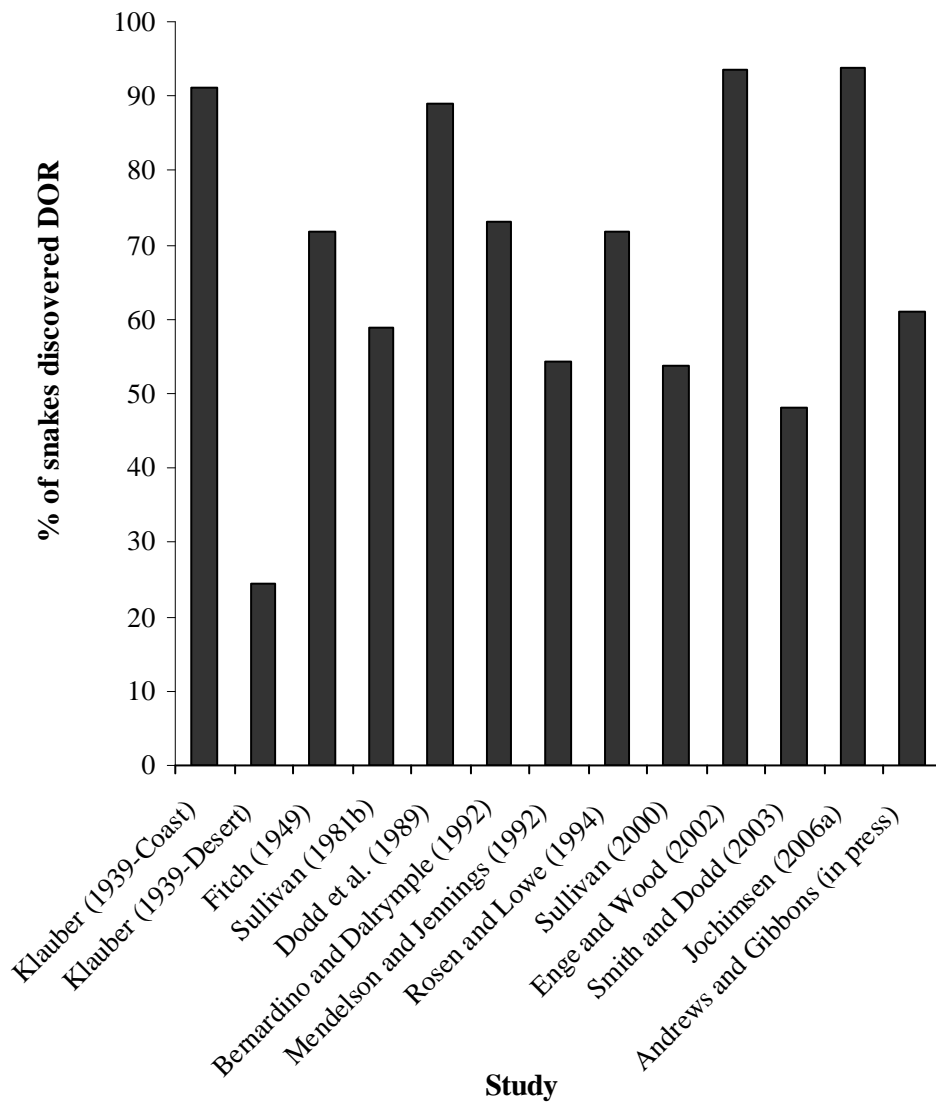


FIG. 6. Proportion of snakes that were dead on the road (DOR) of total (alive and dead) found in 14 separate surveys at different times and locations. References for each survey are given on x-axis. Figure adapted from Jochimsen (2006a).