HIGHWAY MORTALITY OF TURTLES AND OTHER HERPETOFAUNA AT LAKE JACKSON, FLORIDA, USA, AND THE EFFICACY OF A TEMPORARY FENCE/CULVERT SYSTEM TO REDUCE ROADKILLS

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Abstract: I investigated highway mortality and the attempted crossings of turtles and other herpetofauna from 2000-2003 on a 1.2-km-section of a four-lane highway crossing Lake Jackson, Florida. U.S. Highway 27 was built directly through the northwest arm of Lake Jackson, separating a 21-ha portion of the lake to the west (now known as "Little Lake Jackson"). U.S. Highway 27 is a virtually impassable barrier to wildlife (21,500 vehicles per day) and prevents normal movements, dispersal, and migration of most species both during non-drought periods and periodic natural drydowns (on average every 12 yrs). During periods of drought, Little Lake Jackson maintains water and is the destination for large numbers of migrating turtles and other wildlife that leave the drying lake until it refills. The objectives of this study were to: (1) determine the level of road mortality and attempted crossings of turtles and other herpetofauna, (2) examine the potential effects of road mortality on turtle demography including sex ratios and female population size, and (3) design and evaluate the effectiveness of a temporary drift fence-culvert system to both reduce road mortality and facilitate migration. Two drift fences (885 and 600m) were constructed to divert animals away from the north and southbound lanes and direct them into an existing 3.5-m-diameter culvert. Monitoring of road kills and attempted crossings consisted of multiple daily surveys for 43 months (5558 h) including a pre-fence (40 d) and post-fence (1274 d) survey during a drought migration and non-drought conditions.

A total of 10,180 reptiles and amphibians of 44 species were found either road killed or alive behind drift fences: 8,833 turtles, 825 frogs, 344 snakes, 145 lizards, 31 alligators, and 2 salamanders. Diversity among taxonomic groups included 10 species of turtles, 15 species of snakes, 10 species of anurans, 6 species of lizards, 2 salamander species, and 1 crocodilian. Drift fences combined with intensive monitoring greatly reduced turtle road kills and facilitated the use of an under-highway culvert. Pre-fence turtle mortality (9.7/km/day) was significantly greater than post-fence mortality (0.08/km/day), and only 84 of 8,466 turtles climbed or penetrated the temporary fences. Pre-fence data provided strong evidence that turtles cannot successfully cross all four lanes of U.S. Highway 27, with 95 percent of 343 turtles killed as they first entered the highway adjacent to the shoulder and the remaining five percent killed in the first two traffic lanes. I used the equation, $P_{killed} = 1 - e^{-Na/v}$, to estimate the probability of being struck in one attempted crossing of U.S. Highway 27, where N is traffic rate in vehicles/lane/sec during 80 percent of daily volume, a = width of the kill zone (2 tire widths per lane plus 2 times weighted average shell length of 5 species), and v = turtle velocity (m/sec). Solving this equation results in a 98 percent probability of a turtle being killed in one attempted crossing, closely matching my direct observations. Using this model and historic traffic data, the probability of a turtle successfully crossing U.S. Highway 27 decreased from 32 percent in 1977 to only two percent in 2001. Therefore, at least 98 percent of turtles diverted by the fences would have been killed on U.S. Highway 27 during this study if fences were not in place, and the road kill rate is estimated at 1,294/km/yr. Based on a literature survey, this is the highest attempted crossing rate ever documented for turtles. Sex ratios (M:F) of *Pseudemys floridana* (4:1), *Trachemys scripta* (3:1), and *Sternotherus odoratus* (2:1) were significantly male-biased and low numbers of mature females are likely due to 5-10 percent annual road mortality during attempted nesting forays. Because of demographic and life history constraints, turtle populations cannot compensate for the combined effects of annual road mortality (5-10%) and periodic mass road mortality (95-99%) during lake dry-downs.

Introduction

Highways can be detrimental to wildlife populations by causing significant levels of direct mortality and habitat fragmentation. Differential road mortality within populations can affect the demography and the dynamics of populations (Mumme et al. 2000). Highways can create impassable barriers to migration, dispersal, and genetic exchange within populations (Wilkins 1982, Reh and Seitz 1990; Vos and Chardon 1998). In addition, population and community-level effects can alter how adjacent ecosystems function. Thus, understanding the ecological consequences of highways and developing ways to mitigate their effects has become an important field of conservation biology (Oxley et al. 1974, Mader 1984, Rodda 1990, Rosen and Lowe 1994, Groot Bruinderink and Hazebroek 1996, Forman and Alexander 1998, Trombulak and Frissell 2000).

Before current wetland protection laws were enacted, thousands of miles of roads constructed through wetlands caused direct habitat loss, habitat fragmentation, and habitat degradation via dredging and filling and alteration of hydrologic regimes (Evink 1980, Johnston 1994, Mitsch and Gosselink 2000). Prior to the mid-1970's, highways were planned and constructed without consideration of their ecological damage (Adamus 1983, Forman et al. 1997).

Reptiles and amphibians are among the fauna most negatively affected by poor transportation planning associated with wetlands and their mortality can be significant (Ehmann and Cogger 1985, Fahrig et al. 1995, Ashley and Robinson 1996, Clevenger et al. 2001, Smith and Dodd 2003). Highways can be significant barriers to breeding migrations, seasonal and/or drought migrations due to water level fluctuations, and normal foraging forays and dispersal of reptiles and amphibians (Bernadino and Dalrymple 1992, Gibbs 1998, Carr and Fahrig 2001). The "road-effect zone," the maximum distance from a road at which significant ecological effects can be detected, varies depending on the maximum movement distance and frequency (from <200m for sedentary species to >2.0km for turtles, crocodilians, and some frogs (Forman and Alexander 1998, Forman 2000, Carr and Fahrig 2001). Thus, road mortality can reduce the densities of reptiles and amphibians in wetlands for substantial distances from highways and can cause population declines and other negative demographic effects, such as altered sex ratios (Kuslan 1988, Fahrig et al. 1995).

The objectives of this study were to: (1) determine the level of road mortality and attempted crossings of turtles and other herpetofauna on a highway built through a northern Florida lake, (2) examine the potential effects of road mortality on the sex ratios and female population sizes of turtles, and (3) design and evaluate the effectiveness of a temporary drift fence-culvert system to reduce road mortality and to facilitate migration. The design of the temporary ecopassage used vinyl fencing as a guiding structure to divert animals through an existing under-highway drainage culvert. The overall goals were to document road mortality and attempted crossing rates of reptiles and amphibians and to conserve these species until a permanent ecopassage is constructed.

Methods

This study was conducted at Lake Jackson, a 1,620ha lake 11km north of Tallahassee in northwestern Florida, USA. Lake Jackson is a closed basin, and the water depth fluctuates widely. Water level is controlled naturally by variation in rainfall and by two sinkholes. During drought conditions, a lowering of the water table causes leakage into the groundwater through the sinkholes and most of the lake bottom dries, an event that has occurred nine times during the last 100 years (1907, 1909, 1932, 1935, 1936, 1957, 1982, 1999, 2002), drying on average every 12 years (Hughes 1967, Wagner 1984, Carr 1994). Lake Jackson is designated as an Aquatic Preserve by the State of Florida.

From 1963-1965, U.S. Highway 27 was rebuilt as a four-lane, divided highway on a raised road-bed (2.1m above normal high water) directly across a 300m part of Lake Jackson and on 1,000m of the lake shoreline, completely isolating a 21ha portion of the lake to the west (now known as “Little Lake Jackson”) (fig. 1). A 3.5m diameter x 46.6m-long round, corrugated metal drainage culvert under U.S. Highway 27 is now the only connection between Lake Jackson and Little Lake Jackson. Presently, U.S. Highway 27 receives an average traffic flow of 21,500 vehicles per day (224 vehicles/lane/hour) and is a major truck route connecting Interstate 10 to destinations in Georgia and Alabama (FDOT 2002).

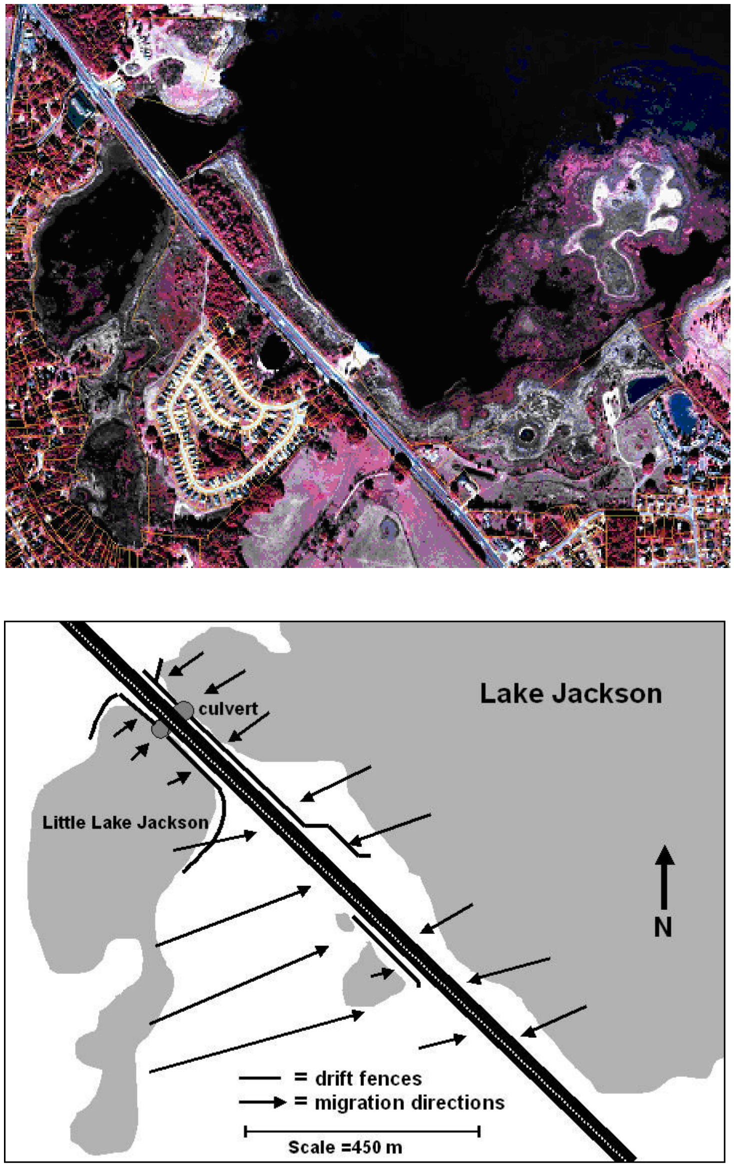

Fig. 1. Aerial photo (above) showing U.S. Highway 27 (center), Lake Jackson (right), and Little Lake Jackson (left) and study area map showing the location of temporary fences and culvert. Arrows indicate direction of migrations by turtles and other herpetofauna.

A large migration of turtles occurred during this study in response to the natural dry down of Lake Jackson in 2000 and the subsequent refilling of the lake in 2001. As Lake Jackson dried, turtles and other herpetofauna emigrated to the west towards Little Lake Jackson, which held water throughout the drought. Heavy rain associated with two tropical storms caused Lake Jackson to refill in 2001, and turtles migrated back from Little Lake Jackson. In 2002-2003, both Lake Jackson and Little Lake Jackson held water.

Monitoring and Fence Design

My daily surveying consisted of two intervals: a pre-fence survey of road kills (22 February - 3 April 2000) and a post-fence survey of the highway and fences (4 April 2000 - 8 September 2003). In the pre-fence survey, I searched the highway, right-of-way, and grassy median of both the north and southbound lanes for live and dead animals two to four times daily between 22 February and 3 April 2000.

Because of the high number of road-killed animals found during the pre-fence survey, I designed and constructed a temporary barrier consisting of 0.6m high woven vinyl erosion control fencing with pre-attached wooden stakes. The fence was installed at the edge of the mowed right-of-way along 885m of U.S. Highway 27N during 31 March - 4 April 2000. The bottom edge was buried ca. 20cm so that the above-ground height of the fence was ca. 0.4m. The barrier was designed to work as a drift fence and divert animals away from the highway and direct them into the under-highway culvert (fig. 1). The north and south ends of the fences were turned back gradually towards the lake at least 80-100 m to prevent animals from simply wandering around the ends and onto the highway (fig .1). From 8-11 September 2000, a 600m fence of the same design was installed along the right-of-way and shore of Little Lake Jackson on the west side of U.S. Highway 27 (fig. 1). On 26-27 April 2002, I constructed a 118m fence along the roadside margin of a 0.6ha pond located on the west side of U.S. Highway 27 opposite Lake Jackson.

All fences were monitored for migrating animals daily from the date of construction to 8 September 2003. I walked along the inside edge of the entire length of each fence. I monitored the fences four times daily in 2000 and 2001 (0900-1100h, 1200-1400h, 1600-1700h, 1800h-2000h) and two times daily in 2002-2003 (1100-1200h and 1600-1700h). In addition, both the culvert and roadway were monitored for live and dead animals. Total sampling effort was 1,314 days and a total of 5,558h. The identity and number of tracks observed on the sand and mud in the culvert were recorded whenever possible. From November-February, daily monitoring of fences was reduced to once per day during months of reduced activity of herpetofauna, and the fences were not monitored when the maximum daytime temperature fell below 14° C.

I recorded the identity and number of all species observed, captured, or found dead. The location of each road kill on the highway was also recorded. All road kills were removed from the highway to assure that they were counted only once. I collected all animals along each fence, placed them in large plastic containers, and transported and released them on the opposite side of the highway (in the direction that they were traveling) at the edge of the water. Terrestrial species (e.g., black racer, *Coluber constrictor*, five-lined skink, *Eumeces fasciatus)* and some semi-aquatic species (e.g., leopard frog, *Rana sphenocephala*) observed along the fences were not transported across the highway unless they were obviously attempting to cross the fence and move directly towards the road. Green anoles (*Anolis carolinensis*) were abundant on the fences and in the adjacent vegetation, and numbers of this species were not counted. Nesting females, gravid females searching for nest sites (i.e., voiding large volume of bladder-fluid when handled; or post-nesting females, (i.e., soil on rear margin of shell and rear legs) were left alone and not transported across the highway.

Animals found alive or dead along the fences or on the highway were placed into one of five categories: (1) alive at fence (LAF), (2) alive on road (AOR), (3) alive on drying lake bottom adjacent to fences (LOB), (4) dead at fence (DAF), or (5) dead on road (DOR). Animals classified as LOB were primarily turtles that were collected as they left drying pools and began migrating towards the highway.

Sex Ratios and Estimates of Numbers of Mature Females

In most studies of freshwater turtles, sex ratios of individual species and female population size are difficult to assess accurately because of sampling biases, variation in local conditions, and differences in habitat preference (Bury 1979, Lovich and Gibbons 1990). However, because of the unique situation at Lake Jackson (i.e., all individuals of all species were migrating from the drying lake in one direction in 2000), I was able to obtain nearly complete data on absolute abundance and population structure including sex ratios and total number of mature females of individual species. In order to examine possible demographic effects of long-term road mortality, I determined if sex ratios of five turtle species differed from 1:1. For inclusion in this analysis, I only included adult turtles (of the known minimum size at maturity for each sex) captured during the initial migration in 2000. Sex ratios were tested for significant deviation from 1:1 with Chi-square tests at an alpha level of 0.05. The road shoulder and fences were monitored for nesting female turtles and depredated turtle nests. Nesting females, gravid females searching for nest sites (i.e., voiding large volume of bladder-fluid when handled; Jackson and Walker 1997), or post-nesting females (i.e., soil on rear margin of shell and rear legs) were left alone and not transported across the highway.

Mark-Recapture of Turtles and Estimating Number of Individual Crossings

I measured and sexed all turtles and individually marked 16 percent of Florida cooters (*Pseudemys floridana*), 10 percent of yellow-bellied sliders (*Trachemys scripta*), and 34 percent of eastern mud turtles (*Kinosternon subrubrum*). In 2001, all captured Florida softshells (*Apalone ferox*) (n=95) were individually marked using specially engraved Monel cattle-ear tags attached to the rear margin of the carapace.

In order to estimate the proportion of turtles that moved from Little Lake Jackson to Lake Jackson that were already counted when migrating earlier from Lake Jackson to Little Lake Jackson, I used recapture rates of marked turtles to estimate the total number of turtles encountered (number of individuals = total captures - (total post-fence captures x proportion of marked individuals recaptured). I did not use a standard mark-recapture method to estimate population size (e.g., Jolly-Seber method) because I did not initially mark all captured individuals migrating from Lake Jackson in 2000.

Funnel Trapping

In order to determine the number and species of reptiles and amphibians that may not be encountered during daylight monitoring of fences and highway, I sampled these species with single-entrance screen funnel traps in October-November 2002. Seven traps were placed every 10 m on the inside of the Little Lake Jackson fence along 10 percent of the fence adjacent to the southbound lane of U.S. Highway 27 and checked twice daily.

Evaluating the Effectiveness of Temporary Fences

I evaluated the effectiveness of the temporary fences in reducing road mortality of turtles by comparing the rate of DOR+AOR turtles (turtles/km/day) found on the 885m stretch of highway before and after fences were installed. I also compared the number of DOR+AOR turtles found on the highway adjacent to the fences to those found on the 300m stretch of highway south of the fences during the post-fence period (4 April 2000 – 8 September 2003). I used Chi-square tests for both comparisons.

Results

Summary of Highway Monitoring

In 43 consecutive months, a total of 10,180 reptiles and amphibians of 44 different species was found either behind the fences or on the highway (Appendix 1). In total, I recorded 8,833 turtles (86.8% of captures), 825 frogs (8.1%), 344 snakes (3.4%), 145 lizards (1.4%), 31 alligators (0.3%), and 2 salamanders (fig. 2). Diversity among taxonomic groups included 10 species of turtles, 15 species of snakes, 10 species of anurans, 6 species of lizards, 2 salamander species, and 1 crocodilian (American alligator, *Alligator mississippiensis*) (Appendix 1).

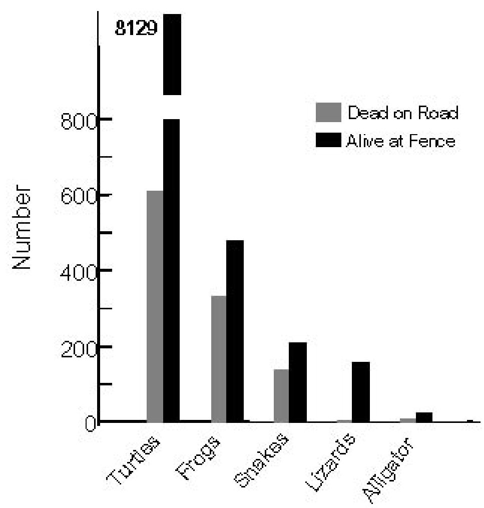

Fig. 2. Number of individuals of each taxon of reptiles and amphibians recorded alive at fences or dead on U.S. Highway 27, Lake Jackson, Florida.

Turtle road mortality and number of attempted crossings

From Feb 2000 - Sept 2003, 4,920 turtles (56%) were found along the Lake Jackson side of U.S. Highway 27 and 3,913 (44%) along the Little Lake Jackson side. Ninety-nine percent of turtles were recorded from March-September. Prior to the construction of the temporary fences, 343 turtles were found DOR on U.S. Highway 27 in 40 days (22 Feb - 3 April 2000) and 24 turtles DOR on U.S. Highway 27 along Little Lake Jackson in 4 days (8-11 September 2000). Following construction of the temporary fences, 8,466 turtles were found along the 1220m on or along the north and southbound lanes of U.S. Highway 27. This total includes 7,526 LAF, 548 LOB, 242 DOR, 95 DAF, and 55 AOR (table 1).

Table 1
Summary data of 10 turtle species found alive behind the fences or on U.S. Highway 27 at Lake Jackson from 22 February 2000 – 8 September 2003. Each individual was classified as alive at fence (LAF), dead on road (DOR), alive on road (AOR), dead behind fence (DAF), or alive on drying lake bottom adjacent to fences (LOB).

Species	*Total*	*LAF*	*DOR*	*AOR*	*DAF*	*LOB*
Apalone ferox	*250*	*206*	*25*	*9*	*1*	*9*
Chelydra serpentina	*17*	*6*	*5*	*1*	*1*	*4*
Deirochelys reticularia	*2*	*2*	*0*	*0*	*0*	*0*
Gopherus polyphemus	*4*	*0*	*2*	*2*	*0*	*0*
Kinosternon subrubrum	*95*	*75*	*20*	*0*	*0*	*0*
Pseudemys concinna	*3*	*2*	*0*	*0*	*0*	*1*
Pseudemys floridana	*3695*	*3303*	*276*	*10*	*68*	*38*
Sternotherus odoratus	*775*	*449*	*61*	*7*	*4*	*254*
Terrapene carolina	*18*	*15*	*2*	*1*	*0*	*0*
Trachemys scripta	*3974*	*3468*	*218*	*25*	*21*	*242*
Total	*8833*	*7526*	*609*	*55*	*95*	*548*

Overall, from 22 Feb - 7 Sept 2000, 4,177 turtles were transported alive across U.S. Highway 27 from Lake Jackson to Little Lake Jackson. Turtles began migrating back to Lake Jackson following heavy rain in early September and a tropical storm on 22 September 2000. From March-June 2001, turtles migrated from Little Lake Jackson back to Lake Jackson as it refilled following heavy early spring rains and a tropical storm (11 June 2001).

Many of the same individuals that were transported across U.S. Highway 27 during the initial migration in 2000 (n=4177) were probably captured again during the return migration in September 2000 and in 2001. Thus, the total number of turtles counted (n=8833) probably represents more than one attempted crossing by many individuals. I used recapture rates of marked turtles to estimate the total number of individual turtles encountered while attempting to cross U.S. Highway 27. Of the 572 *P. floridana* marked during the initial migration from Lake Jackson in 2000, 48 percent (n=236) were recaptured in 2001 during the return migration. Except for *P. floridana*, no other turtle species were marked during the 2000 migration. However, in late 2000 - early 2001, 384 *T. scripta* were marked and released at Little Lake Jackson, and 31 percent (n=119) were later recaptured at the Little Lake Jackson fence as they migrated back to Lake Jackson. In addition, 32 *K. subrubrum* were marked in 2001 with 7 recaptures and 95 *A. ferox* were marked in 2001 with 13 recaptures. In total, 1,185 of 8,466 post-fence turtles were marked, and 33 percent (n=389) were recaptured. Based on the total recapture rate of 33 percent, I estimated that 2794 turtles were captured twice (during both the initial and return migrations), and thus the total number of individual turtles encountered including pre-fence DOR turtles was approximately 5,672.

Efficacy of the Drift Fences for Turtles
The road mortality rate of turtles was significantly less after fences (0.08 DOR/km/day) were installed compared to before (9.7 DOR/km/day) (Chi-square 9.46; $P = 0.002$). After the fences were constructed, significantly fewer turtles were found DOR at the fences than on the road south of the fences. In total, 84 turtles were found DOR+AOR at the fence array and 213 DOR+AOR on the highway to the south of the fences (Table 2) (Chi-square = 56.1; $P < 0.0001$). Thus, only 84 of 8466 (<1%) turtles found post-fence construction actually accessed the highway by climbing or penetrating the temporary fences.

Table 2.
Pre-fence (40 days) and post-fence (1,274 days) comparisons of DOR+AOR turtles on U.S. Highway 27 at Lake Jackson. The location of post-fence turtles was classified as either "At fence" (on U.S. Highway 27 next to the fences) or "Not at fence" (on the 300m stretch of highway south of the fence array).

Species	Pre-fence	Post-fence		Total
		At fence	Not at fence	DOR+AOR
Apalone ferox	0	5	29	34
Chelydra serpentina	1	2	3	6
Kinosternon subrubrum	16	0	4	20
Gopherus polyphemus	0	0	4	4
Pseudemys floridana	217	21	48	286
Sternotherus odoratus	19	39	10	68
Terrapene carolina	0	0	3	3
Trachemys scripta	114	17	112	243
Total	367(55%)	84(13%)	213 (32%)	664

The two most abundant turtle species at U.S. Highway 27 were *T. scripta* and *P. floridana* (table 1). Of 3,974 *T. scripta*, 243 were found DOR+AOR, 114 found pre-fence construction (40 d) and 129 found post-fence construction (1274 d) (tables 1 and 2). Of 3,695 *P. floridana*, 286 were found DOR+AOR, including 76 percent pre-fence and 24 percent post-fence construction (tables 1 and 2). The common musk turtle, *Sternotherus odoratus* represented 8.8 percent of all turtles (n=775) and 68 were found DOR+AOR (table 1). *S. odoratus* demonstrated the greatest ability to climb the fences and represented 46% (n=39) of all turtles found DOR+AOR at the fences after construction. In contrast, *T. scripta* and *P. floridana* combined were 10 times more abundant than *S. odoratus* but represented the same percent of DOR+AOR turtles. Of 220 *A. ferox,* 34 were found DOR+AOR including 5 individuals that climbed over the fences and 29 that attempted to cross on the 300m stretch of highway south of the fence array (tables 1 and 2). *K. subrubrum* exhibited the greatest level of road mortality relative to their abundance. Twenty of 93 *K. subrubrum* were found DOR, 16 pre-fence construction and four that walked around the end of the fence array (tables 1 and 2). Although they represented only 1.1 percent of all turtles, their relative abundance among DOR turtles was 3.3 percent.

Sex Ratios of Turtles and Numbers of Nesting Females and Hatchlings on the Highway
Sex ratios of *P. floridana*, *T. scripta*, and *S. odoratus* were significantly male-biased (Table 3). Number of mature females of *P. floridana* and *T. scripta* represented only 25% and 36% of the total adult population, respectively.

Table 3
Sex ratios and numbers of mature females of five turtle species encountered during the 2000 migration at northwest Lake Jackson and U.S. Highway 27. *P*-values < 0.05 indicate adult male-female ratios that are significantly different from 1:1.

Species	Males	Females	M:F ratio	*P*
Trachemys scripta	1478	539	2.7	<0.0001
Pseudemys floridana	1386	350	4.0	<0.0001
Sternotherus odoratus	293	156	1.9	<0.0001
Apalone ferox	29	23	1.3	NS
Kinosternon subrubrum	14	16	1.0	NS

I observed 221 female turtles nesting directly behind the fences on the road shoulder in 2001-2003. Based on the numbers of adult females counted during the mass migration from Lake Jackson, I estimated that the number of females of each species nesting annually along U.S. Highway 27 represented the following proportions of reproductive females in each population: 6 percent of *P. floridana*, 7 percent of *T. scripta*, 6 percent of *S. odoratus,* and 13 percent of *A. ferox.* Table 4 shows the number of adult males and females found at the fences or on the highway during non-drought years. The observed numbers of females are significantly greater than that expected if turtles were moving on land in numbers equal to the actual population sex ratios (table 4). These data indicate that during non-drought years, female turtles move overland more frequently than males and, thus, have a greater probability of being killed by vehicles, and this may explain the observed male-biased sex ratios.

Table 4
Comparison of the observed and expected number adults of each sex found on land adjacent to or on U.S. Highway 27 at Lake Jackson, Florida in 2002-2003. P-values < 0.05 indicate adult male-female ratios that are significantly different from expected ratios based on population sex ratios.

Species	Observed	Expected	Actual Sex Ratio	*P*
T. scripta				
Male	53	135	2.7:1	<0.0001
Female	132	50		(chi-square=185)
P. floridana				
Male	50	94	4:1	<0.0001
Female	67	23		(chi-square=105)
S. odoratus				
Male	18	39	2:1	<0.0001
Female	42	21		(chi-square=32.3)
A. ferox				
Male	10	22	1.3:1	<0.0001
Female	30	18		(chi-square=14.5)

From 2000-2003, 93 hatchling turtles were found on or along U.S. Highway 27, including 50 *T. scripta*, 34 *P. floridana*, 4 *S. odoratus*, 3 *A. ferox*, and 2 common snapping turtles, *Chelydra serpentina*. Of these 93 hatchlings, 37 percent were DOR.

Road Mortality and Attempted Crossings of Other Herpetofauna and Efficacy of Drift Fences
Other than turtles, 1,064 of 1,346 (79%) of the reptile and amphibian species observed at the fences or on the highway were terrestrial (e.g., *C. constrictor*, corn snake, *Elaphe guttata,* southern toad*, Bufo terrestris*) and semi-aquatic species (e.g., *R. sphenocephala,* cottonmouth, *Agkistrodon piscivorus*, cricket frog, *Acris gryllus*). The upland and semi-aquatic species were often observed foraging or basking in the vegetation at the fences. In total, of the 1,064 upland and semi-aquatic species observed, 26 percent were DOR and 74 percent were LAF. Therefore, three-quarters of the upland and semi-aquatic species either remained at the fences or were diverted from the highway. In contrast, aquatic species had higher road mortality rates. I recorded 282 individuals of aquatic species (e.g., pig frog, *Rana grylio*, water snakes*, Nerodia* spp.), with 76 percent DOR, 22 percent LAF, and 2 percent DAF. Not including turtles, the temporary fences were able to prevent only one-quarter of the aquatic species from being killed on the highway. All of the aquatic, semi-aquatic, and terrestrial species were able to climb or scale the temporary silt fence barrier and access the highway (except for the two-toed amphiuma, *Amphiuma means*, Aresco 2002). The temporary fences apparently diverted some species and may have reduced the overall road-kill rate, especially of small anurans (e.g., *B. terrestris*, eastern narrowmouth toad, *Gastrophryne carolinensis*). Alternatively, many small frogs are difficult to find and count after being killed on the highway (e.g., *Acris* and *Gastrophryne*), as they are either completely obliterated or stick to tires and/or vehicles and are carried away from the study site. Therefore, exact numbers of small frogs actually killed on the highway are difficult to obtain and are probably significantly underestimated (see Funnel Trapping below). Ninety-one percent of non-turtle herpetofauna were recorded from March-September.

Funnel Trapping
A total of 211 reptiles and amphibians from 10 species was captured in 7 trap nights for a catch per unit effort (CPUE) of 4.3 animals/trap night in October-November 2002. Trapped animals are not included in the total numbers in Appendix 1. The two most common species trapped were *G. carolinensis* (n=116) and *A. gryllus dorsalis* (n=71). Two species trapped were not previously encountered at fences or DOR, the central newt, *Notophthalmus viridescens louisianensis*, and the greenhouse frog, *Eleutherodactylus planirostris*.

Culvert Use
I observed *T. scripta* (n=6), *P. floridana* (n=8) and *A. ferox* (n=1) moving into or out of the 3.5m diameter culvert. In addition to direct observations, I recaptured two marked turtles at the Little Lake Jackson fence that were previously marked and released on the Lake Jackson side. These turtles probably moved through the culvert back to Little Lake Jackson. Furthermore, in 2000 and 2001, sets of tracks from >200 individual turtles (primarily *T. scripta* and *P. floridana*) were observed on the sand and mud in the culvert, indicating

that these turtles walked through the culvert. I also observed juvenile and adult *A. mississippiensis* (n=5), numerous *R. sphenocephala, R. catesbeiana, R. grylio,* and an *E. guttata* moving through the culvert. Alligator tracks were also frequently observed (>25 sets of tracks). I did not observe any direct predation on turtles by mammals or alligators in or near the culvert, nor did I find any evidence (e.g., turtle carcasses) of predation by mammals at the culvert.

Discussion

Factors Influencing Frequent Highway Crossings

This study documented that U.S. Highway 27 at Lake Jackson, Florida, is a significant source of mortality for reptiles and amphibians, especially turtles, which attempt to cross the highway in both drought and non-drought years. During the 43-month monitoring period, 10,180 individuals of 44 species of reptiles and amphibians were either found dead on U.S. Highway 27 or intercepted by temporary fences before they accessed the highway. The species encountered represented nearly all reptiles and amphibians known to occur in Lake Jackson and adjacent upland habitats. The frequency of attempted crossings and high levels of road mortality are primarily due to two factors. First, the construction of U.S. Highway 27 along the shore and directly across northwest Lake Jackson created a virtually impassable 1,220m barrier to wildlife that prevents normal terrestrial and aquatic movements, such as dispersal, migration, and nesting activities. Second, the water level of Lake Jackson fluctuates widely in a natural pattern that is typical of shallow, sinkhole lakes in northern Florida (Brenner et al. 1990). Variation in rainfall causes both annual fluctuations and periodic partial and complete drying events during drought conditions (every 12 yrs on average). Little Lake Jackson to the west of the main lake has never dried and is the migration destination for large numbers of migrating turtles and other wildlife when Lake Jackson partially or completely dries. This pattern of emigration and immigration during both normal and drought conditions requires wildlife to attempt to cross U.S. Highway 27, resulting in high road mortality, especially of turtles and other herpetofauna.

Road mortality and attempted crossings of turtles on U.S. Highway 27 is clearly greatest when drought conditions cause Lake Jackson to dry and during subsequent return migrations when the lake refills. In this study, 4,818 turtles were found migrating from Lake Jackson during the dry down in 2000 and 3,783 returning from Little Lake Jackson when the lake refilled in early 2001. I estimated that the fence along U.S. Highway 27 intercepted most of the turtles from a 405ha area of the northwest part of Lake Jackson, as well as many turtles that had migrated to the northern part of the lake in 1999 when the southern part dried. During this study, turtles did not move randomly in all directions from the drying lake and demonstrated the ability to detect water from >1km (Gibbons et al. 1983). Turtle tracks in wet mud on the drying lake bottom were easily visible and indicated that almost all individuals moved directly towards U.S. Highway 27. An aerial photograph taken 150m above drying Lime Sink at Lake Jackson on 17 May 2000 shows a distinct line of hundreds of turtle tracks heading to the northwest in the general direction of Little Lake Jackson approximately 2.1km away (Thomas Scott, Florida Geological Survey, pers. comm.). Therefore, turtles were apparently moving nonrandomly towards Little Lake Jackson, the largest remaining body of water to west. These observations indicate that during mass migrations, a large percentage of the Lake Jackson turtle population will attempt to migrate across U.S. Highway 27.

Probability of Road Mortality in an Attempted Crossing

My observations provide strong evidence that few turtles can successfully cross all four lanes of U.S. Highway 27. Pre-fence data indicated that 95 percent of 343 turtles were killed as they first entered the highway adjacent to the shoulder, and the remaining 5 percent were killed in the first two traffic lanes. In February-March 2000, turtles were observed migrating only from Lake Jackson to Little Lake Jackson (east to west) as Lake Jackson was drying and no DOR or AOR turtles were found west of the median. Based on these observations, traffic volume on the four-lane highway (21,500 vehicles per day; 3.7 vehicles/lane/minute), and turtle movements that correspond with 80 percent of daily traffic volume (0700-2000h), these data demonstrate that virtually no turtles can successfully traverse all four lanes. Further, I used the equation of Gibbs and Shriver (2002) modified from Hels and Buchwald (2001) to estimate the probability that a turtle will be killed in one attempted crossing of U.S. Highway 27:

$$P_{killed} = 1 - e^{-Na/v},$$

where N is traffic rate in vehicles/lane/sec during 80 percent of daily volume, a = width of the kill zone (2 tire widths per lane plus 2 times weighted average shell length of 5 species), and v = turtle velocity (m/sec). I estimated average turtle velocity (v) from direct observations of individuals on U.S. Highway at 0.05m/sec and an average kill zone/lane of 2.4m. Solving this equation for 2001 traffic volume gives a 98 percent probability of a turtle being killed in one attempted crossing which closely matches my direct observations (fig.

3). Therefore, it is reasonable to estimate that at least 98 percent of turtles diverted by the fences (5,558 individuals at a rate of 1,294 road kills/km/yr) would have been killed on U.S. Highway 27 during this study if fences were not in place and turtles were allowed to access the highway. Thus, mass migration events in response to periodic natural dry-downs can potentially decimate the entire populations of six turtle species: *T. scripta, P. floridana, S. odoratus, A. ferox, K. subrubrum, and C. serpentina*.

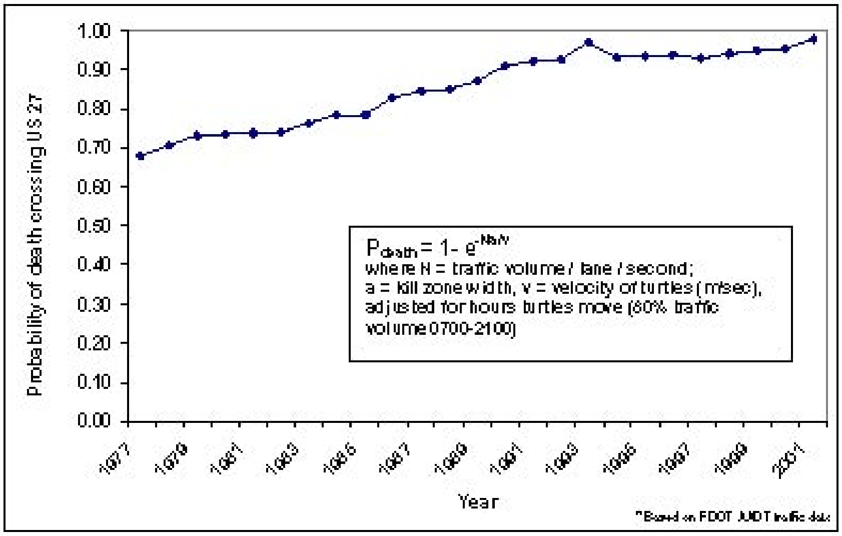

Fig. 3. Annual change in probability of a turtle being killed by a vehicle while attempting to cross U.S. Highway 27 at Lake Jackson as a function of traffic volume (vehicles/lane/second) from 1977-2001 (FDOT 2002). Probability of being killed is calculated using the equation from Gibbs and Shriver (2002) modified from Hels and Buchwald (2001).

Road Mortality Effects on Turtle Population Viability and Demography

Large numbers of turtles are road killed during both periodic dry-downs and in normal years. The mass migration and mortality at U.S. Highway 27 represent turtles from at least 25 percent of the total lake area (400ha northwest sub-basin) and the loss of 25 percent of the entire turtle population every 12 years due to traffic mortality is a severe bottleneck event and a population sink (Pulliam 1988). This mortality alone will likely cause long-term declines that cannot be overcome by immigration from other areas of the lake (Congdon et al. 1993). However, in addition to losses during periodic dry-downs, traffic deaths are also a significant source of mortality for turtles during non-drought years. Frequent terrestrial activity of freshwater turtles is well documented for several species, including *T. scripta, P. floridana, A. ferox, K. subrubrum*, *C. serpentina*, and the chicken turtle (*Deirochelys reticularia*) (Carr 1952; Bennett et al. 1970; Gibbons 1970; Wygoda 1979; Obbard and Brooks 1980; Gibbons et al. 1983; Buhlmann 1995). Such movements are associated with nesting in spring and summer, annual local migration patterns that correspond to hormone cycles (e.g., movements of male turtles over land in late summer and early spring in search of mates), dispersal of juveniles and subadults, and newly emerging hatchlings searching for water. I found 510 turtles DOR or LAF during non-drought years (2002-2003). These turtles included nesting females, migrating males and juveniles, and hatchlings leaving nests. The high rate of terrestrial recaptures (33%) of turtles in this study demonstrates that aquatic turtles move over land frequently at Lake Jackson. These data suggest that even if a turtle successfully crosses the highway one time, it is likely that it will emigrate back across the highway, with a high probability of being killed by vehicles.

In this study, I found strong evidence of demographic effects of long-term road mortality on female population size and sex ratios of three turtle species. For example, only 25 percent of the adult population of *P. floridana* consisted of mature females (table 3). Previous studies of freshwater turtle populations indicate that normal sex ratios are typically 1:1 to 2:1 ratios of males:females in emydid turtle species with earlier maturing males (Bury 1979; Lovich and Gibbons 1990; Gibbons 1990). In this study, the observed sex ratios are not likely due to habitat-related nest temperatures, as *P. floridana* and *T. scripta* have a different pattern of temperature sex determination (TSD) than *S. odoratus* (Ewert and Nelson 1991), yet all three species showed male-biased ratios. Furthermore, it is also unlikely that differential mortality due to predation by alligators would cause the observed male dominated populations, as alligators prey more heavily on males of *T. scripta* and *P. floridana*, as they are significantly smaller than females (Gibbons et al. 1979). Lastly, differential predation on nesting females by mammalian predators (e.g., raccoons) could reduce the number of adult females, but no nesting females were found killed by predators on land during three nesting seasons at Lake Jackson (2001-2003). Therefore, significantly male-biased sex ratios of *P. floridana, T. scripta*, and *S. odoratus* at Lake Jackson may be the result of differential mortality of females due to road kills during annual nesting forays. In 2001-2003, 221 nesting females were observed directly along U.S. Highway 27. In non-drought years (2002-2003) significantly more females than males of *T. scripta, P. floridana, S. odoratus,* and *A. ferox* were found on land along the fences adjacent to the highway (table 4). If 5-10 percent of females are killed annually along the highway during nesting season, this level of mortality by itself could be sufficient to cause long-term population declines when combined with relatively slow growth to maturity and low levels of recruitment (e.g., 10-12 yrs for *P. floridana)* (Congdon et al. 1994, Aresco unpubl. data). Hence, it is unlikely that turtle populations at Lake Jackson can compensate for the combined effects of annual road mortality (5-10%) and periodic mass mortality events (95-99%) during lake dry-downs.

Without appropriate baseline data, it may be difficult to detect if turtle populations have already undergone historic declines in population size. In this case, low, but consistent annual road mortality rates may be causing a long-term population decline that will eventually lead to extinction of local populations. Alternatively, recently abundant species may be experiencing dramatic reductions in population size and alterations in demography due to increased traffic volume and greater road kill probability (Gibbs and Shriver 2002). This scenario best fits the case of U.S. Highway 27 and likely many other highways in North America where formerly rural roads that historically allowed successful crossing of some turtles have experienced a 100-200 percent increase in traffic volume over the last two decades (e.g., 162% increase from 1977-2001 at U.S. Highway 27) (National Research Council 1997, FDOT 2002). For example, the probability of a turtle successfully crossing U.S. Highway 27 decreased from 32 percent in 1977 to only 2 percent in 2001 (fig. 4). Lastly, for new road construction, long-lived species with long generation times may exhibit a lag time between current road mortality rates and observable population declines (Doak 1995, Findlay and Bourdages 2000).

Road mortality is an increasingly significant threat to population viability of turtles (Gibbons et al. 2000, Gibbs and Shriver 2002). Recent studies provide strong evidence that local populations of freshwater and terrestrial turtles are reduced along highways by direct traffic mortality and the effects of habitat fragmentation (Mitchell and Klemens 2000). For example, road mortality of five species of turtles on the 3.6km Long Point Causeway on Lake Erie was 716 in four years (50/km/yr) (Ashley and Robinson 1996). On the Cape May peninsula in southern New Jersey, northern diamondback terrapins *(Malaclemys terrapin*) attempt to find nest sites on shoulders of raised roadways built across salt marshes, resulting in high annual road mortality of females (Wood and Herlands 1997). In a seven-year census between 1989-1995, they counted 4020 roadkilled females (23/km/yr). In central Ontario, a three-year study found 31 percent (86 of 279) of *C. serpentina* observed on roads were killed during the nesting season (Haxton 2000). In Montana, large numbers of painted turtles *(C. picta)* are killed while crossing between pothole ponds located on either side of U.S. Highway 93 (e.g., 345 in 2002 on 6.5km) (Fowle 1996, K. Griffin, Univ. of Montana, pers. comm.). During a one-year study of wildlife mortality on a 3.2km stretch of U.S. Highway 441 crossing Paynes Prairie, Florida, 187 turtles were found DOR (58/km/yr) (Smith and Dodd 2003). In the present study at Lake Jackson, Florida, I counted 8,833 turtles either DOR or attempting to cross 1.2km of U.S. Highway 27 in 3.6 years (2056/km/yr). After adjusting for >one capture for some individuals the road-kill rate is estimated at 1,294/km/yr. Although road kill rates of turtles could be greater in some areas, the rate of attempted crossing by turtles at Lake Jackson is presently the highest ever recorded worldwide. Clearly, additional studies should be initiated throughout North America to carefully quantify both direct mortality and demographic effects.

Efficacy of Temporary Fences and Existing Culvert

The temporary fences installed along the right-of-ways at U.S. Highway 27 combined with daily monitoring almost completely eliminated road mortality of turtles. Prior to construction of the fences, the road mortality rate of turtles was 9.7km/day but this rate was reduced to only 0.08km/day after fences were installed. In 43 months, only 84 of 8,466 (<1%) turtles found post-fence construction actually accessed the highway by climbing or penetrating the temporary fences. The fences directed some animals towards the pre-existing 3.5m diameter culvert, and turtles (*P. floridana, T. scripta, A. ferox*), alligators, and frogs (*R. grylio, R. catesbeiana. R. sphenocephala*) were directly observed to use the culvert as a crossing under the highway. Turtles did not hesitate to use the culvert that has sufficient light visible from the opposite side and a natural sand/silt substrate. In addition, configuration of the north and south ends of the fence by turning the turtles gradually back towards the lake bottom for several hundred meters was successful in preventing most turtles from accessing the highway from around the ends. However, most turtles were capable of climbing the fencing, especially *A. ferox, S. odoratus, C. serpentina*, and juvenile *P. floridana* and *T. scripta.* Therefore, the temporary fences required vigilant daily monitoring to remove turtles from behind the fences and transport them across the highway before they could climb over. The low rate of trespass of turtles at the fences (<1%) would have undoubtedly been much greater if the array was not intensively patrolled. Although the climbing ability of turtles is not well documented, it must be considered for any permanent barrier, including such design features as a smooth, vertical surface (1m tall) and an overhanging, inward lip.

Most mortality of turtles behind the fences was due to predation. Of 95 turtles found dead behind the fences, 92 were killed by predators, and three apparently overheated. Nocturnal mammalian predators killed turtles that left the water in the early evening (1700-2000h) and were diverted by the fences but failed to locate the culvert before nightfall. *P. lotor* were the primary predators, but I also observed a gray fox (*Urocyon cinereoargenteus*) at dusk carrying a live *T. scripta*. Most DAF turtles were found concentrated in a wooded area 235-300m south of the under-highway culvert. These turtles were primarily adult *P. floridana* and *T. scripta* attempting to migrate from drying Lake Jackson to Little Lake Jackson in May-June 2000. In addition, several hatchling and small juvenile turtles were found being attacked by imported red fire ants (*Solenopsis invicta*) and later died. Several turtles were observed being taken by humans at the fences, either for pets (*P. floridana, T. scripta*) or meat *(A. ferox).* These observations demonstrate that simply installing barriers along a roadway without a sufficient number of culverts will result in high rates of depredation if the barriers are not monitored daily. Clearly, a single culvert along a 1.2-km stretch of road, in this case, is not sufficient to facilitate migration, and additional underpasses must be available (Yanes et al., 1995). Therefore, because of potentially high rates of mammalian predation and the slow walking speed of turtles, under-highway culverts should be installed at least every 200-300m to facilitate relatively rapid migration. Thus, at least three-four additional culverts are required at U.S. Highway 27.

Although the temporary drift fences prevented most turtles from accessing the highway, they were only partially successful in diverting other herpetofauna. The drift fences were only able to prevent about one-half of all herpetofauna (other than turtles) from being killed on the highway. Aquatic, semi-aquatic, and terrestrial species were able to climb, scale, or jump over the temporary fence and access the highway. The fences were not monitored at night, so the sampling method underestimated the presence of nocturnal, secretive animals at the fences. In addition, the ability to detect road kills of small frogs, such as *A. gryllus* and *G. carolinensis* is very difficult after they are killed by vehicles, as carcasses are quickly obliterated (Fahrig et al. 1995, Hels and Buchwald 2001). Thus, it is likely that these common species were killed on U.S. Highway 27 in significantly greater numbers than actually observed. Captures in funnel traps confirm that these species were much more common than observed during daylight monitoring. Animals captured in traps were primarily nocturnal species that were not normally encountered, and, thus, numbers of some species are significantly underestimated, and others are completely missed, by simply walking the fences and highway only during daylight hours.

Despite some problems with animal trespass, maintenance, and depredation, the use of vinyl erosion control fencing is recommended for temporary use in diverting turtles towards existing culverts until a more permanent design can be constructed. The design and construction of wildlife crossings is a challenge to both ecologists and highway engineers (Evink et al. 1996, Clevenger and Waltho 2000, Clevenger et al. 2001, Little et al. 2002). Ideally, ecopassages should be designed to mitigate the effects of highway mortality and habitat fragmentation on the full diversity of fauna affected by a particular highway, including reptiles and amphibians. Therefore, a multi-species approach that seeks to restore the ecological connectivity of fragmented areas should be the primary goal, rather than a single-species or single-group approach. An ideal prototype for a multi-species ecopassage design for reptiles, amphibians, and mammals was recently constructed by the Florida Department of Transportation at the Paynes Prairie State Preserve along 3.2-km of U.S. Highway 441 south of Gainesville, Florida. This design consists of a lipped, 1.1-m high concrete guide wall and a series of underpasses. This system has proven effective in diverting wildlife from the highway, reducing mortality, and facilitating under-highway movements (Barichivich and Dodd 2002).

Implications for Prioritization of Wildlife-Highway Problem Areas for Mitigation

Current wildlife-transportation mitigation planning in many states is based primarily on decision-based prioritization models (Smith et al. 1998, Harris and Smith 1999; Schaefer and Smith 2000, Gilbert et al. 2002). Many states use such models to prioritize funding and rank sites for wildlife-highway mitigation projects, and these are based primarily on the presence of threatened and endangered species. However, in cases such as Lake Jackson where there is severe road mortality of non-listed species that affects viability of local populations, we need a better method of identifying and integrating these sites into GIS-based prioritization models. Prioritization algorithms should account for differential vulnerability to high levels of road mortality of long-lived reptiles, such as turtles, that have unique demographic constraints and are unable to compensate for significant losses of adults (Gilpin and Soulé 1986, Congdon et al. 1994, Doak et al. 1994). It is imperative that such sites are identified and mortality rates documented in order to yield a more complete inventory for statewide transportation planning and ranking for environmental mitigation.

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Appendix 1

44 species of reptiles and amphibians found either behind the fences or on U.S. Highway (dead or alive) at Lake Jackson, Leon County, Florida from 22 February 2000 - 8 September 2003. "Alive" includes number alive at fence (LAF) or alive on the road (AOR) and "Dead" is number found dead on road (DOR) or number in parentheses is dead at fence (DAF). An asterisk indicates a State of Florida Species of Special Concern.

Species	Alive	Dead	Total
Salamanders (n=2)			
Two-toed amphiuma, *Amphiuma means*	0	0 (1)	1
Central newt, *Notophthalmus viridescens*	1	0	1
Anurans (n=825)			
Bullfrog, *Rana catesbeiana*	1	34	35
Cricket frog, *Acris gryllus*	309	2	311
Eastern spadefoot toad, *Scaphiopus holbrookii*	1	4	5
Greenhouse frog, *Eleutherodactylus planirostris*	0	1	1
Green tree frog, *Hyla cinerea*	2	36	38
Leopard frog, *Rana sphenocephala*	68	198	266
Narrowmouth toad, *Gastrophryne carolinensis*	5	0	5
Pig frog, *Rana grylio*	7	52	59
Southern toad, *Bufo terrestris*	84	18	102
Squirrel tree frog, *Hyla squirella*	2	1	3
Turtles (n=8833)			
Box turtle, *Terrapene carolina*	16	2	18
Chicken turtle, *Deirochelys reticularia*	2	0	2
Common musk turtle, *Sternotherus odoratus*	710	61(4)	775
Common snapping turtle, *Chelydra serpentina*	11	5 (1)	17
Eastern mud turtle, *Kinosternon subrubrum*	75	20	95
Florida cooter, *Pseudemys floridana*	3351	276 (68)	3695
Florida softshell, *Apalone ferox*	224	25 (1)	250
Gopher tortoise, *Gopherus polyphemus**	2	2	4
Suwannee cooter, *Pseudemys concinna**	3	0	3
Yellow-bellied slider, *Trachemys scripta*	3735	218 (21)	3974
Snakes (n=344)			
Banded water snake, *Nerodia fasciata*	19	43	62
Black racer, *Coluber constrictor*	96	3	99
Black swamp snake, *Seminatrix pygaea*	1	6	7
Corn snake, *Elaphe guttata*	10	4	14
Cottonmouth, *Agkistrodon piscivorus*	31	8	39
Eastern kingsnake, *Lampropeltis getulus getulus*	7	1	8
Florida green water snake, *Nerodia floridana*	13	55	68
Garter snake, *Thamnophis sirtalis*	12	5	17
Gray rat snake, *Elaphe obsoleta spiloides*	11	4	15
Mud snake, *Farancia abacura*	0	3	3
Red-bellied snake, *Storeria occipitomaculata*	1	0	1
Ribbon snake, *Thamnophis sauritus*	3	1	4
Ringneck snake, *Diadophis punctatus*	1	0	1
Rough green snake, *Opheodrys aestivus*	3	0(2)	5
Scarlet snake, *Cemophora coccinea*	0	1	1
Lizards (n=145)			
Broadhead skink, *Eumeces laticeps*	4	0	4
Eastern glass lizard, *Ophisaurus ventralis*	11	0	11
Five-lined skink, *Eumeces fasciatus*	122	0	122
Green anole, *Anolis carolinensis*	NA	NA	NA
Ground skink, *Scincella lateralis*	7	0	7
Six-lined racerunner, *Cnemidophorus sexlineatus*	0	1	1
Crocodilians (n=31)			
Alligator, *Alligator mississippiensis*	24	7	30
Total	8985	1195	10180