The effect of sex-specific terrestrial movements and roads on the sex ratio of freshwater turtles

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Abstract

Differential road mortality may affect the demography of vertebrate populations when movements associated with foraging, reproduction, or dispersal cause a greater proportion of one sex or stage to frequently contact roads. In the case of turtles, roadsides create artificial disturbed and open habitats that may be attractive to nesting females but may cause significant road mortality. I tested this possibility by comparing the sex ratios of turtle populations in a lake that is bisected by a high-traffic, four-lane highway to those in nearby ponds located away from major roads in northwestern Florida (USA). I evaluated the potential role of road mortality as the cause of skewed sex ratios by determining whether adult female freshwater turtles move overland more frequently than that expected from actual sex ratios and the proportions of turtles of four species that attempt to nest annually along the roadside. Population sex ratios were dramatically biased toward males in the Florida cooter (*Pseudemys floridana*) (80% males), yellow-bellied slider (*Trachemys scripta*) (73% males), and common musk turtle (*Sternotherus odoratus*) (65% males) in the lake adjacent to the highway compared to those in ponds not affected by road mortality, where the proportion of males ranged from 39% to 60%. Despite male-biased population sex ratios, under normal (non-drought) conditions a significantly greater proportion of adult females (57–72%) than males were found on land along the highway and, thus, have a greater annual probability of being killed by vehicles. An estimated 6–29% of all adult females in four turtle species nested annually along the highway shoulder. If this phenomenon is general for freshwater turtle populations located near roadways, male-biased sex ratios and low numbers of adult female turtles elsewhere may be the result of cumulative differential mortality of nesting females struck by vehicles as they enter the highway during annual nesting forays.
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1. Introduction

Roads increase mortality rates in some species (Rosen and Lowe, 1994; Fahrig et al., 1995; Ashley and Robinson, 1996) and may create barriers to migration, dispersal, and genetic exchange (Wilkins, 1982; Mader, 1984; Reh and Seitz, 1990; Vos and Chardon, 1998). Many studies have documented high mortality of individuals (reviewed in Forman and Alexander, 1998; Trombulak and Frissell, 2000). However, few studies have documented the effects of roads on demography or population viability caused by direct mortality or indirect effects of habitat fragmentation or modification (Hels and Buchwald, 2001).

Artificial roadside habitats may attract wildlife and increase the risk of mortality from vehicle collisions. Some species prefer early successional, open habitats along roads for nesting or foraging (e.g., Florida scrub jay, *Aphelocoma coerulescens*; Mumme et al., 2000). Other species (e.g., mallards, *Anas platyrhynchos*, Cowardin et al., 1985; leopard frogs, *Rana sphenocephala*, Smith and Dodd, 2003) prefer nesting or breeding in man-made stormwater retention ponds or dredge

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canals along roads. In such situations, these altered habitats may be ecological traps when behavioral cues or evolved habitat preferences that are normally correlated with reproductive success instead result in low reproductive output or high adult mortality (Schlaepfer et al., 2002).

Differential road mortality resulting from sex or stage-specific differences in habitat use, dispersal, foraging behavior, and reproduction could affect sex ratios or demographic structure and affect population dynamics (Mumme et al., 2000). For example, Moore and Mangel (1996) found higher road mortality rates for female barn owls (*Tyto alba*) foraging along roads than for males and predicted population declines with relatively low rates of road mortality. In sexually dimorphic species, males typically have higher mortality rates and lower life expectancy than females (Comfort, 1979; Clutton-Brock et al., 1985). In most mating systems, the number of females in the population is relatively more important than number of males for population growth, and fluctuations in the sex ratio will affect reproduction (Caswell, 2001). Demographic dimorphisms in survivorship as small as 20% may destabilize local population dynamics (Caswell and Weeks, 1986; Lindström and Kokko, 1998). Thus, increases in female mortality from roads may destabilize sex-ratio dynamics and increase the risk of local extinctions.

Road mortality is a significant threat to the population viability of turtles in many areas (Ashley and Robinson, 1996; Fowle, 1996; Guyot and Clobert, 1997; Haxton, 2000; Mitchell and Klemens, 2000; Gibbs and Shriver, 2002; Aresco, 2005). Turtles are especially vulnerable to the effects of road mortality because of slow population growth rates and low levels of recruitment (Crouse et al., 1987; Congdon et al., 1993, 1994; Doak et al., 1994). An increase of less than 10% annual mortality of mature females may lead to population declines (Brooks et al., 1991; Congdon et al., 1993). Recent studies provide strong evidence that local populations of freshwater and terrestrial turtles are reduced along roads by traffic mortality and the effects of habitat fragmentation (Bury and Luckenbach, 2002; von Seckendorff Hoff and Marlow, 2002; Marchand and Litvaitis, 2004).

Behavioral differences in terrestrial movements between the sexes of freshwater turtles may lead to sex-specific road mortality and skewed sex ratios (i.e., male-biased), especially in areas of dense roads and human development (Marchand and Litvaitis, 2004; Steen and Gibbs, 2004). Because female freshwater turtles nest on land and may travel up to 1 km from water while searching for appropriate nest sites (Carr, 1952; Congdon et al., 1987), these individuals must often attempt to cross roads (Ashley and Robinson, 1996; Haxton, 2000; Aresco, 2004; Marchand and Litvaitis, 2004). Roadsides are disturbed habitats that attract nesting females but may increase the risk of road mortality (Wood and Herlands, 1997).

Here, I evaluate the potential effect of road mortality on sex ratios and female mortality rates in four species of freshwater turtles in a lake that is bisected by a major road. I use three lines of evidence to build the case that road mortality affects the sex ratios of turtles in this lake: (1) a comparison of the sex ratios of turtles in this lake to those in nearby ponds distant from major roads, (2) an estimate of the extent to which adult female movement rates on land are greater than for males and, (3) an estimate of the proportion of adult females in the population that attempt to nest annually along the road.

2. Methods

2.1. Study area and background

This study was conducted at Lake Jackson in northwestern Florida, USA, a 1620 ha lake 11 km north of Tallahassee. Lake Jackson is a closed basin and the water depth fluctuates widely as a result of rainfall variation. The lake bottom has dried in 9 of the last 100 years. This study was conducted from 2000 to 2003 both during and following a severe three-year drought (1998–2000: 97.4 cm rainfall deficit). Average annual rainfall at Tallahassee, Florida is 165.6 cm (Northwest Florida Water Management District, unpublished data). In 2000, rainfall was 59.1 cm below the normal average. Rainfall was near average to above average in 2001–2003: 1.0 cm above normal in 2001, 3.25 cm below normal in 2002, and 21.8 cm above normal in 2003 (Northwest Florida Water Management District, unpublished data). In 1965, US Highway 27 was rebuilt as a four-lane, divided highway directly across a 300 m wide arm of Lake Jackson, isolating a 21 ha portion of the lake to the west (now known as "Little Lake Jackson"). In 2001, average daily traffic flow on US Highway 27 was 21,500 vehicles (224 vehicles/lane/hour) (Florida Department of Transportation, 2002).

US Highway 27 is a significant source of mortality for turtles in both drought and non-drought years (Aresco, 2005). From 2000 to 2003, 8842 individuals of 10 species were either found dead on Highway 27 or intercepted by drift fences before accessing the road (Aresco, 2005). Little Lake Jackson has not dried in the past 100 years and is the migration destination for large numbers of migrating turtles and other wildlife when Lake Jackson partially or completely dries. A migration of turtles from drying northwest Lake Jackson began in late February 2000 when turtles became active after winter dormancy and continued until mid-July 2000. In that year, 4818 turtles were found trying to migrate across the road. In 2001, 3299 turtles migrated from Little Lake Jackson back to Lake Jackson as it refilled (Aresco, 2005). In

2002 and 2003, both Lake Jackson and Little Lake Jackson held water and normal seasonal movements of turtles occurred in both directions.

2.2. Data collection

2.2.1. Lake Jackson

I counted turtles during a mass migration event to determine population sex ratios. Sex ratios and female population sizes of freshwater turtles 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, since virtually all individuals of all turtle species were migrating west from the north part of the drying Lake Jackson in 2000, I was able to determine absolute abundance and population structure, including sex ratios and total number of mature females. I also counted turtles found on land during two average rainfall years to determine whether one sex moves overland more frequently than expected from known sex ratios.

Daily monitoring of the road and road shoulder consisted of two intervals: a pre-fence survey (22 February–3 April 2000) and a post-fence survey of the road and fences (4 April 2000–1 November 2003) (Aresco, 2005). During the pre-fence survey, I walked the road and shoulder at least 4 h per day. Because Lake Jackson was starting to dry during this period, turtles were only migrating from east to west and 95% of turtles found were killed on the road in the first traffic lane and the remaining 5% in the second traffic lane before reaching the median (Aresco, 2005). These observations provided strong evidence that few turtles could successfully cross both northbound lanes of Highway 27 and, thus, it was unlikely that turtles that attempted to cross the road prior to the construction of the drift fence were undetected.

Because of the high number of road killed turtles found during the pre-fence survey (343 turtles in 40 days), I installed drift fences along 700 m of the east side of Highway 27 in early April 2000 and along 600 m of the west side of the road in September 2000. I walked along the inside edge of the entire length of each fence four times daily in 2000 and 2001 and two times daily in 2002–2003. Total sampling effort was 1367 days and a total of 5664 h. All turtles were individually marked and carapace length (CL) and sex were recorded. The road shoulder and fences were monitored each day for gravid (verified by X-ray) or nesting female turtles and depredated turtle nests (Aresco, 2004).

2.2.2. Three other ponds

I collected all turtles from three natural ponds located within suburban parks in Tallahassee, Leon County, Florida: McCord Pond (2.0 ha), Harriman Pond (0.5 ha), and Hidden Pond (1.7 ha). Each pond is distant from major roads and no significant road mortality of turtles has been observed. Collection methods at these ponds allowed for virtually complete data on absolute abundance and population structure, including adult sex ratios (Aresco and Gunzburger, 2004). Abundance of yellow-bellied sliders (*Trachemys scripta*) was sufficient at all three ponds for comparison with the Lake Jackson population, whereas only abundance at McCord Pond was sufficient for comparison for *Sternotherus odoratus*, *Pseudemys floridana*, and *Apalone ferox*.

2.3. Data analysis

I used log-linear models to compare sex ratios of four species at Lake Jackson with those at nearby ponds unaffected by road mortality. Only adult turtles of the known minimum size at maturity captured during the initial migration in 2000 at Lake Jackson were included in the analyses. I calculated 95% confidence intervals for the proportion of males captured in each population using binomial probabilities (Zar, 1999). I also used log-linear models to test whether sex ratios of turtles observed on land along the road in two average rainfall years differed from that expected from known population sex ratios.

3. Results

Sex ratios in three of four species were significantly more male-biased at Lake Jackson than in other populations (Table 1). The Lake Jackson population of *P. floridana* was 80% male, while the McCord Pond population was only 60% male ($G^2 = 6.04$, df = 1, $P < 0.014$). Similarly, *T. scripta* was 73% male at Lake Jackson vs. only 57% male in the three pond populations ($G^2 = 35.4$, df = 3, $P < 0.0001$). For *S. odoratus*, the Lake Jackson population was 65% male, while the McCord Pond population exhibited a female bias (39% male) ($G^2 = 10.6$, df = 1, $P = 0.001$). The sex ratios for *A. ferox* did not vary significantly among sites. Narrow 95% confidence intervals for the proportion of males of *T. scripta*, *P. floridana*, and *S. odoratus* at Lake Jackson, with a lower limit for each not less than 60%, strengthened the evidence that sex ratios are significantly male-biased, whereas wide 95% confidence intervals for each species at the other ponds included 50% and hence there was no evidence of deviation from a 1:1 sex ratio (Table 1).

During two average rainfall years (2002–2003), females of all four species were significantly more likely to show terrestrial movements than were males (Table 2). Seventy-one percent of *T. scripta* found on land were female, significantly more than the 27% expected based on the population sex ratio. Similarly, 57% of *P. floridana* observed on land were female whereas the expectation

Table 1
Abundances and adult sex ratios (male:female) of four turtle species at northwest Lake Jackson, located adjacent to US Highway 27, and nearby ponds located away from major roads, all in Leon County, Florida

Species and location (ha)	Males	Females	% Males	Ratio
Trachemys scripta				
NW Lake Jackson (405)	1478	539	73 [71–75]	2.74[b]
McCord Pond (2.0)	108	79	58 [49–67]	1.37[a]
Hidden Pond (1.7)	51	42	55 [41–69]	1.21[a]
Harriman Pond (0.5)	40	28	59 [44–74]	1.43[a]
Pseudemys floridana				
NW Lake Jackson	1386	350	80 [78–82]	3.96[b]
McCord Pond	18	12	60 [37–82]	1.50[a]
Sternotherus odoratus				
NW Lake Jackson	293	156	65 [60–71]	1.88[b]
McCord Pond	15	24	39 [14–64]	0.63[a]
Apalone ferox				
NW Lake Jackson	29	23	56 [38–74]	1.26[a]
McCord Pond	8	12	40 [6–74]	0.67[a]

95% confidence intervals for % males are shown in brackets. Different letters denote adult male–female ratios that are significantly different among populations using pairwise log-likelihood ratio tests. Sex ratios are based on turtles collected during natural and anthropogenic drying events. Virtually all individuals in each population were captured (see Section 2).

Table 2
Comparison of the observed and expected number of adults of each sex found on land adjacent to or on US Highway 27 at Lake Jackson, Florida in two non-drought years (2002–2003)

Species	Observed	Expected	Population sex ratio	χ^2	P
T. scripta					
Male	53	135	2.74:1	185	<0.0001
Female	132	50			
P. floridana					
Male	50	94	3.96:1	105	<0.0001
Female	67	23			
S. odoratus					
Male	18	42	1.88:1	38.8	<0.0001
Female	47	23			
A. ferox					
Male	10	19	1.26:1	9.67	0.002
Female	24	15			

P values <0.05 indicate adult male–female ratios that are significantly different from expected ratios based on population sex ratios using χ^2 tests (1 df).

based on the population sex ratio was only 20%. For *S. odoratus*, 72% of individuals found on land were female compared to an expectation of only 35%. Seventy-one percent of *A. ferox* observed on land were female vs. an expected proportion of only 44%.

I observed 235 female turtles nesting directly behind the fences on the road shoulder in 2001–2003, and no nesting activity of turtles during drought conditions in 2000 at Lake Jackson. Based on the number of adult females counted during the mass migration and those found nesting along the road in 2001–2003, I estimated that the number of females of each species nesting annually along US Highway 27 represented the following proportions of reproductive females in each population: 6.1% of *P. floridana*, 7.4%

of *T. scripta*, 9.9% of *S. odoratus*, and 29.1% of *A. ferox* (Table 3).

4. Discussion

Populations of three species of turtles at Lake Jackson adjacent to a road were significantly male biased. Turtle sex ratios may be affected by sexual differences in size at maturity, mortality rates, immigration/emigration rates, and by sex ratios of hatchlings (Lovich and Gibbons, 1990; Gibbons, 1990). The proportion of adult males in freshwater turtle populations ranges from 50% to 63% in species with earlier maturing males (e.g., *T. scripta* and *P. floridana*; Bury, 1979; Lovich and Gib-

Table 3
Average number of females of four turtle species found nesting along US Highway 27 at northwest Lake Jackson, Florida from 2001 to 2003 as a proportion of estimated female population size

Species	Average/ yr (SD)	Female population	Nesting at road (%)
A. ferox	6.7 (3.8)	23	29.1 [10.5–47.7]
P. floridana	21.3 (7.0)	350	6.1 [3.6–8.6]
S. odoratus	15.5 (10.6)	156	9.9 [5.2–14.6]
T. scripta	40.0 (5.9)	539	7.4 [5.2–9.6]

95% confidence intervals of the proportion of females nesting annually at the road are shown in brackets.

bons, 1990; Gibbons, 1990) but are closer to 50% in non-dimorphic species (e.g., *S. odoratus*; Tinkle, 1961). Similarly, I found that the percent of adult males ranged from 39% to 60% in ponds without significant road mortality compared to 65–80% at Lake Jackson. Age at maturity is similar among all sites (Aresco, unpublished data). Therefore, the male-biased sex ratios observed at Lake Jackson are not attributable to differential age at maturity.

It is unlikely that male-biased sex ratios at Lake Jackson are due to temperature dependent sex determination. The sex of *T. scripta*, *P. floridana*, and *S. odoratus* hatchlings is determined by nest temperature during incubation, whereas sex of *A. ferox* is determined genetically (Bull and Vogt, 1979; Ewert and Nelson, 1991). In *T. scripta* and *P. floridana*, incubation temperatures below 29 °C produce only males and temperatures at 29 °C or greater produce only females (Ewert and Nelson, 1991). However, the pattern of sex determination in *S. odoratus* differs in that two transition zones exist: intermediate temperatures (ca. 25 °C) produce 80-94% males, whereas incubation temperatures at both extremes produce mostly females (70–100% at 24 °C or less; 77–100% at 27 °C or greater) (Vogt et al., 1982; Ewert and Nelson, 1991). In northern Florida, the lower temperature thresholds of turtle nests (24 °C or less) can occur by some combination of the following conditions: early spring nests (March–April), those under a closed canopy, and in years with above-average rainfall that lowers average daily air and soil temperatures (Jackson and Walker, 1997). Thus, the observed sex ratios at Lake Jackson are unlikely to have been caused by habitat-related nest temperatures that favor the production of males (e.g., primarily cool nests shaded by vegetation) because *P. floridana* and *T. scripta* have a different pattern of temperature sex determination than does *S. odoratus* (Ewert and Nelson, 1991), yet all three species showed the same pattern of significantly male-biased sex ratios.

Turtles typically nested along 1.2 km of the roadway on the mowed, grassy shoulder with no shading vegetation. Higher soil temperatures adjacent to roads due to an open canopy and the heat sink of pavement may cre-

ate nest conditions that cause the production of greater numbers of female turtles in *P. floridana*, *T. scripta*, and *S. odoratus* (Bull and Vogt, 1979; Vogt and Bull, 1984). Therefore, hatchling sex ratios might actually be female-biased in nests along the road, which strengthens the evidence that observed male-biased adult sex ratios at Lake Jackson are the result of greater female-specific rates of road mortality. In contrast to Lake Jackson, nesting habitats available to turtles at McCord, Harriman, and Hidden Ponds included a mosaic of shaded and open habitats that did not seem to favor the production of one sex over another so that differences in observed adult sex ratios among populations in this study are probably not a result of environmental factors. In order to confirm this hypothesis, it would be useful to compare temperature profiles of natural nests among these populations.

Observed male-biased sex ratios at Lake Jackson are probably not caused by differential predation on females in either the aquatic or terrestrial environment. Differential mortality due to predation by alligators would not cause the observed male biases since alligators prey more heavily on males of *T. scripta* and *P. floridana*, which are significantly smaller than females (Gibbons et al., 1979), whereas they prey equally on male and female *S. odoratus*. Differential predation on nesting females by mammalian predators (e.g., raccoons) could reduce the number of adult females (e.g., Seigel, 1980), but no evidence of predation on nesting females was found during three nesting seasons at Lake Jackson (Aresco, 2004). Therefore, strongly male-biased sex ratios of *P. floridana*, *T. scripta*, and *S. odoratus* observed in this study are best explained by cumulative differential mortality of females struck by vehicles during annual nesting forays.

During severe drought, virtually all individuals of all species emigrate from the drying lake and the observed sex ratios reflect the true population sex ratios. However, in non-drought years, a greater number of females should be seen on land because they must emerge from water to lay eggs, whereas most males do not migrate (Marchand and Litvaitis, 2004). A striking result of my study was that overland movements of all four turtle species were significantly female biased during two non-drought years despite male-biased population sex ratios. Thus, adult females have a greater probability of mortality from vehicles. This may explain the strongly male-biased populations. Long-term population declines could result if females nesting on the roadside each year were killed by vehicles (6–29% of the population). Moreover, many freshwater turtle species lay multiple clutches of eggs each season (Gibbons et al., 1982) which would further increase the probability of annual road mortality in habitats fragmented by roads.

Upland nesting habitat in the vicinity of wetlands are increasingly subject to human alteration and

development, thus female turtles may be attracted to available nesting habitat on roadsides (Burke and Gibbons, 1995; Mitchell and Klemens, 2000; Buhlmann and Gibbons, 2001). However, turtle nests along roadways are rarely successful because of predation by raccoons and imported fire ants (*Solenopsis invicta*) (Temple, 1987; Aresco, 2004). Also, both nesting females and newly emerged hatchlings have a high probability of being crushed by vehicles (Nelson and Scardamalia-Nelson, 2003; Aresco, 2005). Hence, roadside nesting habitats may create a significant ecological trap for turtles, as the open canopy, short vegetation, and friable soil are the preferred conditions for oviposition and incubation but the road causes high mortality of females and hatchlings (Schlaepfer et al., 2002).

Conservation measures for freshwater turtles should consider their frequent annual and seasonal overland movements that often require crossing roads (Gibbons, 1970; Joyal et al., 2001). In many areas low, but consistent, adult female road mortality rates may cause skewed sex ratios and/or long-term population declines that could eventually lead to extirpation of local populations (Crouse et al., 1987; Doak et al., 1994; Mitro, 2003). Population effects of road mortality may be exacerbated for species in wetland habitats when periodic drying results in mass migrations and catastrophic mortality as observed here (see also Gibbons et al., 1983; Aresco, 2005). In cases of small, single remaining populations of endangered species, annual road mortality of nesting females may lead to extinction (e.g., Alabama red-bellied turtle, *Pseudemys alabamensis*; Nelson and Scardamalia-Nelson, 2003).

Many formerly rural roads that historically allowed successful crossing of some turtles have experienced increases in traffic volume over the last two decades. For example, traffic increased 162% from 1977 to 2001 on US Highway 27 at Lake Jackson and the probability of a turtle successfully crossing decreased from 32% in 1977 to only 2% in 2001 (Aresco, 2005). Long-lived species with long generation times and low reproductive rates may exhibit a lag time between observed road mortality rates and population declines (Doak, 1995; Findlay and Bourdages, 2000). Without historic baseline data or careful monitoring, it may be difficult to detect turtle population declines. Thus, the effects of road mortality might not be recognized until they become severe. In many habitats impacted by roads, turtle populations may already be significantly reduced or population structures altered (Steen and Gibbs, 2004).

Direct mortality is frequently measured in studies of wildlife-road conflicts. However, the demographic consequences of road mortality such as skewed sex ratios are equally important in determining population level effects and for planning appropriate mitigation measures, but are more difficult to quantify (Lovich, 1996). Increasingly, such data are required to justify costly mit-

igation measures such as the construction of wildlife barriers and crossing structures (Forman et al., 2003; Dodd et al., 2004).

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