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Relative vulnerability of female turtles to road mortality

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Abstract

Recent studies suggest that freshwater turtle populations are becoming increasingly male-biased. A hypothesized cause is a greater vulnerability of female turtles to road mortality. We evaluated this hypothesis by comparing sex ratios from published and unpublished population surveys of turtles conducted on- versus off-roads. Among 38 166 turtles from 157 studies reporting sex ratios, we found a consistently larger female fraction in samples from on-roads (61%) than off-roads (41%). We conclude that female turtles are indeed more likely to cross roadways than are males, which may explain recently reported skewed sex ratios near roadways and signify eventual population declines as females are differentially eliminated.

Introduction

Turtles are regularly killed by vehicles while traveling overland (e.g. Ashley & Robinson, 1996), potentially influencing the size and structure of populations. Recent research has reported male-skew in sex ratios of aquatic turtle populations relative to roads in various parts of the United States, including New Hampshire (Marchand & Litvaitis, 2004*a*), New York (Steen & Gibbs, 2004) and Florida (Aresco, 2005*a*). Moreover, aquatic turtle populations across the United States have evidently become male-biased over the last century, coincident with the expansion of the nation's transportation network (Gibbs & Steen, 2005). The cause of this demographic change in aquatic turtle populations has been hypothesized to be the disproportionate vulnerability of females to road mortality.

Because of the life-history traits of turtles, specifically low recruitment and delayed sexual maturity (Congdon *et al.*, 1993), populations cannot effectively compensate for the loss of sexually mature individuals (Heppell, 1998). An increase in the mortality of adult turtles, particularly females, has the potential to lead to skewed sex ratios (Steen & Gibbs, 2004; Aresco, 2005*a*), as well as population declines (Brooks, Brown & Galbraith, 1991). As the road network within the United States expands, turtles are becoming increasingly susceptible to road mortality as they undertake terrestrial movements.

Turtles undertake terrestrial migrations for many reasons (Gibbons, 1986), but adult female freshwater turtles make nesting migrations that males do not and females may also be attracted to road shoulders and embankments as nesting habitat (e.g. Jackson & Walker, 1997). For many terrestrial species, the sex-associated size of an individual's home range may determine its relative vulnerability to vehicular road mortality (e.g. Stickel, 1950; Eubanks *et al*., 2002; Eubanks, Michener & Guyer, 2003) and males may undertake migrations to find mates. Determining whether female freshwater turtles are indeed more vulnerable to road mortality is critical for inferring causes of skewed sex ratios in turtles reported from roadside populations throughout the United States (Marchand & Litvaitis, 2004*a*; Steen & Gibbs, 2004; Aresco, 2005*a*). Therefore, we compiled datasets from the published literature and the unpublished notes of field herpetologists on the characteristics of turtles found specifically on- versus off-roads.

Methods

We compiled all published reports we could locate of turtle population surveys conducted along roadways in North America. We also solicited unpublished reports from researchers known to be active in surveying turtles on roadways. Information requested included the number of males, females and juvenile turtles found on the road. We contrasted these 'on roads' data with an extensive compilation of turtle population surveys conducted 'off roads' as reported by Gibbs & Steen (2005). Data categorized as 'on roads' consisted of both live and dead individuals found on roads and roadsides and turtles intercepted at drift fences bordering roads. Data were categorized as 'off roads' as long as the sampling method used did not (1) survey turtles on roads, (2) did not involve methods that targeted one sex, and (3) did not include museum specimens, which are often drawn from scattered areas and vary significantly in date of collection. Some studies consisted of observations compiled over a broad region and do not necessarily represent individuals from one local population. We treated single reports that consisted of information pertaining to several different species as multiple studies. Only studies reporting ≥10 individuals of a particular species were included in the sample to restrict the analysis to studies with a substantial focus on the species of interest.

We classified species based on propensity for overland movement and hence susceptibility to road mortality. To this end, each species was categorized by its 'ecological habit' (Iverson, 1982), that is, as either 'aquatic' (those largely sedentary species that inhabit aquatic environments year-round, e.g. snapping turtle *Chelydra serpentina*), 'semi-aquatic' (those that may be found in either aquatic or terrestrial habitat depending on the season, e.g. wood turtle *Glyptemys insculpta*) or 'terrestrial' (those that are typically encountered in terrestrial habitats and do not rely on wetlands, e.g. gopher tortoise *Gopherus polyphemus*), based on Ernst, Lovich & Barbour (1994). Marine turtles were excluded from the analysis. A complete list of data used is available here: http://www.esf.edu/efb/gibbs/turtles/turtle_roaddata.doc.

Our statistical analysis followed two approaches. The first used 'population' as the replicate, enabling aggregation of estimates from all studies compiled but resulting in the more frequently studied species exerting a disproportionate influence on results. The second approach used 'species' as the replicate, with frequencies from all studies on a particular species pooled. The second approach equalized contributions of different species but reduced sample sizes by restricting analysis only to those species studied both on- and off-roads. Under both approaches, the response variable, p, was the fraction of females within any given replicate, transformed as arcsin $\sqrt{p}$ (Zar, 1984, p. 239), and contrasted among the two fixed factors of interest, ecological habit and road association, using a general linear model general factorial procedure of SPSS (version 7.5). Year was included as a covariate in the case of populations as replicates (average year of study pooled across species was meaningless and therefore not included).

Results

Using populations as replicates, our compilation of the identities of 38 166 turtles from 157 studies reporting sex ratios revealed a consistently larger fraction of females on- versus off-roads (Tables 1 and 2). Ecological habit interacted significantly with road association (Table 1), likely due to the larger difference in female fraction on- versus off-roads in aquatic turtles (Table 2). The effect of year of

Table 1 General linear model analysis of female fraction in turtle populations in relation to road association ('road' – surveys conducted on- vs. off-roadways), ecological habit ('habit'–aquatic, semi-aquatic or terrestrial), and date of study ('year') (sample size = 106 studies off-roads, 51 studies on-roads, model adjusted $R^2 = 0.26$)

Source	Type III sum of squares	d.f.	Mean square	F	Significance
Corrected model	2.171	6	0.362	9.9	0.000
Intercept	0.405	1	0.405	11.1	0.001
Year	0.350	1	0.350	9.6	0.002
Ecological habit	0.167	2	0.083	2.3	0.106
Road association	0.676	1	0.676	18.5	0.000
Ecological habit × road association	0.448	2	0.224	6.1	0.003
Error	5.490	150	0.037		
Total	109.753	157			
Corrected total	7.661	156			

study on female fraction reflects a historical trend toward male-biased sex ratios, as previously reported by Gibbs & Steen (2005). On the basis of confidence intervals ($\alpha = 0.05$) applied to mean female fraction, most population samples could not be distinguished from parity (50%) except for aquatic turtles off-roads (male-biased), aquatic turtles on-roads (female-biased) and semi-aquatic turtles both on- and off-roads (female-biased). Using species as replicates, for the 16 species with both on- and off-road populations samples (Table 3), female fraction was higher on- versus off-roads (Table 4). Ecological habit did not contribute to variation in female fraction, although an interaction between ecological habit and road association was evident (Table 4).

Discussion

Our survey indicates that female turtles were encountered on roads in greater proportion than males for both aquatic and semi-aquatic species. Thus, we conclude that females do indeed represent the class of freshwater turtles most vulnerable to vehicle-induced road mortality. That more female turtles are encountered on roads is somewhat counter-intuitive when viewed in the context that males of many semi-aquatic turtle species are more likely to disperse overland than are females (Morreale, Gibbons & Congdon, 1984; Tuberville, Gibbons & Greene, 1996), but females may seek out roads and roadsides in greater proportion than males because of the roadside's attractiveness as nesting sites. In addition, repeated nesting migrations to a specific area may raise the cumulative risk of females to road mortality relative to males undertaking periodic, one-way movements. This would be particularly true for roads located near wetlands.

Table 2 Mean female fraction in turtle populations [$\pm$1SE (*n*) where *n* is the number of population samples] in relation to road association and ecological habit

Ecological habit	Off-road	On-road
Aquatic	0.43 + 0.02 (65)	0.66 + 0.04 (30)
Semi-aquatic	0.52 + 0.03 (29)	0.64 + 0.06 (10)
Terrestrial	0.49 + 0.04 (12)	0.47 + 0.03 (11)
All	0.46 + 0.01 (106)	0.61 + 0.03 (51)

Table 3 Female fraction (and *n*) in on- and off-road populations of species for which both sorts of samples have been reported

Species	Off-road	On-road
Aquatic		
Apalone ferox	0.44 (52)	0.65 (58)
Chelydra serpentina	0.35 (707)	0.64 (204)
Chrysemys picta	0.41 (6,077)	0.66 (656)
Graptemys geographica	0.38 (576)	1.00 (10)
Pseudemys floridana	0.24 (2,159)	0.58 (158)
Sternotherus odoratus	0.42 (2,960)	0.58 (102)
Trachemys scripta	0.38 (9,139)	0.77 (365)
Semi-aquatic		
Clemmys guttata	0.47 (48)	0.52 (53)
Deirochelys reticularia	0.28 (319)	0.46 (15)
Emydoidea blandingii	0.66 (585)	0.89 (101)
Glyptemys insculpta	0.51 (533)	0.68 (35)
Kinosternon baurii	0.50 (20)	0.66 (42)
Kinosternon subrubrum	0.41 (582)	0.50 (118)
Terrestrial		
Gopherus berlandieri	0.41 (73)	0.36 (106)
Gopherus polyphemus	0.61 (184)	0.35 (206)
Terrapene carolina	0.40 (1,100)	0.49 (608)
All species[a]	0.41 (31,294)	0.83 (6,872)

n is the total number of turtles from all samples of that species.

[a]Note that 'all species' includes species that did not have both on- and off-road samples available and hence sample sizes for all species is greater than the total of the individual species presented.

Although more female turtles are found on roads than males, this pattern could be indicative of a comparatively high prevalence of females in populations, rather than females undertaking terrestrial migrations differing from those of males. However, turtle populations typically possess a background sex ratio of 1:1 among adults (Gibbons, 1970; but see Lovich & Gibbons, 1990), although short-term studies may report considerable temporal variance in sex ratios (e.g. Dodd, 1989). Nonetheless, regardless of cause, populations tend to be male-biased in areas of high road density (Marchand & Litvaitis, 2004*a*; Steen & Gibbs, 2004; Aresco, 2005*a*). Therefore, if sex ratios of turtles on roads were influenced by sex ratios in nearby populations, and not disparate movement patterns, turtles on roads should be male- rather than female-biased. Similarly, many aquatic turtle studies are undertaken within the nesting season (e.g. Wood & Herlands, 1997), a restricted time period when females are more likely to be encountered on land than males. Although such studies present a potential bias, the patterns we observed across this very large sample of studies are consistent with observations conducted year-round in regions where ambient temperatures are conducive to movements of male and female turtles (i.e. the south-eastern United States, e.g. Aresco, 2005*a*). Last, inexperienced observers may be more likely to correctly determine the sex of female turtles by observing nesting behaviour or due to the presence of eggs in individuals dead on the road, yet the same bias would apply to terrestrial turtles and no sex ratio skew was observed in this group.

Sex ratios may also appear skewed because of biases inherent in different trapping methods. For example, baited hoop traps, which are commonly used to trap aquatic and semi-aquatic species away from roads, may yield male-biased captures (Ream & Ream, 1966). Therefore, the disparate sex ratios we describe could be an artefact of a particular methodology and caution should be exercised when comparing these values. However, a previous analysis of primarily off-road studies demonstrated that sampling method did not contribute to variation in reports of sex ratios of turtle populations (Gibbs & Steen, 2005).

These findings lend support for the conclusion of several recent studies (Marchand & Litvaitis, 2004*a*; Steen & Gibbs, 2004; Aresco, 2005*a*; Gibbs & Steen, 2005) that chronic road

Table 4 General linear model analysis of female fraction in turtle species in relation to road association ('road' – surveys conducted on- vs. off-roadways) and ecological habit ('habit'–aquatic, semi-aquatic or terrestrial) for the 16 species of turtles listed in Table 3 (model adjusted $R^2=0.38$)

Source	Type III sum of squares	d.f.	Mean square	*F*	*P*
Corrected model	0.629	5	0.126	4.8	0.003
Intercept	18.106	1	18.106	693.7	0.000
Ecological habit	0.069	2	0.035	1.3	0.283
Road association	0.161	1	0.161	6.2	0.020
Ecological habit × road association	0.216	2	0.108	4.1	0.027
Error	0.679	26	0.026		
Total	22.912	32			
Corrected total	1.308	31			

mortality may deplete females from populations thereby causing male-biased sex ratios in freshwater turtle populations surrounded by a high density of roads. Moreover, the contribution of year to variation in sex ratio in our study is further evidence that sex ratios in turtle populations are generally becoming more biased over time. This result was reported previously by Gibbs & Steen (2005) for the United States, but is also manifested in this extensive dataset drawn from throughout North America. Further study may indicate whether roads have a disproportionately higher impact on some age classes of turtles. The potential implications of these relative vulnerabilities and resulting mortalities are discussed elsewhere (e.g. Gibbs & Shriver, 2002; Steen & Gibbs, 2004; Aresco, 2005*a*), but may implicate road mortality as a significant, ongoing threat to the long-term viability of freshwater turtle populations (Andrews, Gibbons & Jochimsen, in press).

These results argue that mitigation efforts to keep turtles, and especially females, off roads may be warranted. Recently, barrier walls surrounding roads in conjunction with wildlife underpasses have proven effective at reducing mortality of male and female freshwater turtles in Florida (Dodd, Barichivich & Smith, 2004; Aresco, 2005*b*). Further research is required to determine whether other attempts at mitigation, such as creating artificial nesting sites away from roads, dissuade female turtles from venturing onto roadsides, and therefore are effective tools in turtle conservation (Marchand & Litvaitis, 2004*b*). Because of the relative vulnerability of female freshwater turtles to road mortality and the potential effects to turtle populations, mitigation measures should be considered when roads occur in high densities and in proximity to wetlands.

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References

Andrews, K.M., Gibbons, J.W. & Jochimsen, D.M. (in press). Ecological effects of roads on amphibians and reptiles: a literature review. In *Urban herpetology*. *Herpetological Conservation*. Vol. 3. Jung, R.E. & Mitchell, J.C. (Eds). Salt Lake City, UT: Society for the Study of Amphibians and Reptiles.

Aresco, M.J. (2005*a*). The effect of sex-specific terrestrial movements and roads on the sex ratio of freshwater turtles. *Biol. Conserv*. **123**, 37–44.

Aresco, M.J. (2005*b*). Mitigation measures to reduce highway mortality of turtles and other herpetofauna at a north Florida lake. *J. Wildl. Mgmt*. **69**, 549–560.

Ashley, E.P. & Robinson, J.T. (1996). Road mortality of amphibians, reptiles and other wildlife on the Long Point Causeway, Lake Erie, Ontario. *Can. Field-Nat*. **110**, 403–412.

Brooks, R.J., Brown, G.P & Galbraith, D.A. (1991). Effects of a sudden increase in natural mortality of adults on a population of the common snapping turtle (*Chelydra serpentina*). *Can. J. Zool*. **69**, 1314–1320.

Congdon, J.D., Dunham, A.E. & Van Lobel Sels, R.C. (1993). Delayed sexual maturity and demographics of Blanding's turtles (*Emydoidea blandingii*): implications for conservation and management of long-lived organisms. *Conserv. Biol*. **7**, 826–833.

Dodd, C.K. Jr. (1989). Secondary sex ratio variation among populations of the flattened musk turtle, *Sternotherus depressus*. *Copeia* **1989**, 1041–1045.

Dodd, C.K. Jr., Barichivich, W.J. & Smith, L.L. (2004). Effectiveness of a barrier wall and culverts in reducing wildlife mortality on a heavily traveled highway in Florida. *Biol. Conserv*. **118**, 619–631.

Ernst, C.H., Lovich, J.E. & Barbour, R.W. (1994). *Turtles of the United States and Canada*. Washington and London: Smithsonian Institution Press.

Eubanks, J.O., Hollister, J.W., Guyer, C. & Michener, W.K. (2002). Reserve area requirements for gopher tortoises (*Gopherus polyphemus*). *Chel. Conserv. Biol.* **4**, 464–471.

Eubanks, J.O., Michener, W.K. & Guyer, C. (2003). Patterns of movement and burrow use in a population of gopher tortoises (*Gopherus polyphemus*). *Herpetologica* **59**, 311–321.

Gibbons, J.W. (1970). Sex ratios in turtles. *Res. Popul. Ecol.* **12**, 252–254.

Gibbons, J.W. (1986). Movement patterns among turtle populations: applicability to management of the desert tortoise. *Herpetologica* **42**, 104–113.

Gibbs, J.P. & Shriver, W.G. (2002). Estimating the effects of road mortality on turtle populations. *Conserv. Biol.* **16**, 1647–1652.

Gibbs, J.P. & Steen, D.A. (2005). Historic trends in sex ratios of turtle populations in the United States. *Conserv. Biol.* **19**, 552–556.

Heppell, S.S. (1998). Application of life-history theory and population model analysis to turtle conservation. *Copeia.* **1998**, 367–375.

Iverson, J.B. (1982). Biomass in turtle populations: a neglected subject. *Oecologia* **55**, 69–76.

Jackson, D.R. & Walker, R.N. (1997). Reproduction in the Suwannee cooter, *Pseudemys concinna suwanniensis*. *Bull. Flor. Mus. Nat. Hist.* **41**, 69–167.

Lovich, J.E. & Gibbons, J.W. (1990). Age at maturity influences adult sex ratio in the turtle *Malaclemys terrapin*. *Oikos* **59**, 126–134.

Marchand, M.N. & Litvaitis, J.A. (2004*a*). Effects of habitat features and landscape composition on the population structure of a common aquatic turtle in a region undergoing rapid development. *Conserv. Biol.* **18**, 758–767.

Marchand, M.N. & Litvaitis, J.A. (2004*b*). Effects of landscape composition, habitat features, and nest distribution on predation rates of simulated turtle nests. *Biol. Conserv.* **117**, 243–251.

Morreale, S.J., Gibbons, J.W. & Congdon, J.D. (1984). Significance of activity and movement in the yellow-bellied slider turtle (*Pseudemys scripta*). *Can. J. Zool.* **62**, 1038–1042.

Ream, C. & Ream, R. (1966). The influence of sampling methods on the estimation of population structure in painted turtles. *Am. Midl. Nat.* **75**, 325–338.

Steen, D.A. & Gibbs, J.P. (2004). The effects of roads on the structure of freshwater turtle populations. *Conserv. Biol.* **18**, 1143–1148.

Stickel, L.F. (1950). Population and home range relationships of the box turtle, *Terrapene c. carolina* (Linnaeus). *Ecol. Monog.* **20**, 353–378.

Tuberville, T.D., Gibbons, J.W. & Greene, J.L. (1996). Invasion of new aquatic habitats by male freshwater turtles. *Copeia* **1996**, 713–715.

Wood, R.C. & Herlands, R. (1997). Turtles and tires: the impact of roadkills on northern diamondback terrapin, *Malaclemys terrapin terrapin*, populations on the Cape May Peninsula, southern New Jersey, USA. In *Proceedings: conservation, restoration, and management of tortoises and turtles – an international conference*: 46–53. Van Abbema, J. (Ed.), State University of New York, Purchase. New York: New York Turtle and Tortoise Society.

Zar, J.H. (1984). *Biostatistical analysis*. New Jersey: Prentice-Hall.