Trends in Sex Ratios of Turtles in the United States: Implications of Road Mortality

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Abstract: *Road mortality has been implicated as a significant demographic force in turtles, particularly for females, which are killed disproportionately on overland nesting movements. Moreover, the United States' road network has expanded dramatically over the last century. We therefore predicted that historical trends in sex ratios of turtle populations would be male biased. To test this prediction, we synthesized published estimates of population-level sex ratios in freshwater and terrestrial turtles in the United States (165 estimates for 36 species, published 1928–2003). Our analysis suggests that the proportion of males in populations has increased linearly ($p = 0.001$); the trend in male bias is synchronized with the expansion of the surfaced portion of the road network since 1930; sex ratios became more male biased in states with higher densities of roads; and populations have become more male biased in aquatic species, in which movement differentials between males and females are greatest, and are least biased in semiaquatic and terrestrial species, in which overland movements are more comparable between sexes. Our results suggest an ongoing depletion of breeding females from wild turtle populations over the last century because of many factors, including, and perhaps chiefly, road mortality.*

Key Words: climate change, demography, highways, roads

Tendencias en las Proporciones de Sexos de Tortugas en los Estados Unidos: Implicaciones de la Mortalidad en Caminos

Resumen: *La mortalidad en caminos ha sido considerada como una fuerza demográfica significativa en tortugas, particularmente para hembras, que son matadas desproporcionadamente al hacer movimientos por tierra cuando anidan. Más aun, la red caminera se ha expandido dramáticamente en el último siglo en los Estados Unidos. Por lo tanto predijimos que las tendencias históricas en las proporciones de sexos de poblaciones de tortugas estarían sesgadas hacia machos. Para probar esta predicción, sintetizamos estimaciones publicadas sobre proporciones de sexo a nivel población de tortugas dulceacutícolas y terrestres en los Estados Unidos (165 estimaciones para 36 especies, publicadas entre 1928 y 2003) Nuestro análisis sugiere que la proporción de machos en la poblaciones ha incrementado linealmente ($p = 0.001$); la tendencia del sesgo hacia machos esta sincronizada con la expansión de la superficie de la red caminera desde 1930, las proporciones se volvieron más segadas hacia machos en estados con mayores densidades de caminos; las poblaciones están más sesgadas hacia machos en especies acuáticas, en las que son mayores los movimientos diferenciales de hembras y machos, y son menos sesgadas en especies semiacuáticas y terrestres, en los que los movimientos por tierra son más comparables entre sexos. Nuestros resultados sugieren una reducción drástica de hembras reproductivas en poblaciones de tortugas silvestres en el último siglo, debido a muchos factores, incluyendo, quizá principalmente, la mortalidad en caminos.*

Palabras Clave: cambio climático, carreteras, demografía

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Introduction

The road network has expanded substantially in the United States in the last century (National Research Council 1997) and now affects some 20% of the land area (Forman & Alexander 1998; Forman 2000). This is a particular concern for mobile species that must regularly traverse the landscape to complete their life cycles. Turtles are one example. Females of all turtle species make annual movements overland to nest, during which time they are particularly vulnerable to mortality on roads (e.g., Haxton 2000). Moreover, turtle demography is unusual among vertebrates insofar as slight increases in adult mortality can lead to large declines in populations (e.g., Congdon et al. 1993). Notably, sex ratios in freshwater turtles have been demonstrated to be more skewed toward males in populations associated with higher road density (Marchand & Litvaitis 2004; Steen & Gibbs 2004; Aresco 2005), and road mortality has been estimated to potentially limit populations of some types of turtles at a regional scale (Gibbs & Shriver 2002).

If chronic mortality on roads is demographically significant for turtles, particularly females, sex ratios in turtle populations in the United States may have become more male biased over the last century. We tested this prediction by analyzing 165 published estimates of population-level sex ratios in turtle populations obtained from field studies of freshwater and terrestrial turtles published between 1928 and 2003.

Methods

We attempted to locate every published estimate of sex ratio (based on a sample size of $\geq$10) of wild-caught individuals from a population of any freshwater or terrestrial turtle species within the United States. For each study we recorded species, study location, number of females and males captured, sampling method, and years of sampling (from which operative year of study was calculated as the average of the initial and final year of the study). Because studies were inconsistent in discriminating between juveniles and adults, we based sex ratio estimates on counts of all sexed turtles captured. We later recorded predominant ecological habit (aquatic, semiaquatic, or terrestrial) of each species based on Iverson (1982) and Ernst et al. (1994). Studies were excluded if they were based on collecting or trapping methods that would preferentially locate one sex, such as road patrols for aquatic turtles during the nesting season or museum specimens, which are typically drawn from scattered areas. For studies presenting data from multiple sites, we pooled all samples if sites were <100 km from one another. This reduced overall sample size but avoided overrepresenting particular sites where intensive turtle research has occurred. Moreover, because of the extensive publication of data sets from turtle studies at the University of Michigan's E. S. George Reserve and from the Savannah River Ecology Laboratory, we used sex ratio estimates from a single publication—Congdon et al. (1986)—that synthesized population data across the many studies conducted at these sites.

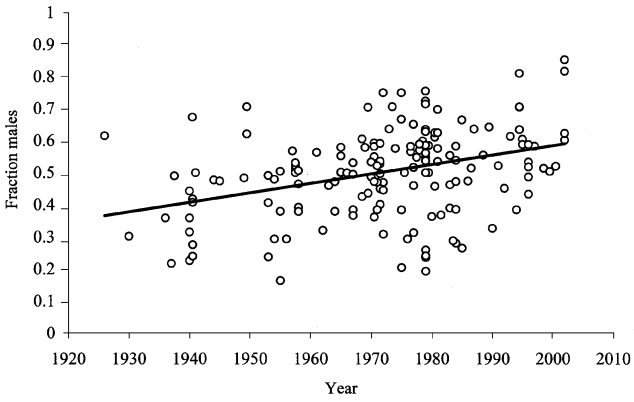

*Figure 1. Relationship between fraction of males in a turtle population versus year study was conducted (*n = *165, adjusted* R^2 = *0.126,* p = *0.0001) in the United States over the last century.*

To examine temporal trends in sex ratios, we contrasted sex ratio with operative year of the study through least-squares regression (Zar 1984). The response variable used was fraction of males in a sample from a particular study because of the undesirable statistical properties of true ratios (e.g., males/females; Berges 1997). To examine the influence of year on sex ratios we arc-sine transformed male fraction and subjected it to analysis of covariance while controlling for the influence of taxon (family), ecological habit, and sampling method (Zar 1984). We did not include Trionychidae (softshell turtles) in the analysis because we obtained too few reports of sex ratio for this family ($n = 4$). Neither did we include the diamondback terrapin (*Malaclemys terrapin*) or any of the sea turtles because these are largely estuarine and marine forms and because accurate estimates of adult sex ratios for them are elusive (Lovich 1996).

Results

We obtained 165 estimates of population-level sex ratios published between 1928 and 2003 for 36 species of turtles in 40 U.S. states. (Citations are available from the authors on request.) Mean and median sample sizes per study were 200 and 107, respectively. Male fraction was positively related to operative year of study for all studies combined (Fig. 1, Table 1). After controlling for the effect of year (Table 1), only ecological habit (aquatic highest, semiaquatic intermediate, terrestrial lowest) contributed to variation in sex ratio (although family also contributed marginally). More specifically, male bias in sex ratio increased over time in aquatic turtles but not in semiaquatic

Table 1. Analysis of covariance of male fraction in freshwater and terrestrial turtle populations in relation to taxonomic affiliation (family), ecological habit (aquatic, semiaquatic, terrestrial), and sampling method (baited traps only, mixed methods, hand capture), with year of study as the covariate ($n = 138$ studies with complete information for all variables).

Family	*df*	*Type III SS*	*Mean square error*	F	p
Family	3	0.151	0.05	2.518	0.061
Habit	2	0.26	0.13	6.481	0.002
Method	2	0.07	0.035	1.74	0.18
Year	1	0.435	0.435	21.712	0.001
Error	129	2.584	0.02	—	—

or terrestrial species (Table 2). Because ecological habit contributed to variation in sex ratios, we considered that the temporal trend observed in sex ratios might be an artifact of changes in the classes of turtles researchers have chosen to study over time. The proportion of studies focusing on any of the three groups of turtles was, however, not correlated with decade of study (e.g., aquatic turtles [$r = 0.091, p = 0.830$]). In relation to geographic region of study, male fraction increased among studies conducted in states with intermediate to high road density but did not increase among studies conducted in states with low road densities (Table 2). In contrast, male fraction did not increase in heavily forested states but did increase in regions with intermediate and low levels of forest cover (Table 2).

Table 2. Historical trends in the fraction of males in freshwater and terrestrial turtle populations in relation to road density, forest cover, and ecological habit within the United States over the last century.

	n	*Slope* ± *1SE* [a]	t	p	*Model adjusted* R^2
Road density (km/km^2) in state where study was conducted[b]					
<0.75	55	0.003 ± 0.001	1.58	0.118	0.028
0.75–1.00	54	0.004 ± 0.001	4	0.001	0.217
>1.00	56	0.003 ± 0.001	3.37	0.001	0.159
Forest cover (%) in state where study was conducted[c]					
<20	56	0.003 ± 0.001	3.21	0.002	0.165
20–50	55	0.003 ± 0.001	2.72	0.009	0.123
>50	54	0.002 ± 0.001	1.91	0.061	0.063
Ecological habit[d]					
aquatic	103	0.004 ± 0.001	5.51	0.001	0.223
semiaquatic	37	0.002 ± 0.002	1.17	0.25	0.101
terrestrial	28	0.001 ± 0.001	0.73	0.47	0.01

[a] *Estimates reflect arc-sine-transformed male fraction.*
[b] *Source of state-specific road densities: FHA (1999). Classes based on thresholds that divide observations approximately into thirds.*
[c] *Source of state-specific forest cover: U.S. Department of Agriculture National Resources Inventory for 1997. Classes based on those that divide observations approximately into thirds.*
[d] *Based on Iverson (1982) and Ernst et al. (1994).*

Discussion

Literature surveys are effective for summarizing the results of many similar, yet independent studies and for detecting patterns that may not be evident in isolated, short-term research projects (Arnqvist & Wooster 1995). This is particularly true for organisms that have the potential to outlive most, if not all, field studies, such as turtles, whose life spans typically extend for decades (Gibbons 1982). The turtle studies we reviewed lasted, on average, 3.6 years.

Our literature survey indicates that sex ratios in populations of turtles have become increasingly male biased in the United States over the last century. Although the temporal trend in sex ratios was highly significant, the amount of overall variation explained by time was modest (13% for all turtles, 22% for aquatic turtles). The trend may be pervasive, however, if it persists despite enormous sampling "noise" associated with aggregating estimates across hundreds of different studies, each with its own idiosyncrasies. Additionally, although the sex-ratio trends observed may be subtle, slight changes in the sex ratio of turtle populations may be indicative of much larger changes in vital rates of populations, including mortality sufficient to lead to population declines (Brooks et al. 1991; Heppell 1998). For example, a 50-year study of the box turtle (*Terrapene carolina*) revealed a population in steep decline that corresponded with an increasing proportion of males (Hall et al. 1999).

Our finding of increasing male bias contrasts distinctly with the expectation of disproportionate production of females as a consequence of the 1° C climate warming that has occurred over the last century (Hansen et al. 2001). Gradual female skew has been predicted by Janzen (1992, 1994) and others on the basis that most turtle species have temperature-based sex determination, generally with species-specific pivotal temperatures above which females are disproportionately produced (either Type Ia or II patterns of sex determination, Ewert & Nelson 1991). That said, temperature-change scenarios do not rule out a trend toward male bias. Large-scale reforestation of various parts of the country could lead to general cooling of the soils and turtle embryos incubating therein. Forest cover has, however, increased in some regions but decreased in others, remaining largely stable across the United States in aggregate since the 1920s (Whitney 1994). Moreover, contrary to expectation, male fraction increased more rapidly in regions with less forest cover (and therefore presumably warmer; Table 2). We are unaware of other large-scale, temperature-related scenarios that could generate the temporal trend in sex ratios observed.

Imbalanced sex ratios in turtle populations are often attributed to sampling biases (Gibbons 1970, 1990). For example, Ream and Ream (1966) found that baited hoop traps may be male biased in capturing painted turtles.

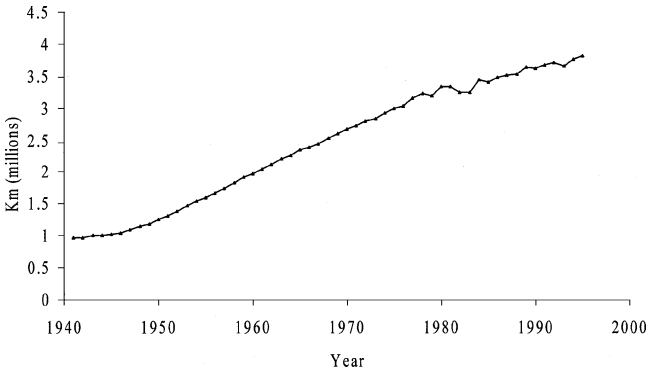

Figure 2. Historical changes in the extent of the paved portion of the road network in the United States (source: FHA 1999).

Our analysis indicated, however, that sampling method, including use of baited traps, did not substantially contribute to variation in sex ratios (Table 1). Thus, we discount a systematic shift in sampling methodologies by researchers as the cause of the trend in sex ratios observed.

We contend that the trend observed toward increasing numbers of males in populations of turtles is most consistent with a hypothesis involving selective mortality of females. This conclusion is corroborated by the observation that the greatest skew in sex ratios (Tables 1, 2) was found in aquatic turtles (the group with the greatest differential in vulnerability between males and females) and least in semiaquatic and terrestrial turtles (the groups in which vulnerability to road mortality is more comparable between sexes). Ideally, we would relate trend in sex-ratio skew with extent of surface movements, but field data on movement distances of particular species or even taxonomic groups are too sparse to support such an analysis (e.g., Bodie 2001).

Road mortality may be the most likely female-selective factor to account for the trends observed. Requisite annual nesting migrations that females undertake likely expose them to higher levels of road mortality. Of turtles found dead on roads, 60% were females in an Ontario (Canada) study (Haxton 2000) and 66% were females in a New Hampshire (U.S.A.) study (Marchand & Litvaitis 2004). Moreover, a dramatic expansion of the network of surfaced roads to accommodate high-volume and high-speed automobile traffic has occurred since the passage of the U.S. Federal Highway Act in the 1930s (Fig. 2). This expansion is closely synchronized with the elevation in male fraction in turtle populations (Figs. 1 & 2), which changed from, on average, ~45% males in the 1930s to ~60% today. Females on nesting migrations may be more vulnerable than males to many hazards, including being collected opportunistically by humans for the meat or for the pet trade (e.g., Garber & Burger 1995), being eaten by predators (whose numbers have escalated in the last several decades [Congdon et al. 1993]), disappearing down storm drains, encountering farm machinery, and experiencing other hazards (Mitchell & Klemens 2000). Thus, the skewed sex ratios we found might well be a product of the multitude of threats females face on nesting migrations, although road mortality will likely remain chief among them given the spatial extent of the nation's road network (Forman 2000).

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