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Fredric J. Janzen, *University of Chicago*



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Climate change and temperature-dependent sex determination in reptiles

(extinction/population demography/rate of evolution/sex ratio/turtles)

FREDRIC J. JANZEN*

Department of Ecology and Evolution, University of Chicago, Chicago, IL 60637

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ABSTRACT Despite increasing concern over the possible impact of global temperature change, there is little empirical evidence of direct temperature effects on biotic interactions in natural systems. Clear assessment of the ecological and evolutionary impact of changing climatic temperature requires a natural system in which populations exhibit a direct unambiguous fitness response to thermal fluctuation. I monitored nests of a population of painted turtles (*Chrysemys picta*) with temperature-dependent sex determination to investigate the causal relationship between local climatic variation in temperature and offspring sex ratio. Consistent with theoretical predictions, annual offspring sex ratio was highly correlated with mean July air temperature, validating concerns about the effect of climate change on population demography. This correlation implies that even modest increases in mean temperature ($<2^{\circ}\text{C}$) may drastically skew the sex ratio. Statistical evaluation of the variance in climate change indicates that an increase in mean temperature of 4°C would effectively eliminate production of male offspring. Quantitative genetic analyses and behavioral data suggest that populations with temperature-dependent sex determination may be unable to evolve rapidly enough to counteract the negative fitness consequences of rapid global temperature change. Populations of species with temperature-dependent sex determination may serve as ideal indicators of the biological impact of global temperature change.

Average global temperatures are expected to rise from 0.6 to 8°C in the next century (1–4). Consequently, scientists are increasingly concerned with the potential impact of global climate change on natural systems. In addition to geophysical matters like rising sea levels (for a review, see ref. 5), considerable attention has been directed recently toward predicting the effects of large-scale temperature shifts on biotic interactions (6–10). Despite a wide array of theoretical predictions, ranging from modifications in geographic range to alterations in community composition to extinction, there is little explicit empirical evidence of direct temperature effects on factors influencing these biological processes (6–10). Temperature-dependent sex determination in reptiles provides an ideal model system with which to test predictions concerning the biological significance of global temperature change.

In contrast to other amniote vertebrates, whose gender is determined genetically at conception, offspring sex in many reptiles is irreversibly determined by temperatures experienced during the middle third of embryonic development (11–15). The sex ratio of offspring in these taxa may be radically altered by as little as a 1°C shift in incubation temperature (15). Hence, sex ratio, a critical demographic parameter, is subject to the vagaries of the thermal environ-

ment in species with temperature-dependent sex determination, even though offspring sex ratio is under strong frequency-dependent selection to be balanced (16–18). Using this unusual system to test hypotheses concerning the biological consequences of climate change (6–10), I combined models of environmental physiology and evolutionary genetics by relating local climatic temperatures to changes in cohort sex ratios in a natural population of turtles with temperature-dependent sex determination. This approach incorporates identification of a key climatic variable with evaluation of its critical rate of change in nature, permitting development of a model that predicts ecological and evolutionary responses to global temperature change.

MATERIALS AND METHODS

Between 1988 and 1993, I monitored 390 natural nests of painted turtles (*Chrysemys picta*: Emydidae). The painted turtle is a common geographically widespread species, ranging throughout most of North America (19). The study site, an island called the Thomson Causeway in the Mississippi River (Whiteside County, IL), was censused almost daily for nesting activity in June of each year (20). No viable nests were constructed in May or July; hence, data for hatchling sex ratios were derived only from nests laid in June. All nests constructed at the Thomson Causeway were probably detected because the nesting beaches on the island were moderate in size and predation never occurred on a previously undetected nest (20). Furthermore, no hatchlings emerged prior to my excavation of nests in each year. In contrast to most species of turtles, offspring of *Chrysemys picta* hatch during the summer but remain buried in the nests until the following spring (19).

After incubation was completed, hatchling turtles were removed from all 116 viable nests in the third week of September. Up to 10 individuals from each clutch were randomly chosen for sex determination. Sex of the hatchlings (529 males, 397 females, and 6 intersexes) was determined by macroscopic examination of the gonads (21). Temperature data for each summer were obtained from the nearest National Weather Service recording station (5.5 km south of the Thomson Causeway). Monthly mean air temperatures for June, July, and August were calculated by averaging the high and low daily temperatures for each month and dividing the sum of these values by the number of days in the month. Regression analysis was employed to evaluate the relationship between cohort sex ratio and among-year variation in local climatic temperature.

RESULTS

The majority of nests in each year produced hatchlings of only one sex (20). Most unisexual nests in 1988, 1989, and

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*Permanent address: Department of Zoology and Genetics, Iowa State University, Ames, IA 50011.

1991 were female-biased and all unisexual nests in 1990 and 1992 were male-biased (all nests in 1993 were destroyed by flooding). The consequent heterogeneity in sex ratio of all hatchlings among years was statistically significant ($G = 376$; $df = 4$; $P < 0.0001$). To illustrate the extent of this heterogeneity in sex ratio at the site, all hatchlings censused in 1988 were female and all individuals produced in 1992 were male.

Annual cohort sex ratio of hatchling painted turtles was significantly correlated with mean July air temperature ($r = -0.91$; $P = 0.03$; Fig. 1). This correlation is particularly informative because July corresponds to the developmental period when embryonic sex is determined (11–15, 21). Also in accordance with laboratory results (11–15), more male hatchlings were produced in summers with a cooler July (and vice versa) and the sex ratio was not significantly correlated with either mean June or mean August air temperature ($r = -0.57$; $P = 0.32$ and $r = -0.83$; $P = 0.08$, respectively). These results confirm a strong relationship between annual cohort sex ratio in hatchling painted turtles and a simple measure of summer temperature and provide evidence that sex ratios in such species are highly susceptible to local fluctuations in ambient temperature.

July air temperatures were also significantly associated with July soil temperatures at depths approximately equal to the top and bottom of painted turtle nests. For example, in July 1992 in nearby Iowa City, IA (22), mean daily ambient temperatures were significantly correlated with mean daily soil temperatures at 5 cm ($r = 0.74$; $P < 0.0001$) and at 10 cm ($r = 0.76$; $P < 0.0001$). This result also was obtained for July in other years at this site and solidifies a general functional link among ambient temperatures, soil temperatures in the shallow nests of painted turtles, and sex ratios of the offspring that emerge from these nests.

Data for mean July temperature from the last 49 years at the Thomson Causeway predict an unbiased overall hatchling sex ratio (47.8% male), though some years probably produced all male offspring (e.g., 1962 and 1992) or all female offspring (e.g., 1955 and 1983) (Fig. 2). Although there was no apparent trend for an increase or decrease in cohort sex ratios with time, the regression equation from Fig. 1 implies that an increase in mean July temperature of merely 1.85°C over the mean for the last 49 years ($\bar{x} \pm \text{SD} = 23.60 \pm 1.11^\circ\text{C}$) would cause 100% female offspring to be produced in an average year. Nonetheless, male turtles would be produced at least

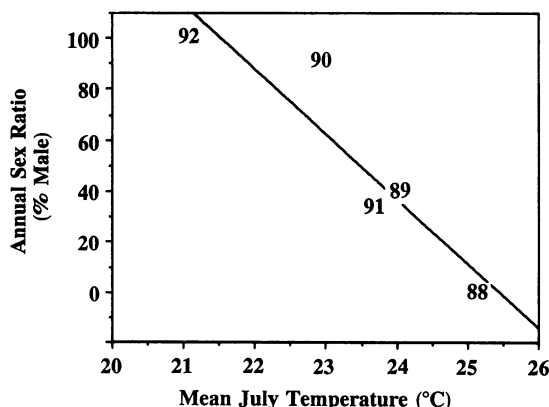


FIG. 1. Annual cohort sex ratio (% male) of hatchling painted turtles (*Chrysemys picta*) from 1988 to 1993 as a function of the mean ambient temperature in July. No data are presented for 1993 because all nests were destroyed by flooding. The linear regression of annual cohort sex ratio on mean July temperature is $Y = -25.59X + 651.25$; $r = -0.91$; $P = 0.03$. The negative relationship between sex ratio and air temperature is strongly consistent with results of laboratory studies of temperature-dependent sex determination (11–15): cooler summers produced mostly male offspring and warmer summers produced mostly female offspring.

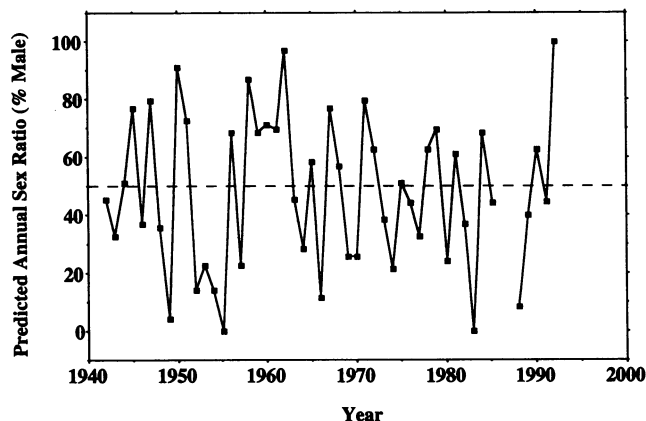


FIG. 2. Temporal change in predicted annual cohort sex ratio (% male) of hatchling painted turtles at the Thomson Causeway since 1942. The dashed line indicates an equal sex ratio of male and female offspring. Ambient temperature data for July of 1986 and 1987 were unavailable, thus the equation from Fig. 1 could not be used to predict the sex ratio in these years. Cohort sex ratio exhibited no significant trend through time ($r = 0.02$; $P = 0.87$). The overall hatchling sex ratio of this nesting population since 1942 (excluding 1986 and 1987) is predicted to be 47.8% male.

occasionally because July temperatures vary considerably among years (Fig. 2). When among-year variance in temperatures is incorporated into the analysis of offspring sex ratios, calculations indicate that an increase in the mean July temperature of about 4°C [i.e., $1.85^\circ\text{C} + (2 \times 1.11^\circ\text{C})$] would effectively eliminate the production of male offspring in this population.

DISCUSSION

Based on models of global climate change, a 4°C rise in mean July temperature for central North America is very likely within the next 100 years (1–4). A sustained change of this magnitude may result in the eventual extinction of this painted turtle population because no males will be produced (Fig. 1). Can the Thomson Causeway painted turtles counteract this rise in temperature either evolutionarily or behaviorally? Evolutionary change in the response of sex determination to temperature is unlikely for both historical and contemporary reasons. Contrary to theoretical expectations, reptiles with temperature-dependent sex determination do not exhibit an inverse latitudinal cline in the threshold temperature of sex determination (i.e., the incubation temperature at which offspring sex ratios are equal) (for review, see refs. 23–25). Although the propensity to produce offspring of a given sex has a high heritability (h^2) under constant laboratory conditions (26, 27), the likelihood that this trait would evolve rapidly enough to keep pace with the rate of climatic warming is slim. If mean July temperature rose 4°C , the threshold temperature would also have to increase about 4°C , because it currently produces a balanced sex ratio in the population on average (47.8% males). Given the heritability of this trait ($h^2 \approx 0.10$ in nature) (26, 27), the strength of selection (S) would be 40 ($S = 4/0.10$) (28). Consequently, the intensity of selection (i) would be extraordinarily large, requiring a shift in the mean threshold temperature of 35 SDs over the period of changing climatic temperatures ($i = S/\text{SD}_{\text{threshold temperature}} = 40/1.1275$) (28). Such a rapid rate of adaptive thermal evolution would be difficult to achieve in organisms with short generation times, much less in long-lived species like turtles (29, 30).

Another possible strategy is that female turtles could begin nesting earlier in the season so that temperatures during the sex-determining period of embryonic development would

produce both sexes. There is almost no evidence for this behavior in turtles at lower latitudes compared to their northern conspecifics (31), although a definitive long-term database is presently lacking. There was also no evidence for modification of nesting dates in this population: nearly all nests were constructed in the first half of June every year and still some years produced 100% male or female hatchlings. Likewise, shadier (sunnier) nest sites were not more frequently chosen in advance of warmer (cooler) summers to offset the temperatures in those years ($r = 0.42$; $n = 4$; $P = 0.57$) (20). Even if females employed thermal cues to choose nest sites, this trait may have a very low heritability, as it does in a lizard with temperature-dependent sex determination (32), and clearly would fail in thermally extreme years (e.g., 1992) in this population.

Given the antiquity of temperature-dependent sex determination (11, 13), taxa with this sex-determining mechanism experienced extreme climatic temperature changes in the geologically recent past similar in magnitude to the predicted rise (33, 34). Extinction was relatively minimal for these groups; most taxa shifted their geographic ranges southward in response to advancing glaciers (35–37). Proximate shifts in climatic temperature are expected to be rapid however, which may preclude successful gradualistic responses that functioned historically, like active modification of geographic range (6–10, 38). Furthermore, many species with temperature-dependent sex determination are already threatened or endangered (13): natural populations of these species could be negatively affected by climate changes long before they become as severe as predicted (39).

The causal influence of annual variation in climatic temperature on cohort sex ratios in this population of painted turtles serves as a clear empirical example of the biological impact portended by rapid global temperature change. This study demonstrates that the demography of populations of species with temperature-dependent sex determination may be directly sensitive even to modest deviations in the local thermal environment. These results are entirely consistent with earlier work on a nesting beach of endangered loggerhead sea turtles (*Caretta caretta*), wherein 87–99% of hatchlings from the rookery in each of 3 years were females because sand temperatures at nest level were high (39). If such strongly female-biased cohorts lead to highly skewed adult sex ratios, then the probability of population extinction may be greatly enhanced.

The broader implications of this study may nonetheless be limited by several factors. (i) Because evidence to the contrary is incomplete (31), initiation of the nesting season in species with temperature-dependent sex determination may in fact correlate with latitude (and thus ambient temperature) in a manner that diminishes the impact of local climatic temperature change. Such a behavioral modification could be insufficient for northern populations of painted turtles, however, because hatchlings in nests may be unable to survive extended exposure to hot summer temperatures (e.g., high temperatures greatly reduced hatchling recruitment after the summer of 1988). (ii) The metapopulation structure of painted turtles in the Mississippi River might also mitigate against skewed population sex ratios caused by climate change if there is both sufficient variance among populations in the thermal structure of nesting areas and adequate migration rates among these populations. Unfortunately, this information is known for very few reptile species (but possibly for some sea turtles and crocodilians); still, the sex ratio benefits of these metapopulation dynamics may be unexploitable by numerous isolated (e.g., pond) populations of most species with temperature-dependent sex determination. (iii) Despite statistical evaluation of the effect of environmental variance on sex ratios (see *Results*), among-year variation in ambient temperatures occasionally may produce a small number of

male turtles that could then propagate the female-biased populations. The viability of this scenario to maintain painted turtle populations is greatly reduced, however, by the low probability of reaching sexual maturity ($<1\%$) (40), by a short life expectancy after reproductive maturation (≈ 5 years on average) (41), and by the small number of offspring that realistically could be sired by these few male turtles (*sensu* ref. 42).

Despite the potential limitations of this study, more reliable forecasts of the biological consequences of global temperature change will be possible by linking results of this type with climatological information to design and validate models of species dynamics and ecosystem processes. In particular, the incorporation herein of both mean and variance in environmental conditions into an analysis of alterations in population demography highlights the utility of this system for empirical assessment of the biological impact of climate change. Consequently, populations of species with temperature-dependent sex determination may act as bellwethers for the impending disruption to biological systems posed by global temperature change.

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