

TEMPERATURE CONTROLLED SEX-DETERMINATION IN TURTLES: ECOLOGICAL AND BEHAVIORAL ASPECTS

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ABSTRACT: The sex of many reptiles is determined by incubation temperature. Laboratory studies of 14 genera of turtles in five families show that a developmental temperature of 25 C produces all males in most species, and that 31 C or higher produces all females. Survival of embryos to hatching is sufficiently high in some studies to conclude that this phenomenon is not due to differential death of the sexes. Field studies corroborate the laboratory work and suggest that nest temperature is the chief agent determining sex. The sex ratio of natural populations may be influenced by climatic changes, but natural selection on maternal choice of nest sites and on the embryonic control of sex determination may compensate for climatic change and bring the sex ratio to its equilibrium.

Key words: Reptilia; Testudines; *Graptemys*; Incubation; Reproduction; Sex determination; Temperature

TWO basic types of sex determination occur in reptiles: genotypic sex determination, and temperature-dependent sex determination (Bull, 1980). Genotypic sex determination is known for many lizards and snakes, but for only three turtles and for no crocodylian. The sex of most cryptodiran turtles and a few lizards is determined instead by incubation temperature.

Laboratory studies have shown that incubation temperature controls sex determination in 14 genera of turtles, including the emydids *Chrysemys*, *Emydoidea*, *Emys*, *Graptemys*, *Pseudemys*, and *Terrapene*; the kinosternids *Kinosternon* and *Sternotherus*; the chelydrids *Chelydra* and *Macrochlemmys*; the chelonids *Chelonia*, *Caretta*, and *Lepidochelys*; and the testudinid *Gopherus*. Incubation at 25 C produces primarily males, while incubation at 31 C or higher results in all females. Survival of embryos to hatching was high enough in several studies to refute the hypothesis that the results are due to differential mortality of the sexes (Bull and Vogt, 1979; Bull et al., 1982b; Pieau, 1975; Vogt and Bull, 1982; Vogt et al., 1982; Yntema 1976; Yntema and Mrosovsky, 1980).

Over the last few years, we have conducted a variety of laboratory studies us-

ing constant and fluctuating incubation temperatures with the map turtles *Graptemys pseudogeographica* and *G. ouachitensis*. These experiments clearly substantiate that sex determination in these species is controlled by temperature, and that sex is determined during the middle third of development (Bull and Vogt, 1982). Analysis of variation in sex ratios among clutches of eggs incubated at the same temperature indicates that there are moderate genetic effects on sex determination (Bull et al., 1982a).

To test the applicability of our laboratory results to a natural population, we conducted field experiments to examine sex ratios in both experimental and undisturbed nests. Results from the experimental nests were similar to those from laboratory experiments: hatchlings from eggs buried in the sun were mostly females, whereas those from eggs buried in the shade were all males. In addition, natural nests tended to produce only males or only females (Bull and Vogt, 1979). The combination of laboratory and field experiments with *Graptemys* strongly suggests that incubation temperature is a natural factor controlling sex determination in some species of turtles.

One of the more interesting implications of these studies pertains to the sex

ratio. Because sex of turtles depends on environmental temperature, the hatching (and subsequently, the adult) sex ratio may be subject to both long term and short term variation, merely from climatic changes. The population sex ratio can also evolve in response to climatic variation, however, through both the embryonic response to temperature in becoming male or female and through the choices of nest sites by females. These aspects of turtle populations may thus be studied from the perspective of sex ratio evolution. Here we discuss and review work of ours and others that bears upon the sex ratio question.

A 7 yr study of *G. ouachitensis* and *G. pseudogeographica* in Wisconsin revealed that sex ratios of adults are biased toward females (ca. 0.8 ♀♀ : 0.2 ♂♂; Vogt, 1980a). The bias toward females was detected using each of several collecting techniques, increasing the plausibility that the bias is real rather than due to sampling error (Vogt, 1980b). Several studies of *Malaclemys* populations also demonstrated adult sex ratios biased in favor of females (Cagle, 1952; Hildebrand, 1929; Seigel, 1979). In three different river systems in Mississippi and Alabama, adult sex ratios favoring females were found in four species of *Graptemys*. It may not necessarily be the case that these biased sex ratios result from temperature-dependent sex determination, and the consistent excess of females is not expected if the sex ratio biases are due to climatic variation. Females are much larger than males in both *Graptemys* and *Malaclemys*, so differential mortality of the sexes after sexual maturity may account for the skewed sex ratios (since the size differences arise after males mature [Vogt, 1980a]). However, in *Trionyx*, which lacks temperature-dependent sex determination (Bull and Vogt, 1979; Vogt and Bull, 1982), females are much larger than males, yet sex ratios of nearly 0.5 ♀♀ : 0.5 ♂♂ were observed at some of the same sites where *Graptemys* were studied (Vogt and McCoy, un-

publ. data). If the excess of females in *Graptemys* is due to differential mortality based on size differences of males and females, we might also expect a female-bias among adult *Trionyx*. That *Trionyx* has an adult sex ratio near 0.5:0.5 therefore casts doubt on the differential mortality hypothesis for *Graptemys*.

In view of the evidence from emydids, we suppose that species with temperature-dependent sex determination may experience periodic variation in sex ratio. Consequently, there are several characteristics of these turtles that may be affected by sex-ratio selection: (1) the position of the threshold between male-producing and female-producing temperatures; (2) the length of exposure required at a particular temperature to induce male or female differentiation under daily fluctuations in temperature; (3) maternal choice of nest sites; (4) date of oviposition; and (5) rate of development preceding the temperature-sensitive stages.

THRESHOLD TEMPERATURE

The threshold temperature has been defined as the temperature producing 50% males. It is usually the case that there is an abrupt change in sex ratio in a narrow range around this temperature, such that most temperatures above and below the threshold temperature produce all of one sex (Bull, 1980). In most species of turtles studied, including *Graptemys* (Bull and Vogt, unpubl. data) and *Emys* (Pieau, 1978), there is only one threshold temperature between 20–35 C. Yntema (1979), however, found that *Chelydra* embryos developed as female at both high (30 C) and low (20 C) temperatures and as male at intermediate temperatures. Two threshold temperatures are thus observed, one near 20 C and the other near 28 C. *Chelydra* eggs incubated throughout development at 20 C fail to hatch, so it might be thought that the lower threshold is irrelevant to sex determination in nature. However, if nest temperature fluctuates, temporary expo-

sure to 20 C could affect sex determination but not be lethal. A kinosternid turtle, *Sternotherus odoratus*, also appears to have two thresholds, one between 23 and 25 C and the other between 25 and 28 C (Vogt et al., 1982). It seems likely that the two thresholds are more relevant to natural sex determination in *Sternotherus* than in *Chelydra*, because embryos remain viable throughout development at both thresholds in *Sternotherus*.

In wide-ranging species of turtles exhibiting temperature-dependent sex determination, one means for maintaining a balanced sex ratio in different populations would be adjustment (through selection) of the threshold temperature. Bull et al. (1982a) showed that there is a weak genetic component to sex determination in map turtles, and hence this character could be selected. For example, if the environment cools, leading to production of an excess of males, selection would favor zygotes that become female at a lower temperature than usually is required for female differentiation. Because differences in threshold temperature are heritable, these individuals would then have offspring that also become female at lower than average temperature, and female differentiation could be extended to lower threshold temperatures until the sex ratio equilibrates.

Geographic variation in the threshold temperature was studied in several species of *Graptemys*, *Chrysemys*, and *Pseudemys* from populations in the northern and southern United States (Bull et al., 1982b). The average daily temperature during July is 2–3 C warmer in the southern than in the northern locality. The threshold temperatures generally were between 28 and 30 C. At 28 C, all but one of the populations produced nearly all males, and at 30 C and above all populations produced essentially all females. *Chrysemys* from Tennessee, however, had a threshold temperature 1 C lower than that of *Chrysemys* from Wisconsin. A significantly, though only slightly, lower threshold tempera-

ture was also observed in *G. pseudogeographica* from Tennessee.

These results first suggest that there is only a small difference in the threshold temperatures between populations of closely related species in different geographic areas. But there appears to be no physiological restriction confining the threshold between 28–30 C, as evidenced by the differences observed for *Chrysemys*, so selection could be acting to change the threshold to bring sex ratios to equilibrium. If sex ratio evolution depended solely on the changes in the threshold temperature, we would expect higher threshold temperatures in the South, presuming that nest temperatures are higher than in the North. However, the data for *Chrysemys* and *G. pseudogeographica* show a distinctly lower threshold in Tennessee as compared to Wisconsin—the opposite result from that predicted.

Adult sex ratios do not appear to be biased more towards females in southern populations, as might be expected with the threshold temperatures being so similar. McCoy and Vogt (unpubl. data) studied three riverine turtle communities in Alabama and Mississippi and observed an adult sex ratio of nearly 0.5 ♀♀ : 0.5 ♂♂ in *Pseudemys*. Although females predominated in four species of *Graptemys* at the Alabama/Mississippi study sites, sex ratios biased even more toward females were observed in two species of *Graptemys* in Wisconsin (Vogt, 1980a). Differences in nesting behavior may thus be compensating for the climatic differences between northern and southern populations. Southern turtles commence nesting about 2 wk earlier than northern populations (Vogt, unpubl. data), which reduces the disparity in temperature expected from synchronous climatic comparisons. Yet, even the comparison of June temperatures for the southern localities with July temperatures for the northern ones removes only about half of the differences in climatic temperatures. Differences in nest sites may compensate for

the climatic differences. Limited observations (McCoy and Vogt, unpubl. data) suggest that nest site differences between southern *Pseudemys* and *Graptemys* are consistent with the differences noted in the adult sex ratios, demonstrating the evolutionary flexibility of maternal behavior in choosing nesting habitat.

In a theoretical study of environmental sex determination, Bulmer and Bull (1982) suggested that if there is a steep threshold of sex determination as observed here, then there is little genetic variation in sex determination. Consequently, the threshold temperature change is slow to evolve in response to a bias in sex ratio. If more genetic variation exists for female choice of nest sites, then this will be a major source of sex ratio evolution, rather than a change of threshold temperature.

NEST SITE ECOLOGY AND FEMALE CHOICE

During the summer of 1980, we conducted a study on nesting behavior and the effect of nest site ecology on the sex ratio of hatchling turtles (Vogt and Bull, unpubl. data). We marked 397 nests (mostly *Graptemys ouachitensis* and *G. pseudogeographica* on Turtle Island, Vernon Co., Wisconsin (43°40' N latitude, 93°13' W longitude; see Vogt, 1978, 1980a for a description of the study area). We followed 236 of the marked nests through to hatching in August and September, the rest being lost due to predation or other factors (Vogt, 1981).

Incubation ranged from 52–73 days (median of 56) for nests producing all females and 58–85 days (median of 71) for nests producing only males. This resulted in the emerging hatchlings being nearly all females initially, then all males later in the season. These results are not surprising, since warmer temperatures accelerate development as well as cause femaleness (Bull and Vogt, 1982).

The distribution of the nest sex ratio in this study is bimodal for both species, with intermediate sex ratios occurring in

20% of the *G. ouachitensis* nests and in 30% of the *G. pseudogeographica* nests. Nests that produced females were located in open, sandy areas with scattered low herbaceous cover; nests that produced males were associated with denser clumps of vegetation, usually at the interface between the open sand and shrub zone at the edge of the beach. Soil temperatures at nest depth were, in fact, several degrees cooler in shaded areas than in areas of open sand.

A significantly larger proportion of males was produced on some beaches than on others. Part of this difference was apparently due to a greater density of herbaceous vegetation on the beaches producing the most males. These vegetated areas provided suitable nesting habitat, but were shaded enough to cause male development. The overall hatchling sex ratio observed in 1980 (0.75 ♀♀ : 0.25 ♂♂) concurred amazingly well with the observed adult sex ratio of previous years (ca. 0.8 ♀♀ : 0.2 ♂♂; Vogt, 1980a). If the imbalanced sex ratio of adults were due solely to greater mortality among males than females, then the hatchling sex ratio should not also be female-biased. Of course, the hatchling sex ratio from other nesting areas or in other years may be male-biased, but the present parallel between the adult and hatchling sex ratio should not be overlooked.

Similarly, incubation temperature affects the sex determination of sea turtles. Yntema and Mrosovsky (1980) showed that in loggerheads (*Caretta caretta*) sex determination is affected by incubation temperature in a manner similar to that in freshwater turtles. This finding has important applications to sea turtle management. For over a decade the standard procedure for protecting sea turtle eggs has been to remove eggs from natural nests and to place them in styrofoam boxes filled with moist sand. Eggs then are incubated in the shade, or are reburied in corrals away from the initial nesting site. No attempt has been made to determine sex of hatchlings or to maintain incuba-

tion temperatures similar to those of natural nests. Thus, the seas may have been seeded with an inordinate number of one sex, namely males.

A thorough study on the effect of incubation temperature on the sex of *Chelonia mydas* and *Lepidochelys olivacea* was recently conducted in Costa Rica. Nests in natural situations as well as artificial nests located in shade and sun were monitored throughout incubation. Some eggs also were incubated in styrofoam boxes in an effort to determine what effect this method has on the sex of the hatchlings. Not surprisingly, shade nests produced primarily males in *Chelonia mydas* while sun nests produced all females (Morreale et al., 1982).

Also, it appears that the same generalization holds for *L. olivacea* (Ruiz et al., 1981): females developed in the sun nests, and only males in the shaded nests. The styrofoam boxes held in shaded huts produced only male *Lepidochelys* (Ruiz et al., 1981); in *Chelonia*, boxes in sunny and shaded areas produced female and male hatchlings, respectively. Thus, it appears that sea turtle conservationists may have been releasing thousands of males in the past.

Various studies with sea turtles suggest that animals return to the same nesting beaches in different years, and that they nest several times a year during the nesting season. However, to our knowledge, no study has plotted the exact positions of nests in respect to habitat differences or similarities. This would be important in order to determine a female's influence on the sex ratio and how this might be selected for. Does a female alternate between shade and sun nesting sites, or do individual females have a specific preference of one type of site over another?

In our study of *Graptemys* (Vogt and Bull, 1982), a few marked females were observed on nesting excursions more than once (either twice in 1980 or once each in 1980 and 1981). (This does not indicate a low percentage of females pro-

ducing multiple clutches, however, because most nesting females were not observed.) These few observations suggest that at least some females repeatedly return to the same beach to nest. Six of 8 females found twice on Turtle Island during 1980 were on the same beach both times; of the 5 marked turtles observed nesting in 1981, 4 were on the same beach as in 1980. In addition, 5 females caught adjacent to or on this island in the 1972 season were observed here again in 1980, and 29 captured at a nearby island in one or more previous years back to 1975 were captured there in 1980 (Vogt, 1980a). These data suggest that some females tend to nest repeatedly on the same beach.

Even though the data on female choice of nesting sites are scant, this aspect of reptilian biology presents some intriguing questions regarding sex ratio. A female's choice of nest site affects the offspring's fitness as well as its sex, and the interaction of these selective forces offers unlimited material for the theoretician. Do females nest where they hatched? Clearly not all females do, or they would not be nesting in long-existing shaded sites that produce males (e.g., under old trees). However, females nesting in the general vicinity of their hatching site would be selected for if rates of nest predation are consistently higher in some areas than in others, provided that females can not assess levels of predation. Nesting at the precise site of hatching has the disadvantage that the population sex-ratio would often become female-biased (Bull, 1980). Another disadvantage of nesting at the exact site of hatching is the possible excavation of eggs of close relatives (thus reducing inclusive fitness) or eggs of an earlier clutch of the same female (thus reducing direct fitness).

One aspect of nest ecology that does not seem to be a major source of sex ratio variation for *Graptemys* is nest depth. Adult females do not differ greatly in size, and the nests are shallow enough that there is little temperature gradation

within a nest. Individuals of *Chelydra*, however, vary greatly in size from initial sexual maturity of the female to cessation of growth many years later. Thus, there may be a difference of over 20 cm between the carapace length of turtles laying their first clutches and those that have been reproducing for many years. This allows for the potential of smaller turtles laying eggs in shallower nests, and as they get older, in deeper nests, thus producing females in the earlier years of reproduction and males in the later years. Also, D. Wilhoft (personal communication) has shown in *Chelydra* that there is a temperature gradient in some nests. Eggs at the top of the nest, which received an average of 6 h at 30 C per day, produced females, while the eggs at the bottom of the nest chamber, which seldom reached 30 C, produced males. Morreale et al. (1982) suggest that nest depth may be an occasional factor in natural regulation of the sex ratio in sea turtles.

TEMPERATURE SENSITIVE PERIODS

In *Chelydra* sex is determined during the middle third of development (Yntema, 1979). Similarly, temperatures during the middle third of development are critical to sex determination of *G. ouachitensis* and *Chrysemys picta* embryos from Wisconsin, and temperatures during early and late developmental stages have little or no effect (Bull and Vogt, 1982). The primary sensitive period, defined as the interval of development during which sex is irreversibly determined (Bull and Vogt, 1982), occupies embryonic stages 16–22 in *Chrysemys* and *Graptemys*. In *Chelydra*, the primary sensitive period is similar, but its limits depend on the experimental temperatures used (Yntema, 1976). With 30 C and 26 C, the primary sensitive period occupies stages 14–19, slightly earlier than in emydines. The sensitive period is much briefer when 20 C and 26 C are used, occurring at stages 14–16, suggesting that 20 C is not identical to 30 C in its effect on sex determination in *Chelydra*.

Our experiments showed that sex determination depends upon a cumulative effect of temperature; sex determination during a part of the primary sensitive period is not independent of previous temperatures experienced by the embryo (Bull and Vogt, 1982). The stages prior to the primary sensitive period, in which sex is influenced by temperature but not irreversibly so, are referred to as the secondary sensitive period. The secondary sensitive period marks the onset of temperature sensitivity while the primary sensitive period marks the onset of possible irreversible sex determination. These may be distinct phenomena.

In *Graptemys*, 25 C is dominant to 31 C for sex determination; that is, 25 C can determine sex earlier and with less exposure than is required at 31 C. Yntema (1976) found the converse to be true with 26 and 30 C in *Chelydra*. What this implies about the differences in sex determination is unclear, except that there appear to be many pathways for the embryological control of sex determination that have yet to be fully explored. The point in mentioning the temperature sensitive period is to emphasize that very little is known about the mechanism of environmental sex determination and also to stress that only during a part of the developmental period is the sex of the embryo subject to the control of environmental temperatures. Thus, 2 wk or less of cool, rainy weather during the critical stages could radically change the sex ratio of hatchlings from what it would have been under sunny conditions, regardless of nest habitat.

OVIPOSITION

The nesting season for *Graptemys* in Wisconsin is usually confined to June, but turtles have been found nesting as early as 18 May and as late as 11 July (Vogt, 1980a). In our 1980 study of nest sex ratios, we observed a slight change in the sex ratio of nests depending upon the date of laying. The sex ratio from nests laid in the first half of June was about 0.8

♀♀ : 0.2 ♂♂ for the two species of map turtles (*G. ouachitensis* and *G. pseudo-geographica*), whereas the sex ratio from nests laid in the second half of June was 0.7 ♀♀ : 0.3 ♂♂. Seasonal changes in four factors may have contributed to these differences: (1) selection of nest sites by the females, (2) cooler ambient temperatures early in the summer, (3) growth of vegetation, increasing the amount of shade later in the summer, and (4) a greater effort to locate shaded nests late in June.

It would be interesting to investigate the possibility of a seasonal change in preference of females for sunny versus shaded sites. It would seem disadvantageous for a female to lay a late clutch in the shade, because incubation time in the shade is 2 or more wk longer than in the sun, imposing a risk of having the eggs not hatch until winter. The three nests in this study that failed to hatch by October were laid in shaded sites after 21 June. Hatchlings of some species of turtles are known to overwinter in the nest (Cagle, 1944; Gibbons and Nelson, 1978; Hartweg, 1946; Newman, 1906; Sexton, 1957). *Graptemys* eggs buried late in the nesting season in shady plots failed to hatch before winter and did not survive. Although *Chrysemys picta* and *G. geographica* hatchlings emerge from nests in the spring in some areas, eclosion occurs in the fall.

Other species of turtles, in particular some of the sea turtles, have a much longer nesting season, extending several months. It is more plausible that in these species, where nest temperatures and nesting habitats are often more uniform, the date of oviposition would have a greater influence on the sex ratio of the hatchlings than in map turtles. Preliminary data on *C. mydas*, *C. depressa*, and *C. caretta* in Australia suggest this (J. Miller et al., personal communication). Little stratification of nesting habitat or of nest temperatures at any one time was found, but significant differences among

nest temperatures at different seasons occurred. The Costa Rican sea turtle projects (Morreale et al., 1982; Ruiz et al., 1981) were conducted over only a limited portion of the nesting season and with only a small number of nests, so any such seasonal differences do not appear in their data.

DEVELOPMENTAL RATES

Another mechanism on which selection could be acting is the rate at which an embryo reaches the stages in which temperature influences sex. If the early developmental rate is slowed, so that the temperature-sensitive stages are reached at a later time, the sex ratio would perhaps change, depending upon the seasonal change in climate. The basis for this idea stems from the observation that, in some fall- or winter-nesting species, there is a greatly prolonged development (*Chelodina expansa*: Goode and Russell, 1968; *Staurotypus triporcatus* and *Deirochelys reticulata*: M. Ewert, personal communication). The embryology of this phenomenon is unknown, but it may be due either to a period of retarded, but continuous, development, or to an embryonic diapause. The prolonged development in these species is also associated with highly asynchronous hatching within the clutch (M. Ewert, J. Legler, personal communications; see also Ewert, 1979).

CONCLUDING REMARKS

Our study of sex determination began in August 1977 when two heretics were slowly transformed, one at a time, into believers, despite the fact that the occurrence of this mechanism in turtles would be in direct conflict with theories previously published by one of us (Charnov and Bull, 1977) and it was difficult to interpret citing the gospel according to Fisher. Thus, this presentation is appropriate in a symposium dedicated to Donald Tinkle—mounds of field and laboratory data about what reptiles are actually

doing will often topple the dreams of theoreticians.

If temperature-dependent determination of sex is primitive for turtles, it appears to have worked quite well for a long period of time. Heteromorphic sex chromosomes are of recent origin in turtles, and the genetic control of sex in *Trionyx*, a form lacking differentiated sex chromosomes, also is suggestive that temperature-controlled sex determination may be primitive (Bickham et al., 1981; Bull et al., 1974; Sites et al., 1979; Vogt and Bull, 1982). Turtles thus provide an ideal variety of systems to study the evolution of genetic control of sex determination: species with heteromorphic sex chromosomes, species with genetic control of sex but without heteromorphic sex chromosomes, and species with temperature-dependent sex determination. The only drawback is that generation time is slightly longer than in *Drosophila* populations.

Our research has taken us from the field to the laboratory and back to the field to obtain fortifying evidence that temperature controls sex determination under natural conditions and that this effect may be responsible for the skewed sex ratios observed in some areas. A temperature-sensitive period during embryogenesis has been defined, threshold temperatures have been documented, and incubation temperature has been shown to have a cumulative effect on the embryo in the ultimate sex of the hatchling; yet no one has studied the physiological mechanism causing the directional development of the gonad toward maleness or femaleness. Presently we are continuing our study along similar lines with neotropical turtles, pursuing such topics as: Are threshold temperatures different in the tropics? Does temperature-dependent sex determination occur in genera of turtles endemic to the tropics? What is the effect on the threshold temperature when a predominately temperate zone species invades the tropics—*Chelydra*

and *Pseudemys*? What sex ratios exist in populations of tropical species?

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