Temperature-Dependent Sex Determination in Reptiles [1]

By: Moeller, Karla T. Keywords: Sex determination [2] Reptiles [3] Turtles [4] Hormones [5]

The sex of a reptile [6] embryo partly results from the production of sex hormones [7] during development, and one such process to produce those hormones [8] depends on temperature of the embryo's environment. The production of sex hormones [7] can result solely from genetics or from genetics in combination with the influence of environmental factors. In genotypic sex determination [9], also called genetic or chromosomal sex determination [9], an organism's genes [10] alone determine which hormones [8] are produced. Non-genetic sex determination [9] occurs when the sex of an organism can be altered during a sensitive period of development due to external factors such as temperature, humidity, or social interactions. Temperature-dependent sex determination [9] (TSD), where the temperature of the embryo's environment influences its sex development, is a widespread non-genetic process of sex determination [9] among vertebrates, including reptiles. All crocodilians, most turtles [11], many fish [12], and some lizards exhibit TSD.

One cause of TSD is the enzyme aromatase. Aromatase helps to convert sex steroids, a group of hormones [8] that influence sex development and reproduction, from male sex hormones [7] (androgens [13]) to female sex hormones [7] (estrogens). Individuals with low levels of aromatase during the thermosensitive period will develop male characteristics. High levels of aromatase activity increase the production of female hormones [8], resulting in the development of female characteristics. While aromatase activity remains low for much of development in individuals that exhibit TSD, during the thermosensitive period, variations in temperature increase the activity of aromatase. This increase in aromatase enables individuals to develop into males or females depending on the temperatures experienced. Although other environmental influences can have similar effects, temperature is the most wide-spread factor that alters aromatase activity and sex determination [9].

Madeline Charnier, at the University of Dakar, in Dakar, Senegal, first described vertebrate TSD in Senegal in 1966. Charnier observed that temperature affected sex ratios, which are the number of females versus males in a population or a single clutch of eggs, of the rainbow Agama lizard, *Agama agama [14]*. Charnier published her results in the meeting records of the local *Society of Biology* in West Africa, a journal with limited distribution, and her efforts were not widely recognized for several years.

In 1967, the book *Sex Chromosomes and Sex-Linked Genes* by Susumu Ohno, a researcher at the City of Hope National Medical Center, in Duarte, California, drew attention to the genetic mechanisms and evolution [15] of sex determination [9]. In the late 1970s, James J. Bull, a professor at the University of Texas at Austin [16], argued that Ohno's publication treated TSD only as an aberrant imperfection in sex development, and scientists largely ignored TSD during the 1960s. In 1971 and 1972, Claude Pieau, a researcher at the Université Paris, in Paris, France, published findings on the effects of temperature on sex differentiation [17] of the European pond turtle, *Emys orbicularis [18]*, and on the Mediterranean tortoise, *Testudo graeca [19]*. Although few previous studies had supported the theory in reptiles, Pieau proposed TSD as an alternative to genotypic sex determination [9]. At this point, little evidence supported TSD as a possible mode of sex determination [9].

In 1974 researchers established the existence of genotypic sex determination [9] among turtles [11], a result that weakened support for TSD in reptiles and in vertebrates. When Bull and Eric Charnov, at the University of Utah, in Salt Lake City, Utah, proposed a model for the evolution [15] of environmental sex determination [9] in 1977, they only suggested applying the model to plants and invertebrates, and not to vertebrates. This evolutionary model, called the Charnov-Bull model, outlines the conditions under which the evolution [15] of environmental sex determination [9] occurs, and scientists later applied it to vertebrates with TSD.

In 1979 Bull and Richard Vogt, a researcher at the Instituto Nacional de Pesquisas da Amazônia in Aleixo, Brazil, showed that TSD exists in some reptiles. Bull and Vogt's article, "Temperature-dependent Sex Determination in Turtles", investigated the effects of temperature on the sex of hatchlings in five turtle species under controlled and natural field conditions. The results, which found evidence of TSD in four out of five species, confirmed that some vertebrate species exhibit TSD. As of 2004, sixty-five of seventy-nine tested species of turtles [11] were found to exhibit TSD.

Following Bull and Vogt's 1979 publication, TSD attracted more interest. Over the next two decades, scientists worked to test mechanisms of sex differentiation [17] in more species and to pinpoint pivotal temperatures, which are species-specific temperature ranges in which males and females are produced in equal number. Pieau and his colleagues focused on defining the TSD thermosensitive period, or the time of development during which changes in temperature can alter sexual organ growth.

Turtle species that display TSD are thought to follow one of two patterns of temperature dependence. In some species, low temperatures produce mainly females, and high temperatures produce mostly males. Other species show disproportionately high female production at both high and low temperatures, with intermediate temperatures causing mostly male development.

In the 1990s, David Crews, a biologist at the University of Texas at Austin [16], and colleagues found that some environmental pollutants caused sex-altering effects in turtles [11] and other reptiles. For instance, polychlorinated biphenyls (PCBs) are pollutants whose molecules are structurally similar to some estrogens. PCBs can act as an estrogen [20] replacement, causing feminization of sex organs in growing reptiles. At certain levels of PCBs, the feminizing effects can override the influence of temperature, negating the effects of TSD in an organism.

Scientists are still working to understand the evolution [15] of TSD and the implications of climate change for species that exhibit this mechanism of sex determination [9]. The consequences of TSD on fitness, or reproductive success, are largely unknown. However, a 2008 publication by Daniel Warner, at Iowa State University, in Ames, Iowa, and Richard Shine, at the University of Sydney, in Sydney, Australia, titled, “The Adaptive Significance of Temperature-Dependent Sex Determination in a Reptile”, posited that TSD maximizes reproductive success in some lizards. Warner and Shine used hormonal manipulations to produce males and females across a range of temperatures in a species with TSD. They did so to test the predictions of the Charnov-Bull model. Their results suggest that the temperatures an organism experiences during development significantly affect its reproductive success. Warner and Shine’s publication supports the Charnov-Bull model for evolution [15] of TSD in lizards. The scope of the model for other reptiles, however, requires further research.

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