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Point of view

Temperature-dependent sex determination in an uncertain world: advances and perspectives

Determinación sexual por temperatura en un mundo incierto: avances y perspectivas

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Abstract. Recently, scientific attention has increased around the ecological and evolutionary effects of climate change on species with temperature-dependent sex determination (TSD). Arguably the most significant effect of climate change on TSD species will be the imbalance of sex ratios, which, in turn, would threaten population viability. Recent laboratory studies suggest that current climate change may not necessarily result in skewed sex ratios for most TSD species; these observations could challenge the current perception of interplay between climate change and TSD. Here, I present a brief review of the previous and new insights regarding ecological implications of TSD species to climatic changes.

Key words: climate change, sex determination, sex ratio, reproduction, reptiles.

Resumen. Recientemente, la atención de los científicos ha aumentado en relación a las consecuencias ecológicas y evolutivas del cambio climático sobre las especies con determinación sexual por temperatura. Posiblemente el efecto más significativo del cambio climático sobre las especies sexo dependientes de temperatura sea el desequilibrio en la proporción de sexos y por consiguiente poner en riesgo su viabilidad poblacional. Estudios recientes, en condiciones de laboratorio, sugieren que los diferentes patrones de determinación sexual por temperatura pueden invertir la proporción de sexos en respuesta a las variaciones ambientales, poniendo en entredicho la percepción actual de la interacción entre determinación sexual por temperatura y cambio climático. En esta nota, se presenta un breve resumen de los estudios previos y nuevos sobre las implicaciones ecológicas en especies con determinación sexual por temperatura ante los cambios ambientales.

Palabras clave: cambio climático, determinación sexual, proporción de sexos, reproducción, reptiles.

Reptiles have evolved different mechanisms for sex-determination. In several species, sex is determined by heteromorphic sex chromosome recombination, a process known as genetic sex determination (GSD). In contrast, temperature-dependent sex determination (TSD), where sex is determined by thermal conditions experienced in the lability period during gonadal development, is present in most reptile lineages (many turtles, all sphenodontians, a few lizards and all crocodilians studied) (Bull, 1980; Pieau, 1996). Thus, TSD is a case of phenotypic plasticity where environmental conditions during reproduction represent a powerful driver of population dynamics. TSD

has thus provided an interesting model to understand the interplay between sex ratio selection, sex determination and environmental factors, and thereby the evolutionary significance of phenotypic plasticity (Bull, 1980; Janzen, 1994; Van Dooren and Leimar, 2003; Warner and Shine, 2008).

Recently, the ecological and evolutionary impacts of environmental changes on TSD species have aroused considerable interest (e.g., Janzen, 1994; Hulin et al., 2009; Mitchell and Janzen, 2010). This interest lies in the hypothesis that TSD species may have an adaptive disadvantage in light of current environmental changes, leading to skewed sex ratios and potentially an increased risk of local population extirpations. Yet, recent TSD studies suggest that the interplay between sex determination and

environment are more complex than has been previously envisioned. These observations have challenged the current perception of potential consequences of environmental changes on TSD species. Here, I discuss some of these new insights regarding TSD species' responses to climatic changes, and the associated ecological implications.

The role of incubation temperature on sex determination was first reported over 46 years ago in the African agamid lizard *Agama agama* by Charnier (1966). Since then, studies mainly in laboratory conditions in the context of TSD mechanism in reptiles continue to accumulate. The molecular basis to explain sex differentiation remain rather complex, due to variety among species, some gene regulatory networks in GSD species are also found in TSD species, therefore the form to regulate the gene expression and hormonal precursors depends on genetic or environmental factors (reviewed in Lance, 2009; Merchant-Larios and Díaz-Hernández, 2013).

TSD pattern are characterized by showing a pivotal temperature (i.e., temperature which produces a balanced sex ratio at constant incubation temperature) and a transitional range of temperature (i.e., the range of temperatures that yield both sexes in variable proportions). Based on available information from the laboratory studies at constant temperature, simple experiments suggest that mean temperature variations above or below one of the pivotal temperatures during the lability period would drastically alter the offspring sex ratio (e.g., Glen and Mrosovsky, 2004; Hawkes et al. 2007; Katselidis et al., 2012; Patiño-Martínez et al., 2012), which, in turn, would have important ecological implications for field studies.

Recently, Neuwald and Valenzuela (2011) and Warner and Shine (2011) showed under controlled conditions that offspring sex-determination can be reversed under increasing thermal fluctuation. Both studies used laboratory incubation regimes that mimic thermal fluctuations within natural nests. Neuwald and Valenzuela (2011) observed for the painted turtle *Chrysemys picta* (TSD pattern Ia; Bull and Vogt, 1979), that eggs incubated at male-promoting temperature with low thermal variation ($26 \pm 3^\circ\text{C}$) showed the expected sex ratio as if they were incubated at constant temperature; while eggs incubated at the same temperature but with higher thermal variation ($26 \pm 5^\circ\text{C}$) produced a female-biased sex ratio. The opposite occurred when eggs were exposed at female-promoting temperature with low ($31 \pm 3^\circ\text{C}$) and high ($31 \pm 5^\circ\text{C}$) thermal variation: the expected sex ratio resulted in the former and male-biased offspring in the later. In the other study, Warner and Shine (2011) experimented with the TSD II jacky dragon *Amphibolurus muricatus*, in which females are produced at low ($\leq 26^\circ\text{C}$) and high ($\geq 30^\circ\text{C}$) temperatures, and

males at intermediate temperatures ($26\text{--}30^\circ\text{C}$) (Harlow and Taylor, 2000). Warner and Shine (2011) observed that constant female-promoting temperature (25°C) produced a female-biased sex ratio, but when increasing thermal variation (low: $25 \pm 4^\circ\text{C}$ and high: $25 \pm 8^\circ\text{C}$) sex ratio approached a balanced proportion. When eggs were exposed to an intermediate temperature (28°C) a balanced sex ratio was produced, but when thermal variation was increased (low: $28 \pm 4^\circ\text{C}$ and high: $28 \pm 8^\circ\text{C}$), sex ratio was female-biased. On the other hand, Inamdar et al. (2012) studying the Indian oviparous lizard *Calotes versicolor* observed that eggs incubated at $23.5 \pm 0.5^\circ\text{C}$ and $31.5 \pm 0.5^\circ\text{C}$ produced females, while males were produced at $25.5 \pm 0.5^\circ\text{C}$ and $31.4 \pm 0.5^\circ\text{C}$, suggesting that *C. versicolor* shows 3 threshold temperatures that produce balanced proportions. In a recent study, a similar pattern (3 threshold temperatures) was observed in the oviparous desert lizard *Crotaphytus collaris* (Santoyo-Brito et al., 2012); therefore the female-male-female-male pattern may be more common than was previously thought.

Future climate projections indicate a rise of the mean global temperature at least during the current century, but offer little information regarding changes in thermal fluctuations. This limits our ability to foresee the potential effects of climate change on TSD species under natural conditions. Yet, new insights suggest that different TSD species could shift sex ratio in response to thermal fluctuations, specifically reversing the sex ratio or balance sex ratios in TSD species. Also, these observations shed new light on the adaptive significance of TSD strategies to maintaining sex ratios in the face of environmental changes (Neuwald and Valenzuela, 2011; Warner and Shine, 2011; Inamdar et al., 2012), thus current climate change may not necessarily result in skewed sex ratios for most TSD species. However, this suggestion is not entirely new. In the early 1980's, Bull and Vogt (1981) and Bull (1985) observed that offspring sex ratio is the outcome between daily thermal fluctuation and daily proportion of time in which gonadal development spent above threshold temperature. Thereafter, Georges et al. (1994) proposed, 19 years ago, that threshold temperature established in laboratory conditions at constant temperature is poorly relevant to natural conditions wherein the nest temperature fluctuate daily. Yet, unfortunately, some laboratory and field studies that evaluate the potential effect of climatic variations on sex ratio in TSD species in the context of climate change have ignored previous work wherein mean temperature in the natural nest failed to explain hatchling sex ratio. In addition, we still know surprisingly little about the role of heat shock proteins (HSPs) during thermo-sensitive period of sex differentiation (Harry et al., 1990; Kohno et al., 2010), which may be the key to

understanding the physiological mechanisms of adjustment to environmental changes.

In sum, based on the previous and new insights, considering only the mean incubation temperature as the thermal parameter to predict the resulting sex ratio in natural conditions and the consequences of climate change on TSD species could lead to erroneous conclusions, and misleading conservation strategies for TSD species. Therefore, there are many missing pieces that need to be in place before it will be possible to predict the effects of climate change on TSD species. Future work should address questions regarding how temperature fluctuations influence sex determination under natural conditions and how environmental changes affect offspring fitness. This information will help provide a broader and more precise view about the consequences of contemporary environmental variations, and the responsiveness of TSD species to these changes.

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