
A fifth hypothesis for the evolution of TSD in reptiles

In a recent paper, Shine reviewed the evolutionary origin of temperature-dependent sex determination (TSD) in reptiles¹. He discussed four models explaining its widespread occurrence and detailed the differential fitness hypothesis. In this model, TSD is selected for when fitness of individuals is influenced by both incubation temperature and sexual phenotype. However, more than 30 years after the discovery of temperature-dependent biased sex ratio in a squamate² and turtle³, the only strong biological support for the differential fitness theory comes from a species that possesses genetic sex determination (GSD)⁴.

We have previously proposed a fifth model that, contrary to the others, does not attempt to provide an advantage of TSD but rather investigates any disadvantages of this kind of sex determination, as opposed to GSD (Ref. 5). Two possible disadvantages have been considered. First, although intersex gonads can be produced during development, we have recently shown that this intersexuality is generally transient and does not hinder the reproductive capacity at adult stage⁶. Second, TSD promotes fluctuation of primary sex ratio as a result of climatic variation.

When sex ratio varies between years, individuals that develop into the predominant sex are counter-selected. Consequently, the genetic characteristics that enhance the lability of sex determination are also counter-selected and TSD is less favourable compared with GSD. However, intrasexual competition (males versus males and

females versus females) does not hold only for individuals within a cohort but also among cohorts. Thus, the sex ratio under selection that should be taken into account is not the primary sex ratio of each cohort but rather the mean of the primary sex ratios of all the cohorts participating in reproduction weighted by their numeric representation in the population.

For long-lived species, the average of several tenth years of primary sex ratio should be taken into account, which considerably reduces the potential fluctuation of the sex ratio under selection; therefore, TSD becomes quasi-neutral compared with GSD when a large number of overlapping generations contribute to reproduction⁵. Reptile species with TSD are long-lived species (e.g. turtles, crocodylians and sphenodonts) or among the longest-lived species for squamates (agamidae or geckonidae). Moreover, turtles with TSD have higher annual adult survivorship than turtle species with GSD (Ref. 7).

Finally, any genetic component involved in the sex determination of species with TSD gives strong support to the quasi-neutral hypothesis for the evolution of TSD. Indeed, when a genetic component acts in natural conditions, individuals develop towards the 'wrong' sex compared with what is expected based on a selective hypothesis. The influence of a genetic component in sex determination has been proved not only in laboratory conditions in several turtles and crocodylians⁸⁻¹¹, but also in natural conditions in the European freshwater turtle, *Emys orbicularis*¹².

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Marc Girondot

UMR 8570, Evolution et Adaptation des Systèmes Ostéomusculaires, Case 7077, Université Paris 7-Denis Diderot, CNRS, Collège de France et MNHN de Paris, 2 place Jussieu, 75251 Paris Cedex 05, France (mgi@ccr.jussieu.fr)

Claude Pieau

Laboratoire de Biochimie du Développement, Institut Jacques Monod, CNRS, Université Paris 7 et Paris 6, 2 place Jussieu, 75251 Paris Cedex 05, France (pieau@ccr.jussieu.fr)

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