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Horizons

Temperature dependent sex determination and climate change

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One possible response of species to climate change is shifting their geographical range so as to track their climatic niche. Many concerns have been raised about the species ability to disperse effectively. I argue that species may have mechanisms, like temperature-dependent sex determination (TSD), that are responsive to climate change and may facilitate an appropriate shift in their geographical range. More specifically, I hypothesize that, under stable climatic conditions, populations of some TSD species at the edge of their range are regulated by reduced growth rate (due to skewed sex ratios or due to limited availability of suitable nesting sites). Under climate change, these populations face new climatic conditions that trigger fast population growth (e.g. by more balanced sex ratio, or greater availability of nesting sites). Increased population size may lead to increased dispersal, and thus efficient colonization of the newly created habitat patches. So, the species rapidly tracks the geographical position of its climatic niche. This conceptual model is speculative but it leads to specific hypotheses, and opens up new research questions about the existence of prior adaptations that will enable the appropriate response to climate change.

Ecologists investigate the way species will respond to climate change. Species may change their phenology and shift their activity temporally (Both and Visser 2001, Mazaris et al. 2008), or alternatively they may shift their geographic range to cooler regions (Warren et al. 2001), or finally they may evolve new adaptations (Davis et al. 2005).

Studies document the range shift of species to cooler regions and assess the impacts of various scenarios of climate change on species distributions (Davis and Shaw 2001). As Thuiller et al. (2008) point out, these models are based on a wide range of assumptions and scenarios, but few, if any, focus on the critical role of migration processes, and more specifically on what happens at the leading and trailing edge of the species range.

In this paper, I examine the role of temperature-dependent sex determination in regulating the populations at the leading and trailing edge of the species range, and how TSD may facilitate migration in the face of climate change. I argue that species may already have mechanisms, like TSD, that respond to climate change, and facilitate species to shift their geographic ranges.

The conceptual model

In some reptile species and some other taxa (e.g. fish like salmon Conover and Kynard 1981, or even birds like *Alectura lathanii* Goth and Booth 2005) sex is determined by incubation temperature. There are three main patterns of TSD: 1) males are produced at low temperatures, and females at high temperatures (pattern Ia), 2) the exact opposite, females at low temperatures and males at high temperatures (pattern Ib), and 3) fmales are produced at both high and low temperatures and males at intermediate temperatures (pattern II) (Janzen 2002).

Studies document a relationship between surface air temperature and temperature in nests of TSD species, i.e. incubation temperature (Janzen 1994, Hawkes et al. 2007), as Fig. 1 schematically illustrates. A corollary is the relationship between surface air temperature and offspring sex ratio (Janzen 1994, Hays et al. 2003, Mitchell et al. 2008). I assume that the population's adult sex ratio is determined by the offspring sex ratio, because mechanisms causing sex-dependent juvenile mortality or recruitment are either absent or not strong enough to completely counteract the offspring sex ratio. Given the relationship between latitude and temperature, I postulate that the sex ratio varies geographically, with balanced sex ratio in the core of the species range and skewed sex ratios at the edges of the species range. As far as I know, there are no detailed reports of a TSD species sex ratio throughout its range, but studies document northern populations with male biased sex ratio as postulated (Edmonds and Brooks 1996, Bishop and Echternacht 2003). Thus, under stable climatic conditions population growth at the edges of the species range is regulated (Fig. 1), due to the under-representation of either males or females. This is a more efficient control on population growth when females are missing, but the lack of males may also efficiently cap population growth in species with high mate fidelity. Although many TSD species

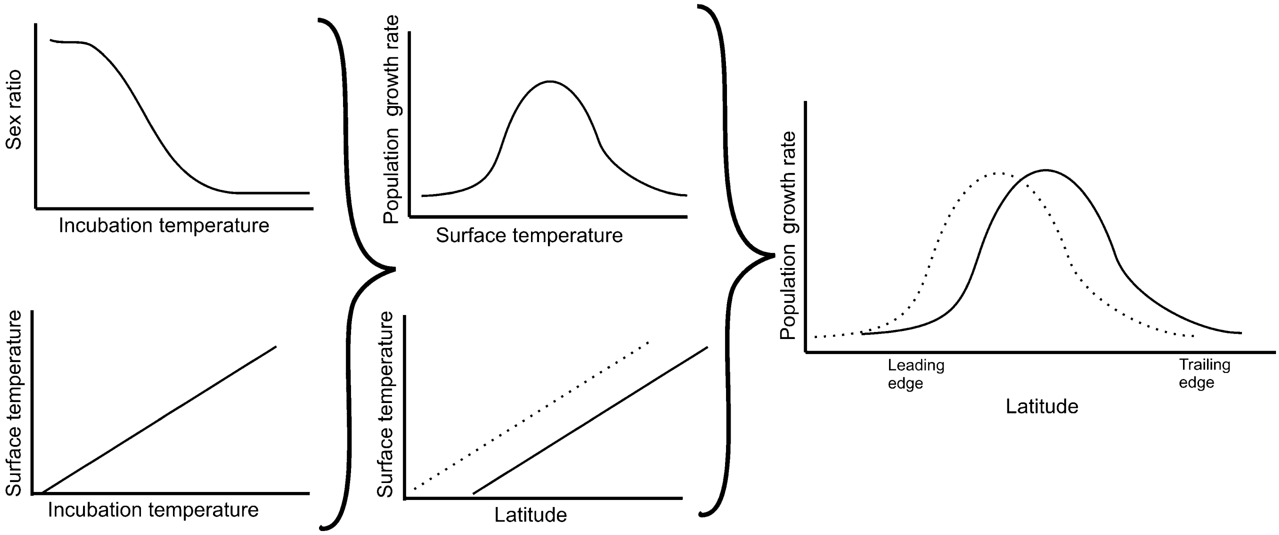

Figure 1. A schematic illustration of the conceptual model. The incubation temperature affects the offspring sex ratio, but it is also correlated to surface temperature. Thus surface temperature affects a population's growth rate either by skewing the sex ratio or by limiting the availability of nesting sites producing balanced sex ratio. But surface temperature is related to latitude (with solid line is the present day relationship, and with dotted lines the relationship after global warming). Thus the population's growth rate is related to latitude (solid line the present, dotted line after global warming). So the leading edge populations, that formerly faced low growth rate, will have increased growth rate with climate change, and thus have more potential dispersers to colonize the new locations, that their climate niche will be located after climate change. Trailing edge populations will see their growth rate drop to zero, and probably face increased extinction risk.

are polygynous or promiscuous (Hofmann and Henle 2006), there are species with high mate fidelity (O'Connor and Shine 2003).

There also exist examples like the geckos, in which many species have TSD, with sex ratio rarely deviating from an equal sex ratio even at the edge of their range (Henle 1990a, 1990b). Such species may regulate their sex ratio through maternal behaviour in choosing nest sites (Doody et al. 2006). However, it remains an open question whether a female chooses a nesting site in order to produce a balanced sex ratio or to maximize offspring survivorship, e.g. when nest sites with appropriate temperature face increased predation risk or inappropriate moisture conditions (Morjan 2003, Houghton et al. 2007). Even assuming that females choose nesting sites producing balanced sex ratio, the edge populations of TSD species still face reduced population growth rates. In extreme temperature conditions the suitable nesting sites will be limited (Mitchell et al. 2008 for tuataras). Thus a limiting resource (i.e. nesting sites) decreases the population's growth rate at the edge of the species range (Fig. 1).

TSD is only one possible mechanism that may produce such pattern of decreased population growth at the edge of the species range. In *Podarcis sicula* winter mortality may limit population growth at the northern part of its range. In other species, factors like juvenile growth, duration of the nesting season or adult density might also lead to similar patterns.

So what will happen under climate change?

At the leading edge, low temperatures decrease the population's growth rate (by skewed sex ratio, or by limited availability of nest sites). Under global warming these populations will face increased temperatures (Fig. 1 dotted lines compared to solid lines); consequently they may undergo rapid growth (due to balanced sex ratio, or increased availability of nest sites), which means an increase in population density, and thus a greater availability of individual dispersers at the species range margin. These new dispersers are strategically located at the part of the species range nearer to the suitable habitat patches that would be created by climate change in locations outside the present day species range. And thus there is a greater availability of potential dispersers to colonize these patches and track the new geographic location of the species climatic niche. So the model predicts that as the climate changes the dispersal propensity at the leading edge of the species range will increase, with greater number of individuals dispersing.

At the trailing edge, high temperatures restrict population growth. Here, global warming will further increase temperatures, by decreasing suitable nesting sites, or producing hatchlings of only one sex (Mitchell et al. 2008). So population growth will effectively become null (Fig. 1), before climatic conditions cross the species physiological tolerance threshold, and individuals start to perish. So unless refuges could be established, trailing edge populations would find it difficult to persist and serve as stores of genetic diversity.

An important feature of this mechanism is that it is equally plausible for both global warming and global cooling. So this mechanism needs not be invoked as an ad hoc mechanism for humanly induced global warming, but might be useful in both the cooling and warming phases of a glacial cycle. The difference will be which edge is leading and which is trailing.

Discussion

The main point of my model is that some species face reduced population growth rate at the edge of their range due to climatic conditions. Under global warming, this restriction on population growth at the cold end of the species range is lifted. So, these populations grow rapidly, building a pool of potential dispersers, which may be able to track the new geographic location of their climatic niche. This might mean that their extinction risk in the face of climate change is lower than previously estimated.

However, I should point out three caveats. Firstly, this model examines only the population's migration. This range expansion is based on the rapid growth of the populations at the leading edge of the species range. These populations are usually small due to restricted population growth, and thus they may possess a limited gene pool. The small size of the gene pool might result in phenomena like colonization bottlenecks or founder effects. These phenomena might have important effects for the species extinction risk and evolutionary potential, but fall outside the scope of this study. Secondly, and most important, this mechanism reduces the extinction risk only if new habitat patches become available at the new geographic location of the climatic niche. If this is not the case (e.g. the new location is over human dominated land uses or in uninhabitable areas like the ocean for a terrestrial species) then the increased dispersal propensity leads to nowhere, and in combination with the decreased population growth of the trailing edge, leads to increased extinction risk (in accordance with Janzen 1994, Mitchell et al. 2008). Thirdly, I assume that TSD and sex ratio are the limiting factors driving the dynamics of a population, and that other factors (e.g. growth of juveniles) are not strong enough to completely counteract the sex ratio imprinted by offspring sex ratio. I am not aware of any studies examining this question, but hope that this study may stimulate such investigations.

Furthermore, TSD species also display other responses to climate change (Huey and Janzen 2008). Species may alter their thermal sensitivity of TSD (an example offered by Ewert et al. (2005) over the geographical variation in the pivotal temperature) or their behaviour, e.g. earlier onset of reproductive events (Mazaris et al. 2008, Schwanz and Janzen 2008).

It remains an open research question why did species evolve TSD (Shine 1999, Janzen and Phillips 2006). I do not claim that TSD evolved as an adaptation to climate change. I only argue that a pre-existing adaptation (TSD) has a fortuitous side effect to enable the appropriate response to climate change, something that might be viewed as a preadaptation. The acceptance that there might already exist mechanisms that allow species to adapt faster to climate change, opens a new research agenda in the quest for such mechanisms or life history traits. And even though the model was built around TSD, I should point out that it could apply to other species, provided there is a mechanism restricting their population growth at the edge of their range in response to the site's temperature.

References

Bishop, D. C. and Echternacht, A. C. 2003. Winter growth and sex ratio of a northern population of *Anolis carolinensis* (Sauria: Polychrotidae) – Copeia 4: 906–909.

Both, C. and Visser, M. E. 2001. Adjustment to climate change is constrained by arrival date in a long-distance migrant bird. – Nature 411: 296–298.

Conover, D. O. and Kynard, B. E. 1981. Environmental sex determination: interaction of temperature and genotype in a fish. – Science 213: 577–579.

Davis, M. B. and Shaw, R. G. 2001. Range shifts and adaptive responses to Quaternary climate change. – Science 292: 673–679.

Davis, M. B. et al. 2005. Evolutionary responses to changing climate. – Ecology 86: 1704–1714.

Doody, J. S. et al. 2006. Nest site choice compensates for climate effects on sex ratios in a lizard with environmental sex determination. – Evol. Ecol. 20: 307–330.

Edmonds, J. H. and Brooks, R. J. 1996. Demography, sex ratio and sexual size dimorphism in a northern population of common musk turtles (*Sternotherus odoratus*) – Can. J. Zool. 74: 918–925.

Ewert, M. A. et al. 2005. Geographic variation in the pattern of temperature-dependent sex determination in the American snapping turtle (*Chelydra serpentina*). – J. Zool. 265: 81–95.

Goth, A. and Booth, D. T. 2005. Temperature-dependent sex ratio in a bird. – Biol. Lett. 1: 31–33.

Hawkes, L. A. et al. 2007. Investigating the potential impacts of climate change on a marine turtle population. – Global Change Biol. 13: 923–932.

Hays, G. C. et al. 2003. Climate change and sea turtles: a 150 year reconstruction of incubation temperatures at a major marine turtle rookery. – Global Change Biol. 9: 642–646.

Henle, K. 1990a. Population ecology and life history of the arboreal gecko *Gehyra variegata* in arid Australia. – Herpetol. Monogr. 4: 30–60.

Henle, K. 1990b. Population ecology and life history of three terrestrial geckos in arid Australia. – Copeia 1990: 759–781.

Hofmann, S. and Henle, K. 2006. Male reproductive success and intrasexual selection in the common lizard determined by DNA-microsatellites. – J. Herpetol. 40: 1–6.

Houghton, D. R. J. et al. 2007. Protracted rainfall decreases temperature within leatherback turtle (*Dermochelys coriacea*) clutches in Grenada, West Indies: ecological implications for a species displaying temperature dependent sex determination. – J. Exp. Mar. Biol. Ecol. 345: 71–77.

Huey, R. B. and Janzen, F. J. 2008. Climate warming and environmental sex determination in tuatara: the last of the sphenodontians? – Proc. R. Soc. Lond. B 275: 2181–2183.

Janzen, F. J. 1994. Climate change and temperature-dependent sex determination in reptiles. – Proc. Natl Acad. Sci. USA 91: 7487–7490.

Janzen, F. J. 2002. Temperature and sex. – In: Halliday, T. and Adler, K. (eds), The new encyclopedia of reptiles and amphibians. Oxford Univ. Press, pp. 116–117.

Janzen, F. J. and Phillips, P. C. 2006. Exploring the evolution of environmental sex determination, especially in reptiles. – J. Evol. Biol. 19: 1775–1784.

Mazaris, A. D. et al. 2008. Do long-term changes in sea surface temperature at the breeding areas affect the breeding dates and reproduction performance of Mediterranean loggerhead turtles? Implications for climate change – J. Exp. Mar. Biol. Ecol. 367: 219–226.

Mitchell, N. J. et al. 2008. Predicting the fate of a living fossil: how will global warming affect sex determination and hatching

phenology in tuatara? – Proc. R. Soc. Lond. B 275: 2185–2193.
Morjan, C. L. 2003. Variation in nesting patterns affecting nest temperatures in two populations of painted turtles (*Chrysemys picta*) with temperature-dependent sex determination. – Behav. Ecol. Sociobiol. 53: 254–261.
O'Connor, D. and Shine, R. 2003. Lizards in 'nuclear families': a novel reptilian social system in *Egernia saxatilis* (Scincidae). – Mol. Ecol. 12: 743–752.
Schwanz, L. E. and Janzen, F. J. 2008. Climate change and temperature-dependent sex determination: can individual plasticity in nesting phenology prevent extreme sex ratios? – Phys. Biochem. Zool. 81: 826–834.
Shine, R. 1999. Why is sex determined by nest temperature in many reptiles? – Trends Ecol. Evol. 14: 186–189.
Thuiller, W. et al. 2008. Predicting global change impacts on plant species' distributions: future challenges. – Persp. Plant Ecol. Evol. Syst. 9: 137–152.
Warren, M. S et al. 2001. Rapid responses of British butterflies to opposing forces of climate and habitat change. – Nature 414: 65–69.