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RESPONSE

Experimental field studies of species' responses to climate change: challenges and future directions

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The outcomes of climate change on biota are difficult to predict because they involve indirect effects of environmental changes on a multitude of organisms and occur via complex pathways. However, some thermally sensitive traits are directly impacted by climate and have demographic consequences for populations. One such trait is temperature-dependent sex determination (TSD), in which offspring sex is irreversibly determined by the temperature experienced by developing embryos; the extreme sensitivity of the TSD pathway means that a small change in environmental temperature could dramatically alter offspring sex ratio. Behavioral adjustment of maternal nest-site choice has been proposed as a mechanism allowing reptile populations to maintain even sex ratios despite climatic changes over evolutionary time. The rapid rate of human-induced climate change, however, may outpace the capacity of behavioral plasticity in long-lived species to adjust to a changing climate. We found that the adjustment in nest depth required to affect sex ratio in a model turtle species may be too great to keep pace with climate change, and therefore maternal adjustment of nest depth seems unlikely to compensate for sex ratio skews in small-bodied, freshwater turtles (Refsnider *et al*., 2013).

One advantage of our experimental approach, which used natural nests under field conditions, was that nests experienced natural incubation regimes in terms of both mean and daily variation in temperature. As Georges (2013) points out, daily variation in nest temperature is as important as mean temperature in determining offspring sex ratios (Georges, 1989), and studies are increasingly finding effects of fluctuating temperatures during embryonic development on later life stages (e.g. Mullins & Janzen, 2006; Les, Paitz & Bowden, 2007; Refsnider, 2013). Moreover, whether temperature variation occurs near the upper or lower thermal limit differentially affects offspring survival (Les, Paitz & Bowden, 2009) and sex ratio (Neuwald & Valenzuela, 2011). These complications emphasize the importance of incorporating natural levels of temperature fluctuations in incubation experiments involving species with TSD. Furthermore, understanding how juvenile performance (particularly as a result of incubation temperature during development) relates to fitness in adults would enhance our ability to predict the phenotypes of later life stages from the performance of earlier ones (Refsnider, 2013; Schwanz, 2013).

A disadvantage of conducting 'controlled' experiments under field conditions, as Rödder & Ihlow (2013) discuss, is that sample sizes are often small. In our study on how turtles may respond to climate change, sample sizes were halved after many nests were (perhaps ironically) destroyed by a flood, the likelihood of which also increases as climate change progresses (Milly *et al*., 2002; Solomon *et al*., 2007). Despite the difficulties of conducting experiments in the field, such an approach will provide valuable insight into species' responses to climate change, and similar studies on a variety of species will greatly advance our understanding of the interactions between biodiversity and climate change (Georges, 2013; Rödder & Ihlow, 2013; Schwanz, 2013).

An important area for continued research is the degree to which traits associated with nest-site choice, embryonic development and sex determination are genetically controlled. For example, studies that split clutches to parse out genetic variation due to parental effects (Rödder & Ihlow, 2013) will provide important insight into genetic versus. environmental drivers of traits related to sex ratio. Heritability has been estimated for some such traits (McGaugh & Janzen, 2011; McGaugh *et al*., 2011), but not yet for nest depth. In addition, researchers should strive to measure selection intensity on sex ratio-related traits (Schwanz, 2013). The strength of selection on traits related to TSD is likely to change as the climate continues to warm; moreover, selection strength on survival relative to sex ratio may also vary as climate change progresses (Schwanz, 2013). If we are to predict reptiles' response to climate change with any accuracy, we need a vastly improved understanding of the selective pressures posed by climate change and how they drive evolutionary responses of reptile populations.

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