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# Geographic variation in the age of temperate-zone reptile and amphibian species: Southern Hemisphere species are older

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**Despite controversy over alternative definitions, the species is the fundamental operational unit of biodiversity, and species are the building-blocks of conservation. But is a 'species' from one part of the world the same as a 'species' from elsewhere? Our meta-analysis of molecular phylogenetic data reveals that reptile and amphibian species distributed in temperate-zone areas of the Northern Hemisphere are younger than taxa from the Southern Hemisphere, probably reflecting the greater impact of past climatic variation on Northern Hemisphere habitats. Because a species' age may influence its vulnerability to anthropogenic threats, geographical variation in species ages should be incorporated into conservation planning.**

**Keywords:** reptile; amphibian; molecular dating; intraspecific diversification; conservation status

## 1. INTRODUCTION

Climate fluctuations (including glaciation events) in the Pleistocene (1.8–0.012 Ma; [1]) rendered many Nearctic and Palearctic regions unsuitable for ectothermic animals such as reptiles and amphibians, with the result that most present-day populations of such animals in these areas are the result of relatively recent (postglacial) recolonization [2,3]. In contrast, less intense glaciation over the same period in Southern Hemisphere continents (Australasia, South America [4]) placed fewer constraints on reptile viability, enabling populations to persist over large areas [5]. Based on the briefer duration of stable ectotherm-friendly conditions in temperate-zone North America, North Africa and Eurasia, we predicted that species in these areas would be younger, on average, than ecologically analogous taxa from Australasia, South Africa or South America. To test this prediction, we assembled data from molecular phylogenies on species ages in reptiles and amphibians.

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## 2. MATERIAL AND METHODS

To estimate the age of a species, we used the oldest intraspecific diversification event (as based on molecular dating) within each taxon. This measure estimates the amount of time since existing populations within a species last shared a common ancestor. Actual dates at which a species diverged from its closest relatives might be much earlier than this date, if local extinctions have eliminated older lineages. We reviewed phylogenetic papers on 157 species of amphibians (Anura) and reptiles (Squamata and Testudines) in temperate (non-tropical) areas to test for differences in age between taxa from the Northern versus Southern Hemispheres (see the electronic supplementary material). Urodeles (salamanders and newts) were excluded from the analyses, as they do not occur in temperate-zone areas of the Southern Hemisphere. Studies on non-monophyletic species were excluded to avoid inaccurate species age estimations. The statistical significance of the difference between Hemispheres in mean ages of species was tested with a two-way ANOVA with Hemisphere and orders (Anura, Squamata and Testudines) as factors and mean species age as the dependent variable, using JMP 7.0 [6]. We also examined latitudinal subsets of the data, to check that the same patterns were evident when we restricted attention to taxa found in directly comparable latitudinal zones. Thus, we repeated the above analysis for two mutually exclusive categories within the broader dataset: (i) species restricted to moderate latitudes only (between the tropics and 40° N or S), and (ii) species distributed at higher latitudes only (above 40° N or S). Species distributed in both of the above latitudinal ranges were excluded from these tests.

## 3. RESULTS

As predicted, present-day species of reptiles and amphibians from temperate-zone habitats of the Northern Hemisphere were on average younger than those from the Southern Hemisphere (two-way ANOVA: Northern versus Southern Hemisphere effect,  $F_{1,156} = 15.48$ ,  $p = 0.0001$ ; Squamate versus turtle versus anuran,  $F_{2,156} = 2.53$ ,  $p = 0.08$ ). This pattern was stronger in anurans and turtles than in lizards and snakes (interaction term,  $F_{2,156} = 3.98$ ,  $p = 0.02$ ; see figure 1).

Similar patterns were evident when the analysis was restricted to species that are found in moderate latitudes only (between the tropics and 40° N or S, including all orders: Northern versus Southern Hemisphere effect,  $F_{1,85} = 9.21$ ,  $p = 0.003$ ). For the analysis of high-latitude species (above 40° N or S), the only taxa represented in our dataset for the Southern Hemisphere were squamates, so we conducted a one-factor ANOVA with hemisphere as the factor and age of squamate taxa as the dependent variable. In this relatively small dataset, species from this latitudinal zone were again younger, on average, in the Northern Hemisphere than in the Southern Hemisphere ( $F_{1,8} = 8.48$ ,  $p = 0.02$ ).

## 4. DISCUSSION

Our data reveal a consistent geographical disparity in mean ages of species: at similar latitudes, reptile and amphibian species from the Southern Hemisphere tend to be older than species from the Northern Hemisphere. A geographical difference in the historical intensity of harsh climatic conditions (e.g. during Pleistocene glacial cycles) offers a plausible reason for this pattern. That is, the current distribution of many Northern Hemisphere taxa reflects relatively recent recolonization, from southern refugia, of areas that were unsuitable for species persistence at the height of glaciation. This is particularly true for species in relatively high-latitude areas of the Northern Hemisphere, where glacial events were most extreme [2]; other processes may have affected species ages in less severely cold regions. Southern Hemisphere species

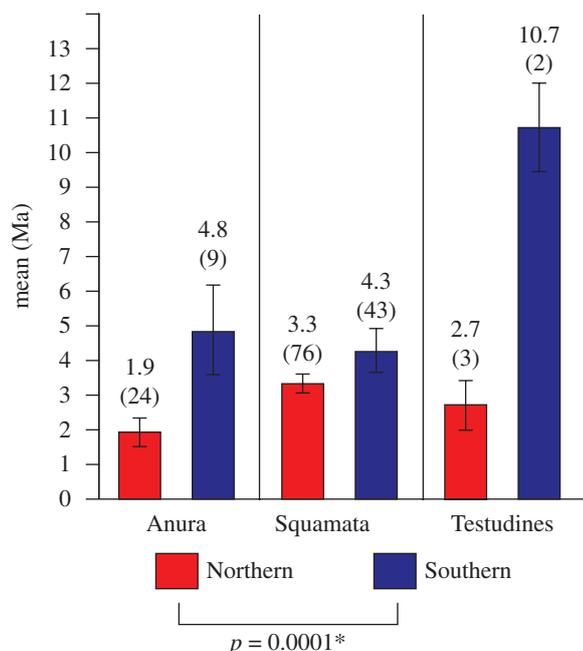


Figure 1. Based on the oldest known dates for intraspecific diversification events, species of reptiles and amphibians from the Southern Hemisphere are older than those from the Northern Hemisphere. The figure shows means and standard errors for the ages (millions of years ago = Ma) of Northern Hemisphere versus Southern Hemisphere species in each order of amphibians and reptiles that occurs in both Southern and Northern Hemispheres (Anura, Squamata and Testudines), and the number of species included in our dataset.

may have been more likely to persist in or near their current ranges over this period (at similar latitudes, Pleistocene climatic conditions were more extreme in the Northern than in the Southern Hemisphere [4]). Nonetheless, we note that alternative processes also could explain the disparity in mean species age. For example, some Southern Hemisphere lineages may contain a disproportionate number of older taxa, or the average ages of species in the Northern Hemisphere may be due to extinction of older lineages within each species rather than to a more recent divergence of each taxon from its closest relatives. In addition, more intensive research on the Northern Hemisphere fauna may have resulted in finer-scale understanding of phylogeographic affinities; and thus, some of the 'species' in Southern Hemisphere sites may ultimately prove to be composite taxa, with each component species younger than the combined lineage currently afforded species status. Finally, we note that the Northern and Southern Hemisphere areas that we compared differ in a range of tectonic, topographic and ecological traits, that may have had additional impacts on the mean age of species. On balance, however, geographical differences in climatic regimes seem the most probable explanation for the patterns that we have documented.

Does a species' age matter? Analyses of birds, Bornean mammals and Australian marsupials all identify species age as a predictor of vulnerability to extinction in the face of anthropogenic habitat destruction [7–10]. Although causal mechanisms remain unclear, 'older' species consistently are less resilient to the challenges

imposed by human activities [9]. Hence, all else being equal, Southern Hemisphere ectothermic vertebrates may be less able to cope with threats (such as those driven by changes in climate, habitat quality, invasive species and habitat fragmentation [11–13]) than are ecologically analogous taxa from the Northern Hemisphere. Understanding such broadscale geographical biases in species vulnerability may help us to understand why extinction rates are so much higher in some parts of the world than others [14], and to allocate conservation and management efforts to regions where endemic taxa may be at particular risk [15].

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