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REPLY

No rattlesnakes in the rainforests: reply to Gosling and Bush

WOLFGANG WÜSTER,* JULIA E. FERGUSON,* J. ADRIAN QUIJADA-MASCAREÑAS,* CATHARINE E. POOK,* MARIA DA GRAÇA SALOMÃO† and ROGER S. THORPE*

**School of Biological Sciences, University of Wales, Bangor LL57 2UW, Wales, UK, †Laboratório de Herpetologia, Instituto Butantan, Avenida Vital Brazil 1500, 05503–900 São Paulo — SP, Brazil*

Gosling & Bush (2005) criticize our interpretation (Wüster *et al*. 2005) of a phylogeographic analysis of the Neotropical rattlesnake (*Crotalus durissus*) as supporting a hypothesis of Pleistocene fragmentation of the Amazonian rainforests. We thank these two authors for the opportunity to further discuss issues concerning the ecological and biogeographical history of the Amazon Basin.

Gosling and Bush quite rightly comment on the diversity of the ecosystems that are often grouped together as 'Amazonian rainforest', and also note the dynamic changes of community composition throughout the Pleistocene. They go on to comment that these two factors make any extrapolation from present-day distribution patterns difficult, and question the use of *C. durissus* to determine the possible past extent of rainforest fragmentation. We reject these doubts, and maintain that the presence of *C. durissus* on both sides of the Amazon Basin does represent evidence of profound changes in the distribution of rainforests in the Pleistocene and cannot be explained by relatively minor changes in rainforest community composition.

Despite the dynamic nature of community composition in Neotropical forests, a typical rainforest physiognomy can be defined and can be traced back through the vegetational history of South America to at least the Eocene (Burnham & Johnson 2004). Moreover, the many different identifiable Amazonian forest types all have one factor in common: *C. durissus* does not occur in them. The few available records of *C. durissus* in forest zones (e.g. Beebe 1946) are all of occasional specimens from ecotonal zones close to established populations in open formations. Kartabo (6°23′N, 58°41′W), the site of Beebe's records, is situated at the edge of the documented distribution of *C. durissus* in Guyana (Campbell & Lamar 2004). Numerous intensive herpetofaunal surveys in many parts of the Amazon and adjacent moist forests, including many different forest types, have consistently failed to locate *C. durissus* in rainforest areas (e.g. Duellman 1978; Dixon & Soini 1986; Cunha & Nascimento 1993; Martins & Oliveira 1998), including in other parts of Guyana (Donnelly *et al*. 2005), and no established moist forest populations are known (Campbell & Lamar 2004). On the other hand, *C. durissus* has proven quick to occupy anthropogenically deforested areas in tropical South America (Sazima & Haddad 1992; Melgarejo & Aguiar 1995; Marques *et al*. 1998; Antunes 2003). Altogether, this suggests that *C. durissus* is a species that is unable to persist in a wide range of moist forest types.

We reject the suggestion that *C. durissus* may have occupied rainforest formations in the past as entirely unsupported. Apart from the absence of forest-dwelling populations at present, we also note that no other species of *Crotalus* occupies tropical rainforests (Campbell & Lamar 2004). Indeed, the closest relatives of *C. durissus*, such as *Crotalus molossus* and *Crotalus basiliscus*, occupy highly seasonal or xeric formations (Campbell & Lamar 2004), and the ancestral habitat for rattlesnakes is most likely to have been upland pine–oak forest (Place & Abramson 2004), a much more open formation than any Amazonian rainforest. This makes an assumption of Pleistocene rainforest occupancy by *C. durissus* highly unparsimonious.

Gosling & Bush (2005) suggest several alternative scenarios for the present-day distribution of *C. durissus*. They back these scenarios up with late Pleistocene palynological information and climatic models for the Last Glacial Maximum. The suggestion that the forests of eastern Amazonia, which surround the isolated Santarém population of *C. durissus*, may have been particularly susceptible to opening up as a result of reduced moisture during the Pleistocene is precisely the kind of scenario our data support: it clearly implies the isolation of the Guyanan rainforests from those of the western Amazon Basin, i.e. rainforest fragmentation, perhaps as illustrated by Hooghiemstra & van der Hammen (1998; Fig. 3).

However, in any case, we re-emphasize that our data on *C. durissus* suggest that forest fragmentation occurred in the Middle Pleistocene, and thus provide no information on late Pleistocene events. Published palynological data have increasingly been interpreted as contradicting extensive

Correspondence: Dr. Wolfgang Wüster, Fax: +44 1248 371644; E-mail: w.wuster@bangor.ac.uk

rainforest fragmentation in the Late Pleistocene (Colinvaux *et al*. 1996, 2001; Haberle & Maslin 1999; Kastner & Goñi 2003; Bush *et al*. 2004), but pollen records from the Early and Middle Pleistocene are lacking. There is therefore no palynological evidence to reject a hypothesis of rainforest fragmentation in the Middle or Early Pleistocene.

The precise nature and extent of this fragmentation remain to be ascertained: our data do not necessarily call for the same extent of rainforest fragmentation as the early formulations of the refugia hypothesis (Haffer 1969), and neither do they predict to what extent any intervening vegetation would have consisted of deciduous forests (Prado & Gibbs 1993), tree savannahs (e.g. Rossetti *et al*. 2004), savannah–forest mosaics (Webb & Rancy 1996) or true savannahs (Haffer 1969). All of these provide suitable habitat for *C. durissus*, and all are inconsistent with the view that the Amazon Basin remained cloaked in rainforest throughout the Pleistocene (e.g. Colinvaux *et al*. 2000, 2001; Bush *et al*. 2004).

Lastly, the alternative scenarios suggested by Gosling & Bush (2005) to account for the present-day distribution of *C. durissus* are to a large extent just-so stories based on speculation rather than data. In contrast, our hypothesis of mid-Pleistocene forest fragmentation generated on the basis of the *C. durissus* data makes clear, testable predictions of patterns that we may expect to see in other nonrainforest organisms distributed on both sides of the Amazon Basin. The very similar findings of Eberhard & Bermingham (2004) in *Amazona ochrocephala* and the existence of multiple open-formation plant species distributed on different sides of the Amazonian evergreen forests, including both north and south of the Amazon Basin (Prado & Gibbs 1993; Pennington *et al*. 2000, 2004), encourage us in our belief that intraspecific phylogeographic studies of nonrainforest organisms, complementing the interspecific approach adopted by Pennington *et al*. (2004), have much to contribute to the debate about the history of the New World tropics. We thus hope that our study of the phylogeography of *C. durissus* will stimulate further studies along similar lines to test for the existence of common patterns that may reveal common causes.

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