

Into the canyons: The phylogeography of the Malagasy frogs *Mantella expectata* and *Scaphiophryne gottlebei* in the arid Isalo Massif, and its significance for conservation (Amphibia: Mantellidae and Microhylidae)

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Abstract

Scaphiophryne gottlebei and *Mantella expectata* are two endemic and threatened frog species that live syntopically in the arid Isalo Massif in southern Madagascar. They share large parts of their distribution areas but differ in their natural history. *Scaphiophryne gottlebei* is more often found in canyons, while *M. expectata* prefers open habitats. Using samples from their known distribution areas, we investigated the genetic variability of these species by analyzing an approximately 600 base-pair fragment of the mitochondrial cytochrome *b* gene. Both species include a few widespread and common haplotypes as well as a number of other, geographically restricted ones. However, *M. expectata* exhibits more geographic substructure than *S. gottlebei*, in which one main haplotype represents individuals from various localities across the largest part of the distribution range. Comparing populations inside and outside of the Parc National de l'Isalo showed that the park does not harbour the bulk of the overall genetic diversity of the two species. These results emphasize the importance of so far unprotected habitats for the conservation of genetic variation in the endemic fauna of the Isalo region and of Madagascar in general.

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Keywords: *Scaphiophryne gottlebei*; *Mantella expectata*; Cytochrome *b*; Madagascar; Conservation; Gene flow

Introduction

Madagascar is renowned for its unique biota (Goodman and Benstead 2003), which are threatened by habitat destruction and degradation (Myers et al. 2000). Recent zoological studies integrating intensive field surveys and the application of molecular methods have revealed an astonishing degree of microendemism within the

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island, with a few widespread species and many others that are restricted to smaller, sometimes very small ranges. Various hypotheses have been proposed to explain this phenomenon, e.g. isolation within mountain refuges (Raxworthy and Nussbaum 1995), rivers as barriers to gene flow (Pastorini et al. 2003; Louis et al. 2006) or isolation in river drainages (Wilmé et al. 2006). Microendemism presents particular challenges to conservation strategies, which require adequate and simultaneous consideration of a variety of taxa to be representative (Kremen et al. 2008).

While the rainforest of eastern Madagascar is known for its richness in amphibian diversity, comparatively little attention has been paid to the arid areas of Madagascar. Recent analyses have shown that some of the latter are of paramount relevance to the conservation of amphibians (Andreone et al. 2005a). One of them is the Isalo Massif in south-western Madagascar, a huge mass of rocky sandstone crossed by numerous canyons of various length, width and depth (ANGAP 2003; Mercurio et al. 2008) that harbours a comparatively large number of endemic species of amphibians and reptiles (Andreone et al. 2006; Mercurio et al. 2008). Part of the Massif is currently included in the network of protected areas of Madagascar, in the form of the Isalo National Park, one of the country's most important tourist destinations (ANGAP 2003). Most of the natural habitats within the park's boundaries can be considered as relatively safe at present, mainly due to control by park guides and to the fact that the inner parts of the park are difficult to access except by several days of walking. However, human population pressures (e.g. activities related to tourism, land management and sapphire mining) are threatening the areas outside of the park (Duffy 2006).

The outline of Isalo National Park (INP) cannot be considered as a barrier to gene flow, as it largely constitutes an arbitrary, legal border rather than a natural one. Outside of the INP, collecting animals for the pet trade is allowed and habitat degradation is higher, but even inside, close to the borders, there is little control by the authorities, resulting in considerable numbers of illegal fires in the lowlands and illegal wood exploitation in the canyons. For conservation purposes it is therefore relevant to assess which proportion of the genetic diversity of locally endemic species is restricted to the area outside of the park.

Among the 21 species of amphibians found at Isalo (Mercurio et al. 2008), five are currently classified as “endangered” according to IUCN criteria (IUCN 2008) among which: *Scaphiophryne gottlebei* Busse & Böhme, 1992 and *Mantella expectata* Busse & Böhme, 1992. Both species have been discovered relatively recently (Busse and Böhme 1992), and are likely to be affected by similar threats such as the continuous decline of suitable habitat and overcollection for the pet trade due to their peculiar colouration (Andreone et al. 2005a). The two species are

also included in Appendix II of the Convention on the International Trade in Endangered Species (CITES).

Scaphiophryne gottlebei is a mainly nocturnal and fossorial microhylid toad, occurs mainly in rocky pools deep inside the canyons (Mercurio and Andreone 2006), and shows highly seasonal breeding behaviour (Andreone et al. 2006). Because its description was based on specimens supplied by local collectors, the precise distribution range of this species has long remained unknown. Detailed field data have become available only recently, along with new populations discovered mainly in the northeast of the Isalo region (Andreone et al. 2005b).

Mantella expectata is a colourful diurnal frog with alkaloid toxins in its skin (Daly et al. 1996; Vences et al. 1999). In contrast to *S. gottlebei*, individuals of *M. expectata* are only rarely found in deep canyons. These frogs prefer open, sun-exposed areas near the canyons, where temporary small water pools are available (Andreone et al. 2005b, 2006; Mercurio and Andreone 2006; Mercurio et al. 2008). At some sites *M. expectata* occurs in close proximity to, or even in syntopy with, the phylogenetically closely related *M. betsileo* Grandidier, 1872 (Rabemananjara et al. 2007). Although hybridization between these two species has not been documented (Rabemananjara et al. 2007), specimens with apparently intermediate chromatic traits have been observed (Mercurio and Andreone 2006).

Due to the more restricted microhabitat preferences of *S. gottlebei*, its populations can be expected to be more isolated and fragmented than those of *M. expectata*. This could result in more geographically structured genetic variation in *S. gottlebei*. Furthermore, since most populations of *S. gottlebei* had been found in the northern part of the Isalo Massif, together with isolated populations of *M. expectata* with a peculiar reddish colouration, we hypothesized that the geomorphology of the Isalo Massif could have influenced the distribution of these two frog species.

Here we analyse the population-genetic structure of these two microendemic and codistributed frog species as reflected by DNA sequences of a fragment of the mitochondrial cytochrome *b* gene. We test (1) whether *Scaphiophryne gottlebei* and *Mantella expectata* differ in genetic population substructure, and (2) whether the protected area (Isalo National Park) harbours the bulk of the respective genetic variation in these two threatened species or whether other yet unprotected sites are equally or more important for their conservation.

Material and methods

Sampling localities and tissue samples

We sampled 104 individuals of *S. gottlebei* from 14 different localities, and 155 specimens of *M. expectata*

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