Chapter 4. Amphibian conservation in Madagascar: old and novel threats for a peculiar fauna


Franco Andreone
Museo Regionale di Scienze Naturali


Angus I. Carpenter
University of Cumbria


Angelica Crottini
University of Porto


Neil D'Cruze
World Animal Protection

White N. J. (eds) Defining and Defeating the Intolerable Burden of Malaria III: Progress and Perspectives: Supplement to Volume 77(6) of American Journal of Tropical Medicine and Hygiene. Northbrook (IL): American Society of Tropical Medicine and Hygiene; 2007 Dec. Available from: *http://www.ncbi.nlm.nih.gov/books/NBK1724/*.
Schneider M. F., Buramuge V. A., Aliasse L. & Serfontein F. 2005. Checklist and centres of vertebrate diversity in Mozambique. Forestry Department (DEF), Eduardo Mondlane University, Maputo, Mozambique.
Schulze R. E. 1997. South African atlas of agrohydrology and climatology: Contribution towards a final report to the Water Research Commission on Project 492: Modelling impacts of the agricultural environment on water resources: TT82-96, Water Research Commission.
Schwann A., Adams M. & Dawood A. 2013. Critically endangered frogs find safe haven at the National Zoo. NZG eNewsletter 28. Available online: *www.nzg.ac.za/newsletter/issues/28/index.php*. Downloaded on 11 April 2014.
Stewart M. M. 1967. Amphibians of Malawi. State University of New York Press.
Sullivan K. B. & Spence K. M. 2003. Effects of sublethal concentrations of atrazine and nitrate on metamorphosis of the African clawed frog. Environmental Toxicology and Chemistry 22: 627–635.
Tarrant J. 2014. The EWT's threatened amphibian programme (TAP): Amathole Toad Conservation Project. Endangered Wildlife Trust.
Tarrant J. & Armstrong A. J. 2013a. Biodiversity management plan for Pickersgill's reed frog: Background information for stakeholders workshop. Endangered Wildlife Trust, South Africa, 16 pp.
Tarrant J. & Armstrong A. J. 2013b. Using predictive modelling to guide the conservation of a critically endangered wetland amphibian. Journal for Nature Conservation 21: 369–381.
Tarrant J. & Cunningham M. J. 2011. Rediscovery of the elusive Amatola Toad *Vandjikophrynus amatolicus*: twice seen in twenty-six years. African Herp News 55: 1–6.
Tarrant J., Cunningham M. J. & Du Preez L. H. 2008. Maluti mystery: A systematic review of *Amietia vertebralis* (Hewitt, 1927) and *Strongylopus hymenopus* (Boulenger, 1920) (Anura: Pyxicephalidae). Zootaxa 1962: 33–48.
Telford N. S., Channing A. & Measey J. 2019. Origin of invasive populations of the Guttural Toad (*Sclerophrys gutturalis*) on Reunion and Mauritius Islands and in Constantia, South Africa. Herpetological Conservation and Biology 14: 380–392.
Tolley K. A., Davies S. J. & Chown S. L. 2007. Deconstructing a controversial local range expansion: conservation biogeography of the Painted Reed Frog (*Hyperolius marmoratus*) in South Africa. Diversity and Distributions 14: 400–411.
Turner A. A. & Channing A. 2008. A new species of *Arthroleptella* Hewitt, 1926 (Anura: Pyxicephalidae) from the Klein Swartberg Mountain, Caledon, South Africa. African Journal of Herpetology 57: 1–12.
Turner A. A. & Channing A. 2017. Three new species of *Arthroleptella* Hewitt, 1926 (Anura: Pyxicephalidae) from the Cape Fold Mountains, South Africa. African Journal of Herpetology 66: 53–78.
Turner A. A., De Villiers A. L., Dawood A. & Channing A. 2004. A new species of *Arthroleptella* Hewitt, 1926 (Anura: Ranidae) from the Groot Winterhoek Mountains of the Western Cape Province, South Africa. African Journal of Herpetology 53: 1–12.
USAID 2008. 118/119 Biodiversity and tropical forest assessment for Angola. Report by Chemonics International Inc.
USGS 2018. North American Amphibian Monitoring Program (NAAMP). United States Geological Survey *https://www.usgs.gov/centers/pwrc/science/north-american-amphibian-monitoring-program*.
Van den Berg H., Manuweera G. & Konradsen, F. 2017. Global trends in the production and use of DDT for control of malaria and other vector-borne disease. Malaria Journal 16: 401.
Van Wyk A. E. 1994. Indian Ocean Coastal Belt: CPD Site AF59. Maputaland-Pondoland region, South Africa, Swaziland and Moçambique. *In*: Davis S. D, Heywood V. H. & Hamilton A. C. (eds) Centres of plant diversity: a guide and strategy for their conservation. Volume 1 Europe, Africa, South West Asia and the Middle East. Cambridge: IUCN Publications Unit, pp. 227–235.
Visser I. 2011. An *ex-situ* conservation and research project for Pickersgill's Reed Frog. AARK Newsletter 16: 14.
Weldon C., Du Preez L. H., Hyatt A. D., Muller R. & Speare R. 2004. Origin of the amphibian chytrid fungus. Emerging Infectious Diseases 10: 2100–2105.
Williamson S., Ball A. & Pretty J. 2008. Trends in pesticide use and drivers for safer pest management in four African countries. Crop Protection 27: 1327–1334.
Yetman C. A. & Ferguson W. H. 2011. Spawning and non-breeding activity of adult giant bullfrogs (*Pyxicephalus adspersus*). African Journal of Herpetology 60: 13–29.
Zielinski S. 2014. Amphibian diseases flow through animal trade. *https://www.sciencenews.org/blog/wild-things/amphibian-diseases-flow-through-animal-trade*.

Chapter 4.

Amphibian Conservation in Madagascar: Old and Novel Threats to a Peculiar Fauna

Franco Andreone, Angus I. Carpenter, Angelica Crottini, Neil D'Cruze, Nicolas Dubos, Devin Edmonds, Gerardo Garcia, Jennifer Luedtke, Steven Megson, Falitiana C. E. Rabemananjara, J. Christian Randrianantoandro, Roma Randrianavelona, Janine Robinson, Denis Vallan, and Gonçalo M. Rosa

Abbreviations and acronyms used in the text and references

ACAP	Amphibian Conservation Action Plan
ACSAM	A Conservation Strategy for the Amphibians of Madagascar
ASG	Amphibian Specialist Group
a.s.l.	above sea level
Bd	*Batrachochytrium dendrobatidis*
BIOPAT	Patenschaften für biologische Vielfalt/Patrons for Biodiversity
CEC	Chytrid Emergency Cell
CEPF	Critical Ecosystem Partnership Fund
CITES	Convention on International Trade in Endangered Species of Wild Fauna and Flora
COBA	Communauté Locale de Base/Grass-Roots Communities
DNA	deoxyribonucleic acid
EAZA	European Association of Zoos and Aquaria
EUR	Euro
GAA	Global Amphibian Assessment
ICTE-MICET	Institute for the Conservation of Tropical Environment/Malagasy Institut pour la Conservation des Ecosystèmes Tropicaux
IUCN	International Union for Conservation of Nature
LAG	line of arrested growth
McAP	*Mantella cowanii* Action Plan
MGA	Malagasy Ariary
NGO	Non Governmental Organization
NSAP	New Sahonagasy Action Plan
PVA	Population Viability Analysis
SAVA	districts of Sambava, Antalaha, Vohémar, and Andapa
SSC	Species Survival Commission
UNEP-WCMC	United Nations Environment Programme-World Conservation Monitoring Centre
UNESCO	United Nations Educational, Scientific and Cultural Organization
UNSD	United Nations Statistics Division
USD	United States dollar
WAZA	World Association of Zoos and Aquariums

I. Madagascar: An Overview of Geography and of Threats to Biodiversity

The island of Madagascar lies in the western Indian Ocean off the southern coast of Africa. It is separated from continental Africa by the deep Mozambique Channel and covering 587 000 km^2, Madagascar is considered the 4th largest island in the world; the three larger islands are Greenland, New Guinea, and Borneo, which have been respectively and repeatedly in contact with North America, Australia and Tasmania, and with Java, Sumatra, and the south-eastern Asian mainland (Mitchell 2019). Madagascar is seen as the world's largest persistent continental island, since its separation from Africa dates approximately from 160–130 million years ago, and from India 80 million years ago (Ali & Aitchison 2008). This is reflected in the extremely high rates of endemism, with more than 90% of Madagascar's vertebrate species living exclusively in its forests and woodlands (Dufils 2003; Crottini *et al.* 2012; Brown *et al.* 2014; Ganzhorn *et al.* 2014). This unparalleled endemism at various taxonomic levels, thus, makes conservation of Madagascar's biota a top global priority (Brooks *et al.* 2006) and is why people have ranked Madagascar as the "8th Continent," a "micro-continent," and an "island continent" (Tyson 2000; de Wit 2003).

A mountainous chain runs from the North to the South with three massifs at an elevation higher than 2 600 m a.s.l.: Tsaratanana in the North (Maromakotro peak at 2 876 m), the Ankaratra Massif in the Centre (Tsiafajavona at 2 643 m) and the huge granitic Andringitra Massif (Pic Boby at 2 658 m). In terms of ecosystems, Madagascar is characterized by the presence of a rainforest belt running along its eastern part, the Sambirano in the North-West, and the isolated Montagne d'Ambre in the North. A wide plateau encompasses the central highlands and part of the South-West. The steep eastern escarpment is cut by several streams and rivers that collectively carry a huge flow of water; these divide the original rainforest belt into several basins that act as biogeographic barriers (Vences *et al.* 2009).

Recent studies suggest that colonization of Madagascar by humans possibly dates to the Early Holocene, although the timing of settlement remains a key topic of debate in archaeology (Douglass *et al.* 2019). Beside this, the island experienced a chain of repeated extinctions, mainly of its megafauna, including large lemurs and other giant endemics, such as the elephant birds: *Aepyornis*, *Mullerornis*, and *Vorombe*. The extinction of Madagascar's megafauna, likely driven by human pressure, led to alteration of habitats and ecosystems and to the loss of pristine habitats, in particular forests (Crowley *et al.* 2017). Madagascar has since suffered environmental degradation over a significant part of its land-mass. Many conservation threats are still currently affecting the island, ranging from deforestation, to landgrabbing, to pollution, and to overexploitation of resources. In particular, Madagascar is well-known for its dramatic rate of deforestation (Harper *et al.* 2007) (see the section "Ongoing threats to Madagascar's amphibians").

The loss in biodiversity and the degradation of natural habitats represents a major threat that is strongly associated with increasing poverty. With over 26 million people and a mean GDP of 1–2 euros per day, Madagascar is one of the poorest countries in the world (International Monetary Fund 2019). Moreover, at least 70% of the population is dependent on resources derived from agriculture and there has been an increase in social instability. Accordingly, Madagascar has suffered a reoccurrence of epidemic diseases, such as the plague (Shinya *et al.* 2017; Ramasindrazana *et al.* 2020), measles (Nimpa *et al.* 2020), and, more recently, SARS-CoV-2 (Evans *et al.* 2020). The projection of population growth for 2100 is also particularly worrying, since it estimates, with a fertility rate of 4.89, a population of 100 million people, which appears to be almost unsustainable taking into account the loss of forest coverage and fertile ground (Vollset *et al.* 2020).

Rainforests originally were present and continuous on the eastern coast, where rainfall is intense, reaching up to 4000 mm per year. The eastern forest belt is now heavily fragmented due to human activity (Harper *et al.* 2007). Although there is debate whether the Central Highlands originally were dominated by montane forests or by a mosaic of grasslands, savannahs, and forests (Solofondranohatra *et al.* 2018), the anthropogenic pressure of recent decades is highly noticeable, with a trail of heavy deforestation and erosion on the now savannah-dominated landscape. A similar scenario of alteration of habitats has been observed in the western forests and in the mangroves of the West and South, which largely have been fragmented and burned (Vieilledent *et al.* 2018).

The general trend of degradation of floral and faunal biodiversity, is caused primarily by destructive practices, such as the clearing of natural habitats and overexploitation of natural resources (see section "Ongoing threats to Madagascar's amphibians").The unsustainable collection of natural products (minerals, plants, animals) represents a further threat for Malagasy biodiversity, together with climatic change and the introduction of alien invasive species (Andreone *et al.* 2015).

In particular, forests are being reduced in size and becoming more isolated from each other. Where forests are lost, the soils erode, which perpetuates loss of biodiversity. A particular problem is caused by slash-and-burn agriculture, called "tavy"(Styger *et al.* 2007). This traditional agricultural method is mostly used for converting forests into rice fields and/or to generate space for zebu pasture and the production of charcoal. Typically, the forest is cut, burned, and planted with rice or other crops. After 1–2 years of production the field is left fallow for 4–6 years before the process is repeated. After two or three such cycles, the soil is deprived of most nutrients and the land usually is colonized by scrub vegetation and alien grasses. Logging for timber is also prevalent, especially on the eastern coast, where precious woods still exist. Large quantities of Malagasy rosewood (genus *Dalbergia*) have been logged illegally and exported at an increasing rate over recent decades (Barrett *et al.* 2010). This takes place almost entirely in protected areas, such as Masoala and Marojejy National Parks, which comprise part of the Atsinanana UNESCO World Heritage Site in the SAVA region (including the districts of Sambava, Antalaha, Vohémar, and Andapa) in north-eastern Madagascar (Schuurman & Lowry 2009; Barrett *et al.* 2010; Andreone *et al.* 2018b).

II. A Land of Astonishing Biodiversity

Madagascar is a land featuring an unparalleled level of biodiversity (Meyers *et al.* 2000; de Wit 2003; Wilmé *et al.* 2006; Ganzhorn *et al.* 2014). Its fauna and flora evolved largely in isolation, and most of its extant fauna colonised the island about 60–70 million years ago, after the island had separated from all other Gondwanian landmasses. The pioneer animals that reached Madagascar and succeeded in adapting to this new environment arrived by rafting over the ocean (Vences *et al.* 2003b; Crottini *et al.* 2012).

With over 100 species, lemurs are Madagascar's most iconic fauna (Mittermeier *et al.* 2010). Yet, the island is also home to an exceptional diversity of reptiles with more than 430 described species (Uetz *et al.* 2020), many of which (at least 40%) are con-

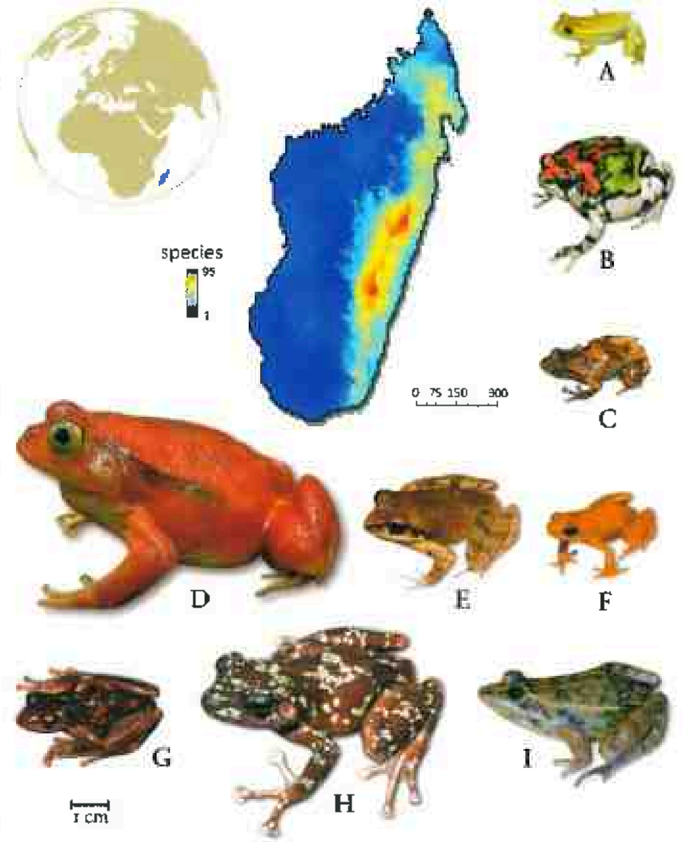

Fig. 4.1: Spatial amphibian diversity patterns in Madagascar and representative species. The map shows the species richness based on the distribution of 325 amphibian species; scale ranges from low (blue) to high (red) number of species per hexagon. Adapted from Brown *et al.* (2016). Representative amphibians:
(A) *Heterixalus luteostriatus*, (Hyperoliidae), Central High Plateau; (B) *Scaphiophryne gottlebei*, (Microhylidae, Scaphiophryninae), Isalo Massif; (C) *Anodonthyla vallani*, (Microhylidae, Cophylinae), Ambohitantely Forest, Central High Plateau; (D) *Dyscophus antongilii* (Microhylidae, Dyscophinae), NE Madagascar; (E) *Aglyptodactylus* sp. (Mantellidae, Laliostominae), Makay Massif; (F) *Mantella aurantiaca* (Mantellidae, Mantellinae), Andasibe-Moramanga area; (G) *Boophis williamsi* (Mantellidae, Boophinae), Ankaratra Massif; (H) *Tsingymantis antitra* (Mantellidae, Mantellinae), Ankarana Massif; (I) *Ptychadena* sp. (Ptychadenidae), all Madagascar.

(All photos by F. Andreone, except (H) by F. Glaw. Graphic elaboration by S.C. Andreone, G. Prono, and G.M. Rosa)

sidered threatened (Jenkins *et al.* 2014). In the past few decades, amphibians have also generated increasing interest, given their extraordinary diversity and endemicity (Andreone 1991). The native amphibian fauna consists of five independent anuran radiations (caudates and gymnophiones are absent) belonging to four families (Fig. 4.1): Hyperoliidae, Mantellidae, Microhylidae, and Ptychadenidae. The Malagasy amphibian fauna is featured by an astonishing diversity, especially the mantellids and the cophyline + scaphiophrynine microhylid lineages (Andreone 2003a, b; Glaw & Vences 2007a; Vieites *et al.* 2009; Perl *et al.* 2014; Crottini *et al.* 2020). Large-scale taxonomic inventories conducted since the 1990s have led to an increase from 133 to over 370 described species and several (about 200) candidate species awaiting formal description. This is largely due to the exploration of new areas and the application of more efficient techniques, such as the combination of morphology, bioacoustics, and molecular genetics. Undescribed diversity may have an important impact on understanding the spatial patterns of endemic radiations on the island, but objective estimates of species' numbers are not yet available (AmphibiaWeb 2021).

The family Hyperoliidae sees its greatest diversification in mainland Africa, but is also represented in the Seychelles Island with one further species, *Tachycnemis seychellensis* (see Chapter 5). In Madagascar, all the 11 recognised species belong to the endemic genus *Heterixalus* (Wollenberg *et al.* 2007; Gehring *et al.* 2012). The family Mantellidae, endemic to Madagascar and to the Comoran island of Mayotte (Glaw *et al.* 2019; Chapter 5), is the largest lineage of frogs within Madagascar, both in terms of species richness and diversity in morphology, ecology, and reproductive modes (Wollenberg *et al.* 2011). This family comprises three subfamilies with diverse ecological and morphological differentiation: Mantellinae, Boophinae, and Laliostominae. Mantellinae has 143 Malagasy species and two from Mayotte (numbers from Amphibia-Web 2021, updated on 15 March 2021) which are represented by many scansorial, semi-aquatic, and arboreal species, which lay eggs terrestrially. They include the genera *Blommersia, Boehmantis, Gephyromantis, Guibemantis, Mantella, Mantidactylus, Spinomantis, Tsingymantis,* and *Wakea*. The subfamily Boophinae includes the mainly arboreal treefrog-like genus *Boophis* (78 Malagasy species and one from Mayotte), while the subfamily Laliostominae (seven species) is represented by the genera *Laliostoma* and *Aglyptodactylus*, both of which are terrestrial but breed in stagnant, temporary bodies of water. The family Microhylidae includes two independent lineages: the subfamily Dyscophinae (three species), related to Asian microhylids, and the subfamilies Scaphiophryninae and Cophylinae (12 and 114 species, respectively) although these still do not have fully resolved relationships (Van der Meijden *et al.* 2007; Wollenberg *et al.* 2008; Scherz *et al.* 2016, 2017). The family Ptychadenidae is present with three mitochondrial lineages likely corresponding to three candidate species (Vences *et al.* 2004; Zimkus *et al.* 2017).

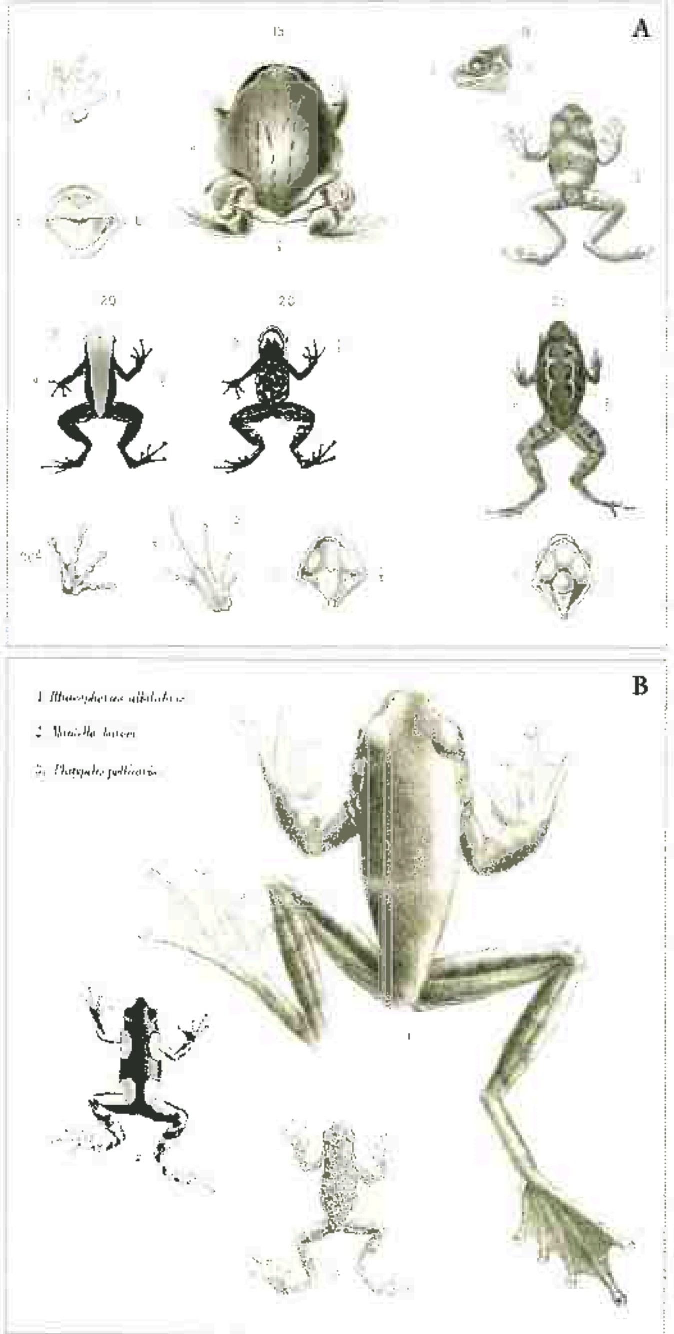

Fig. 4.2: Ancient illustrations from O. Boettger and G.A. Boulenger, depicting some Malagasy frogs. (A) *Rhombophryne testudo* (Boettger 1881, plate IV, fig. 15), *Cophyla phyllodactyla, Mantella ebenaui* (originally described as *Dendrobates Ebenaui* Boettger, 1880), and *Stumpffia psologlossa* (Boettger 1881, plate V, figs. 19–21); (B) *Boophis albilabris* (originally described as *Rhacophorus albilabris* Boulenger, 1888), *Mantella baroni*, and *Platypelis pollicaris* (from Boulenger 1888, plate VI, figs. 1–3).

Two anuran species were introduced by humans. The Indian Bullfrog (*Hoplobatrachus tigerinus*) originated from south-eastern Asia and was likely introduced into Madagascar for the food trade prior to the mid 1900s (Guibé 1953; Penny *et al.* 2017; Mohanty *et al.* 2021). The other is the Asian Toad (*Duttaphrynus melanostictus*), which was introduced around 2010 in the Toamasina (Tamatave) area and is undergoing rapid expansion (Andreone *et al.* 2014c; McClelland *et al.* 2015; Licata *et al.* 2019, 2020).

III. Amphibian Research in Madagascar

Similar to other hyper-rich biodiversity hotspots, such as Brazil or Colombia (Myers *et al.* 2000), inventory surveys leading to species' descriptions and systematics have dominated the research conducted in Madagascar over the past three decades. Fulfilling the scientific documentation of Madagascar's endemic taxa is tightly linked to the conservation of biodiversity and remains one of the most important challenges of forthcoming decades. Particularly important is obtaining data on species-rich groups, surveying poorly documented sites, and clarifying taxonomic relationships (Andriamialisoa & Langrand 2003).

Madagascar has a four-century history of biological exploration that brought about the current extensive (although still incomplete) discovery of its rich biodiversity. With a few exceptions, current knowledge of amphibian species diversity began relatively late. Alfred Grandidier (1836–1921) played a key role in the early natural exploration of Madagascar. He wrote one of the most monumental publications on the natural history of the island: "Histoire physique, naturelle, politique de Madagascar;" it was initially planned to be a 60-volume encyclopedia. His pioneering work on the classification and systematics of Malagasy taxa and his contribution to the knowledge of the island's natural history is unparalleled and has linked his name forever to the country.
Later, George A. Boulenger and Oskar Boettger became leading figures in the study of the amphibians of Madagascar, and between the two of them about 100 species of Malagasy amphibians were described (Boettger 1881; Boulenger 1888, 1889) (Fig. 4.2). Following these researchers, numerous others (e.g., Édouard R. Brygoo, Charles P. Blanc, Rose M.A. Blommers-Schlösser and Jean Guibé to list a few) focused their attention on am-

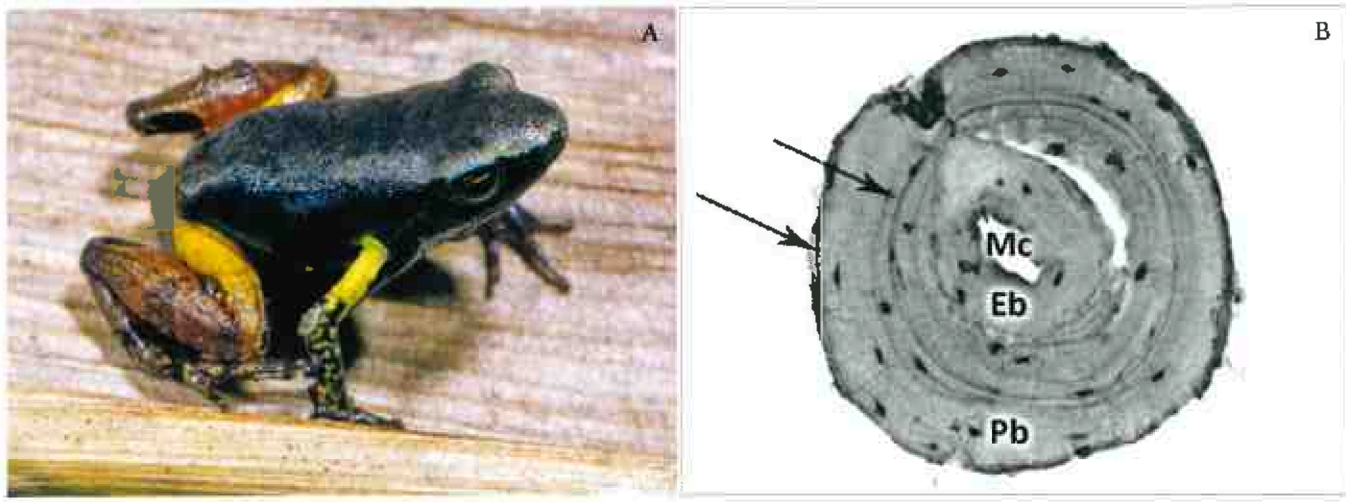

Fig. 4.3: Age estimation in *Mantella bernhardi*. (A) Adult individual; (B) Phalangeal cross section of the individual showing two lines of arrested growth (LAGs: arrows) (adapted from Andreone *et al.* 2011). Abbreviations: Eb, endosteal bone; Mc, medullar cavity; Pb, periosteal bone.
(Photographs by F. Andreone and G. Tessa)

phibians, but it was only in 1978 that Guibé published the first monograph specifically on the amphibians of Madagascar (Guibé 1978). Since the 1980's, a number of publications have increased our understanding of Malagasy amphibians (Andriamialisoa & Langrand 2003). Among these we quote the taxonomic revisions by Blommers-Schlösser (1979a, b, 1981) and two important reference works on Malagasy amphibians (Blommers-Schlösser & Blanc 1991, 1993).

After these contributions, the rate of species descriptions has increased exponentially and certainly is higher than during any other period of scientific exploration of the island (Glaw & Vences 2003; Vences *et al.* 2008a, b). As a result, many new species and taxonomic revisions have been published (e.g., Glaw & Vences 2006; Glaw *et al.* 2010; Andreone 2013; Andreone *et al.* 2010; Vences *et al.* 2010a, b; Crottini *et al.* 2011a, 2020; Lehtinen *et al.* 2011; Scherz *et al.* 2016, 2017; Rakotoarison *et al.* 2017), and even more are known but are awaiting formal description (Perl *et al.* 2014; Hutter *et al.* 2018).

Fig. 4.4: Spatial ecology study in the Rainbow Frog (*Scaphiophryne gottlebei*) in the Isalo Massif. (A) Radio-tracking individuals at a canyon entrance; (B) An adult with external radio attached; (C) A radio-tagged individual hidden in a hole in the canyon wall. (Photographs by P. Eusebio Bergò and G. M. Rosa)

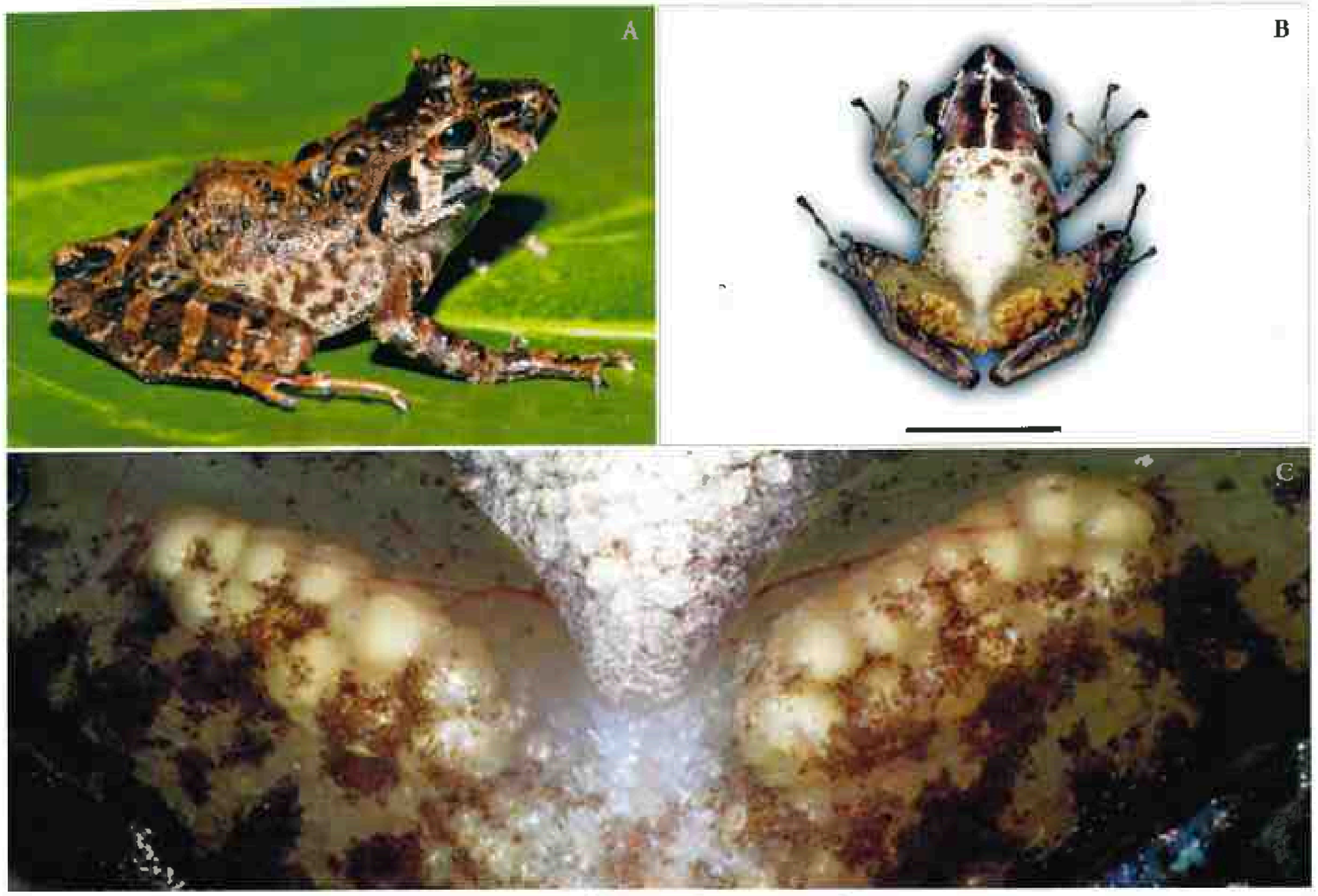

Fig. 4.5: Aspect of femoral glands in an adult male of *Gephyromantis moseri*. (A) Lateral view; (B) Ventral view; (C) Close up of the femoral glands that produce volatile amphibian pheromones most probably used for chemical communication. (Photographs by G. M. Rosa)

A crucial step was the publication of an extensive field guide, which facilitated a rapid identification of species in the field (Glaw & Vences 1994, 2007a). The most recent edition of this guide was published in Malagasy and distributed throughout the island to institutions and organizations involved in conservation and the management of natural resources (Glaw & Vences 2007a, b). In addition to these major works, numerous herpetological research teams have recently carried out many field missions throughout Madagascar (e.g., Andreone 1994; Andreone & Randriamahazo 1997; Raxworthy & Nussbaum 1996a, b; Raxworthy *et al.* 1998; Nussbaum *et al.* 1999; Andreone *et al.* 2000; Vences *et al.* 2002; Mercurio *et al.* 2008; Bora *et al.* 2010; Gehring *et al.* 2010; Crottini *et al.* 2011b; Rosa *et al.* 2012; Cocca *et al.* 2018, 2020). These expeditions resulted in a nearly continuative description of new species and identification of others (Perl *et al.* 2014), leading to a more thorough understanding of the taxonomy and the distribution of the amphibians of Madagascar (Glaw & Vences 2007a; Brown *et al.* 2016). Additionally, to optimize the results of amphibian surveys, it was recommended that standardised field methods are used (Vences *et al.* 2008a, b). These should include: (a) publication of distributional data providing exact reference to at least one voucher specimen of each recorded species per locality; (b) preference for adult males as reference specimens, since they usually exhibit secondary sexual characters that are mostly diagnostic; (c) association of the best voucher reference, when possible, with the recorded vocalization(s); (d) documentation of colouration of live individuals by photographs; and (e) collection of a tissue sample to be used for genetic analysis.

To ensure a nearly complete inventory, the study of Malagasy amphibians should continue with the same intensity for at least another 10-20 years (Andriamialisoa & Langrand 2003; Glaw & Vences 2007a). In addition to the identification and description of new taxa, there has been increasing interest in amphibian ecology (e. g., Andreone *et al.* 2013a; Heinermann *et al.* 2015; Riemann *et al.* 2015; Dubos *et al.* 2020), natural history (e. g., Rosa *et al.* 2011; Rocha *et al.* 2012; Starnberger *et al.* 2013; Lam *et al.* 2020), and conservation (Andreone & Luiselli 2000; Vallan *et al.* 2004). Some remarkable examples include the study of the reproductive phenology of the tomato frog *Dyscophus antongilii* (Segev *et al.* 2012), as well as the regular monitoring of species at some sites, thereby providing valuable data on population dynamics and the status of disease of highly threatened regional endemics (Andreone *et al.* 2014a; Dubos *et al.* 2020). Using the skeletochronological method (Fig. 4.3), which takes into account the number of lines of arrested growth (LAGs) within long bones, it was also possible to estimate the age profile of several amphibian species (Guarino *et al.* 1998, 2010, 2019; Andreone *et al.* 2011; Tessa *et al.* 2011, 2017). Combining the age profile with activity patterns and dispersal abilities with genetic diversity and spatial ecology increased our knowledge of the natural history of *Dyscophus guineti* and *Scaphiophryne gottlebei* (Fig. 4.4), two of the most iconic species of Malagasy amphibians (Crottini *et al.* 2008; Andreone *et al.* 2013a; Andreone 2015; Orozco-Terwengel *et al.* 2013). Examining glandular secretions, Poth *et al.* (2012) demonstrated the emission of volatile pheromones by the femoral glands of mantelline frogs (Fig. 4.5), and the discovery of a modified olfactory anatomy in pheromone-emitting frogs suggests that there is an evolutionary connection in these structures (Nowack *et al.* 2017). In highly diverse species assemblages, chemical communication with these species-specific mixtures of compounds may constitute a hitherto underrated means of distinguishing conspecifics in close proximity.

Recently, morphological description of tadpoles of several species has increased the knowledge of their natural history and larval stages (e.g., Mercurio & Andreone 2006; Randrianiaina *et al.* 2009, 2011a, b; Schmidt *et al.* 2009; Grosjean *et al.* 2011). Analysis of tadpoles also enabled the identification of candidate species previously based solely on DNA sequences and larval morphology (Randrianiaina *et al.* 2012). Focusing on the study of larval communities, functional redundancy and low functional diversity has been found in larval amphibian assemblages from dry-forest (Glos *et al.* 2007a, b) and rainforest habitats (Strauss *et al.* 2010, 2013). Finally, larval behaviour and communication strategies have been observed and described, such as the definition of a new eco-morphological guild for the tadpole of *Scaphiophryne gottlebei*; the so-called "psammo-nektonic" tadpole of this species partially digs into the sandy substrate in bodies of water during diurnal hours only to emerge during the night to actively swim (Mercurio & Andreone 2006). Furthermore, tadpoles of the genus *Gephyromantis* have acoustic underwater signals that probably function during competitive feeding (Reeve *et al.* 2011).

The interest in amphibians has been accompanied by the emergence of a new generation of herpetologists who have invested a great deal of time and energy into the conservation of the island's frogs (Andreone *et al.* 2001). The "A Conservation Strategy for the Amphibians of Madagascar" (ACSAM) initiative represented a crucial step in the implementation at the national level of the Amphibian Conservation Action Plan (ACAP), a strategy put together during a meeting held in Washington, D. C. in September 2005 (Gascon *et al.* 2007; Wren *et al.* 2015). Madagascar's declination of the ACAP is known as the Sahonagasy Action Plan (the term "sahonagasy" is derived from the Malagasy language, meaning "Malagasy frogs") (Andreone & Randriamahazo 2008a, b; Andreone *et al.* 2012; 2016; Gascon *et al.* 2012). The Sahonagasy Action Plan provided the opportunity to prioritize actions and strategies needed to protect the unique amphibian fauna of Madagascar from the multiple threats that it is facing (see the section "Ongoing threats to Madagascar's amphibians"). Furthermore, it was to encourage a better standardization and coordination of future research into amphibians.The implementation of this initiative was supported by a CEPF (Critical Ecosystem Partnership Fund, *http://www.cepf.net*) grant obtained in 2015, and entitled "Building a future for Madagascar's amphibians." This grant provided important opportunities for collaboration and launched a new decade of initiatives for amphibian conservation.

Coordination of research activity has increased in the past two decades, fostering the reciprocal exchange of ideas, skills, results, and information (Andreone & Randriamahazo 2008a, b), and under these initiatives, amphibians now regularly are being considered in the identification of nationally important sites for conservation (Kremen *et al.* 2008).

IV. IUCN Red List and Amphibian Assessments for Madagascar

In 1994, a rigorous approach to determining the risk of extinction of all known species was introduced in conservation biology and has since become a world standard, the IUCN "Red List of Threatened Species" (IUCN 2019; see Chapter 6). Today, the IUCN Red List is widely recognised as the most comprehensive, objective, global approach for evaluating the conservation status of the world's biodiversity. The goal of the Red List is to provide information and analyses on the status, trends, and threats to species' survival in order to inform and catalyze action for conserving biodiversity (IUCN 2012, 2019).

Red List's assessments of species aim to determine the risk of extinction by cataloguing and highlighting 'threatened' species that face a higher risk of global extinction. Threatened species fall within the categories of Vulnerable, Endangered, and Critically Endangered. The Red List also includes information for species that are close to meeting the threatened thresholds, i.e., classed as Near Threatened. Those that are not of immediate conservation concern are classified as Least Concern, while species that cannot be evaluated because of insufficient information are classified as Data Deficient. Red List assessments result from the collaboration of the "International Union for Conservation of Nature" IUCN,

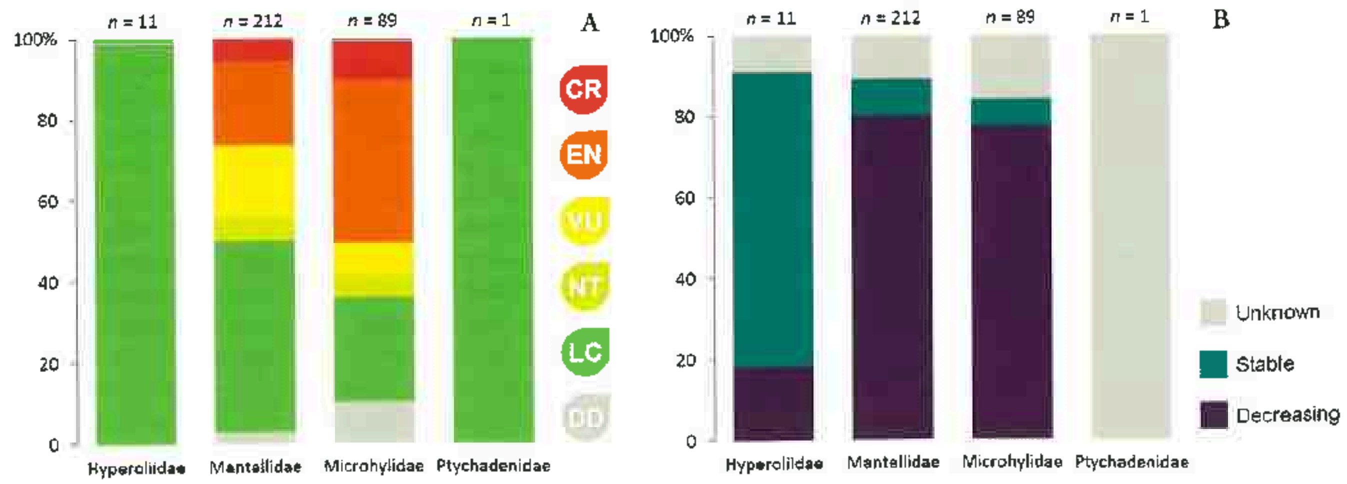

Fig. 4.6: Conservation status in Malagasy amphibians. (A) Proportion of amphibian species (listed by family) in the IUCN Red List categories (IUCN Red List assessment categories: CR, Critically Endangered; EN, Endangered; VU, Vulnerable; NT, Near Threatened; LC, Least Concern; DD, Data Deficient; NE, Not Evaluated). (B) Proportion of Malagasy amphibian species (by family) listed in the IUCN Red List by population trend.

the Global Species Program and the IUCN Species Survival Commission (SSC), to mobilize a network of scientists and partner organisations from across the world.

It was not until the 2004 "Global Amphibian Assessment" (GAA) that the first efforts to assess the conservation status of Malagasy amphibian species were made. This initial effort included the assessment of 218 described species and each was assigned a category of risk based on existing information (Stuart *et al.* 2004; Andreone *et al.* 2005, 2008a, b). In the ten years following this initial effort, a further 29 species were assessed, primarily as a result of the first ACSAM workshop. However, over the same time period 68 additional Malagasy amphibian species were described. As such, it became evident that more effort is required to match the rates of discovery and descriptions of species in Madagascar, with a total of over 370 native species currently listed for Madagascar at the time of finishing the redaction of this chapter (AmphibiaWeb 2021).

Following the ACSAM2 meeting held in 2014 (see details below), a concerted effort to update these assessments was initiated (Andreone *et al.* 2014c). The bulk of the work took place during 2014–2016, with external reviews and final consultations for a few species lasting into 2018. Of the known native species, 312 (88.1%) were assessed with 144 (40.6%) classified within a category of threat (Fig. 4.6A). This huge effort led to a decrease in the number and proportion of Data Deficient species, now as low as 3.7%, versus 19.7% in 2004 (Fig. 4.6A). This leaves 55 species described in 2017 and 2020 to be assessed for the first time during a third GAA initiative, which is set to begin after 2020. The overall IUCN assessment for the Afrotropical amphibians, including Malagasy species, is reported in Chapter 6.

With regards to population trends, only 33 native species (10%) (eight Hyperoliidae, 19 Mantellidae, and six Microhylidae) are considered to have stable populations, according to the amphibian assessments conducted thus far, while 241 species (70%) are considered to be decreasing (two Hyperoliidae, 170 Mantellidae, and 69 Microhylidae). The population trends of the 39 remaining assessed amphibian species (11%) are evaluated as "unknown" (one Hyperoliidae, 23 Mantellidae, 14 Microhylidae, and one Ptychadenidae) (Fig. 4.6B).

Assessing the species-rich amphibians of Madagascar is a challenging and intensive task, especially because we are still far from having a complete species-list and many species are still hidden and/or confused under the same taxonomic name. So far, more than 200 additional confirmed and unconfirmed candidate species have been proposed (Vieites *et al.* 2009; Perl *et al.* 2014). Despite the uncertainties surrounding this estimate, the ongoing discovery and description of new candidate species highlights the vast proportion of Madagascar's undescribed diversity. It also highlights the scale of the task for completing a comprehensive amphibian Red List assessment for the island.

Besides the substantial proportion of amphibian diversity still undescribed, the dynamic nature and fragility of the political and natural environments present significant challenges to Red List assessors. The increase in deforestation and illegal logging in the eastern rainforests, during recent political turbulence (Barrett *et al.* 2010; Innes 2010; Allnutt *et al.* 2013), the detection of a chytrid fungus (Bletz *et al.* 2015a, b) and the invasion of the Asian Toad (Andreone *et al.* 2014a; Kolby *et al.* 2014; Crottini *et al.* 2014a; Marshall *et al.* 2018; Licata *et al.* 2019, 2020) demonstrated that novel threats to the survival of the island's fauna can rapidly emerge.

Red List assessments have become a powerful tool for conservation by providing indications of the species that should be afforded prioritary conservation actions. Globally, amphibian populations are in decline and their associated extinctions are a well-publicised phenomenon (Stuart *et al.* 2004). To date, there have been no known modern amphibian extinctions in Madagascar (Andreone *et al.* 2008b). However, given the level of potential threats (see section "Ongoing threats to Madagascar's amphibians"), as well as climatic change, mining, and over-exploitation for trade (D'Cruze & Kumar 2011), regular assessments of amphibian conservation status will help to monitor the impacts of these threats and help prioritize conservation efforts. However, Red List assessors are confronted by major financial, labour-related, and time-related constraints, and additionally by the challenges presented by the high proportion of undescribed diversity and the dynamic nature of Madagascar's ecosystems. Finally, a comprehensive, accurate, regularly reviewed and updated assessment of the conservation status of the island's amphibians would provide a crucially important tool for conservation.

All described species have been confirmed in recent years. This would lead to the perception that, despite loss of habitat and other threats, the Malagasy amphibians were able to adapt to even small parcels of forest and other original habitats. The enormous number of still undescribed species, the fact that many of these are micro-endemics, combined with the fact that most of Madagascar's natural habitats have already disappeared, makes it very likely that many species went extinct unnoticed. This might be especially true for the Central Highlands, which nowadays are almost deprived of any primary forest cover, and where intense exploitation of natural habitats started several hundreds years ago; or the low elevation and littoral rainforests, which are now highly fragmented and under severe threat of total loss.

V. Ongoing Threats to Madagascar's Amphibians

A. Habitat loss and degradation

Settlements by humans marked the beginning of a great transformation during which forests began to shrink. Loss of forests first took place at a low level, caused mainly by shifting cultivation practiced by the colonizers from south-eastern Asia. Then, about the turn of the first millennium, zebus and other breeds of cattle were introduced from Africa and their interbreeding gave rise to the breed that is now commonly distributed across the island (Rege & Tawah 1999). This event kick-started the practice of burning forests and meadows to create pastures for cattle. By the end of the 16th century, apart from a few sparse remnants, the forests in the Central Highlands largely had disappeared (Gade 1996).

The extent to which Madagascar was covered by forest prior to colonization by humans is still the subject of investigation and discussion (Burney 1987; Quéméré *et al.* 2012; Anderson *et al.* 2018). It is certain that the island was not totally covered by forest, as described by Humbert (1927), but instead consisted of a mosaic of forests and savannahs, particularly in the Central Highlands. Some researchers, such as Humbert & Cours Darne (1965), argued that at least 90% of the island was forested, while others believed the forested area was much smaller (Kull 2000). Be that as it may, before it was settled by man, large areas of Madagascar were forested, so it comes as no surprise that 90% of all Madagascar's organisms are forest-dwellers (Dufils 2003). The proportion

Fig. 4.7: Deforestation in Madagascar. (A) Logs of rosewood (*Dalbergia* spp.) illegally cut and prepared to be floated down to the coast in Masoala National Park and UNESCO World Heritage Site; (B) Mid-altitude rainforest of Vohidrazana near Ambavaniasy cleared for slash-and-burn cultivation known as "tavy," a widely distributed practice in Madagascar to produce rice, the staple food of Madagascan people; (C) One of the few relict high plateau rainforest fragments of Madagascar (Ambohitantely), also highly threatened by logging and burning; (D) Andasibe surroundings. (Photographs by Zoo Zürich [A], D. Vallan [B, C] and F. Andreone [D])

of forest-dwelling amphibians is similarly high. By far the largest number of species of frogs lives in the rainforests along the eastern coast and in the North-East (Andreone *et al.* 2005; Glaw & Vences 2007a). Only a small proportion of amphibian species live in the dry spiny forests of the South, the dry forests of the West, or in open habitats (Glaw & Vences 2007a; Andreone *et al.* 2014d).

At the beginning of the 20th century the French colonial government banned the Malagasy population from practising "tavy" in order to preserve the original rainforest (Jarosz 1993). Unfortunately, this action by the government had little success. In 1950, the coverage of primary forest (rainforests, dry forests, and spiny forests) accounted for 27% of the land area, yet 50 years later only 17% of Madagascar was covered by original forests (Harper *et al.* 2007; Moat & Smith 2007; Irwin *et al.* 2010). However, this reduction did not follow a linear pattern. Between 1950 and 1970 the annual rate of deforestation was 0.3%, yet between 1970 and 1990 it was 1.7%, and in the 1990s 0.9%. Within the same time periods the wet rainforest declined by 0.6%, 1.7%, and 0.9% (Harper *et al.* 2007).

Deforestation is due principally to shifting cultivation, zebu farming, and production of charcoal (Friedberg 2019). Deforestation is exacerbated by population growth of humans, which currently stands at 2.8% per year (UNSD 2014). Increasing demand for rosewood recently has led to a massive increase in logging in the North-East of Madagascar (e.g., Marojejy and Masoala National Parks) (Fig. 4.7) (Barrett *et al.* 2010). In 1998, the number of rosewood trunks leaving the port of Toamasina per month was 332; two years later it had grown to 4108 (Schuurman & Lowry 2009). Political unrest in the past decade has boosted the illegal trade in rosewood, with enormous effects especially on the forests in the North-East. Although logging and exporting rosewood from Madagascar has been prohibited since 2010 (decree number 2010-141), large amounts of rosewood intended for export constantly are being seized. Because of the political instability of Madagascar since 2009, and the resulting limited control, the 1.27% of the forested area of Masoala in the North-East was affected by deforestation between 2010 and 2011, much more than was affected from 2005 to 2008 (0.27% annually) or from 2008 to 2010 (0.01%) (Allnutt *et al.* 2013).

The destruction of natural habitats is one of the greatest threats to amphibians throughout the world, and Madagascar is no exception (Andreone *et al.* 2005) (Fig. 4.7). Loss of habitat affects 89% of threatened amphibian species in the World, followed by emerging diseases, environmental pollution, global warming, and over-collection (Young *et al.* 2004). This makes local endemics particularly at risk (Fig. 4.8) and explains why all Malagasy species listed by the IUCN as Critically Endangered (IUCN 2014) are only locally distributed. Together with deforestation, fragmentation of the remaining habitat also is moving fast and the combination of these two factors is having dramatic consequences. Indeed, due to the edge effect, only small areas of these fragments (core

Fig. 4.8: Some threatened species with local and patchy distributions living in forest fragments of the High Plateau, central Madagascar. (A) *Mantella crocea* (Ambohitantely), Vulnerable; (B) *Anodonthyla vallani* (Ambohitantely), Critically Endangered; (C) *Boophis williamsi* (Ankaratra), Critically Endangered; (D) *Boophis andrangoloaka* (Ambohitantely), Endangered.
(Photographs by F. Andreone [A, B, D] and G.M. Rosa [C])

areas) offer sensitive species an ideal climate, as towards their edges the temperature and wind-speed rise and humidity falls (Murcia 1995; Lehtinen *et al.* 2003). The edge effect can extend more than a kilometer into a fragment. In Madagascar fragmentation has risen sharply, adding to the effect of general deforestation. Between 1950 and 2000 the number of forests with an area of more than 100 km² decreased by more than half, and the forested areas that were not affected by the edge effect (more than 1 kilometer from the forest edge) declined from over 90 000 to less than 20 000 km² (Harper *et al.* 2007). The effect of deforestation (changes in forested areas; fragmentation) on Madagascar's amphibians has been documented by a number of publications in recent years (e.g., Vallan 2002, 2003; Lehtinen *et al.* 2003; Lehtinen & Ramanamanjato 2006, Riemann *et al.* 2015, 2017; Neudert *et al.* 2017; Ndriantsoa *et al.* 2017).

Not all amphibian species are equally affected by deforestation. The influence of habitat-degradation on amphibians seems to be greater in regions with a pronounced dry season alternating with a wet season. In the best case, the moderate, selective exploitation of a rainforest leads to a shift in species-composition (Vallan *et al.* 2004). When exploitation is intense or fragmentation extreme, species with precise requirements and narrow tolerances are prone to disappear (Lehtinen *et al.* 2003; Vallan 2003). This appears particularly true for species that mostly rely on atmospheric humidity for carrying out active life or for breeding. Microhylid frogs belonging to the subfamily Cophylinae have endotrophic larvae and usually live in humid, stable rainforests and lay their eggs in plant internodes (e.g., *Platypelis* and *Cophyla*) or on the ground (e.g., *Stumpffia* and *Rhombophryne*). Deforestation and habitat-fragmentation considerably reduce atmospheric humidity and this is usually reflected in a lowering of species diversity for cophyline microhylids. In fact, these species are very susceptible to alteration of their habitat and hence they are found mainly in continuous forest (Vallan 2000, 2002; Riemann *et al.* 2015). On the other hand, species with exotrophic larvae depend much more time at streams or other bodies of water for breeding. So far, they appear much less affected by alteration of their habitat (Andreone 1994; Vallan 2000; Dixo & Metzger 2010).

In such a context, the most sensitive habitats are the small remnants of montane rainforest of the central high plateau, with a distinct seasonal climate. This is in some ways similar to West Africa where Hillers *et al.* (2008) found little effect from habitat fragmentation when the fragment is still in a rainforest landscape; in contrast the effect of forest degradation was greater. The effects of degradation and fragmentation of forests differ between types of forests (from rainforest to semi-deciduous forest), with the species in drier forests being more at risk after alteration (Ofori-Boateng *et al.* 2013). Degradation and fragmentation of habitats have direct effects on amphibians, which is visible in the medium and long term. Fragmentation can impair genetic exchange within populations, leading to a reduction in genetic diversity with the most affected species being those with restricted dispersal ability (Cushman 2006). There are, however, exceptions to the generalisation that areas with a seasonal dry period are more sensitive to degradation of habitat, like Ambohitantely Special Reserve with a period of low rainfall between May and September (Vallan 2000). Riemann *et al.* (2015), working at Ranomafana, failed to find any effect of forest-fragmentation on species richness.

In 2003, the then president of Madagascar, Marc Ravalomanana, announced at the "Fifth World Park Congress" in Durban, South Africa, that he wanted to triple the area of Madagascar's protected areas within ten years (Corson 2014; Virah-Sawmy *et al.* 2014). Unfortunately, this objective was almost suspended due to the political crisis that took place in 2009, when president Ravalomanana was exiled and his rival, Andry Rajoelina, the former mayor of Antananarivo, took over the presidential role. The management of Protected Areas and biodiversity became much more complicated in the following years, and most protected areas were subjected to uncontrolled exploitation.

B. The impact of emerging diseases

Loss and alteration of habitat have been the leading causes of global amphibian declines; however, multiple factors can act in synergy to cause mortality or sublethal effects. In recent years it has been recognised that the emergence of infectious diseases also plays a role, especially chytridiomycosis and ranavirosis (Berger *et al.* 1998; Stuart *et al.* 2004; Duffus & Cunningham 2010; Rosa *et al.* 2017; Scheele *et al.* 2019). Other diseases also may be linked to mass mortality events in amphibian communities, although there is still little overall understanding of pathogens and their dynamics. This is the case for *Amphibiocystidium*, the causative agent of dermocystidiosis (González-Hernández *et al.* 2010) and some bacterial agents of the family Chlamydiaceae capable of infecting anurans and caudates (Martel *et al.* 2012a, b). As a result, most research on disease undertaken in Madagascar has been centered on chytridiomycosis, an infectious disease caused by pathogenic fungi of the genus *Batrachochytrium* and the first to be associated with declines and extinctions of hundreds of amphibian species (Skerratt *et al.* 2007). This is the most widely studied amphibian disease to date, and two agents are known to cause infections; the amphibian chytrid *B. dendrobatidis* (*Bd*) (Longcore *et al.* 1999) and the salamander chytrid *B. salamandrivorans* (*Bs* or *Bsal*) (Martel *et al.* 2013). The most severe chytridiomycosal epidemiological scenarios were described in the neotropics, where the disease has led to the disappearance of 67% of the species of harlequin frogs (corresponding to 110 species of the genus *Atelopus*) (La Marca *et al.* 2005), as well as the rapid loss of amphibian biodiversity in highly diverse places such as El Copé (Panama), affecting eight families of frogs and salamanders (Lips *et al.* 2006). Severe impacts of *Bd* were also recorded in tropical, temperate, and mountain environments, from the Caribbean, North and South America (especially the Andean region), Australia and Europe (Fisher *et al.* 2009; Catenazzi *et al.* 2011; Rosa *et al.* 2013; Scheele *et al.* 2019; for Africa see Chapters 1 and 2). However, it is interesting to notice that while some species seem to have disappeared completely after outbreaks of chytridiomycosis, others persist without showing evident signs (Retallick *et al.* 2004). Thus, although not fully understood, the susceptibility of hosts is highly variable, not only among species, but also within the same species (Searle *et al.* 2011).

When infecting the epidermis of the host, the chytrid fungus leads to a proliferation of keratinous cells causing hyperkeratosis and hyperplasia in post-metamorphic individuals (Berger *et al.* 1998; Kilpatrick *et al.* 2010). The pathogenesis of *Bd* infection is characterised by the breakdown of cutaneous function, which leads to a loss of homeostasis and consequent heart failure. In larvae, *Bd* infection is confined to the mouthparts (the only keratinized area), leading to depigmentation and, sometimes, to oral lesions (Marantelli *et al.* 2004; Knapp & Morgan 2006). In adults, the clinical signs of chytridiomycosis include anorexia, abnormal posture, lethargy, and loss of righting reflex. It is also possible to observe a strong epidermal desquamation and, in some cases, ulcers and hemorrhages in the skin, muscles, and eyes. However, these are non-specific clinical symptoms shared with several other diseases (Berger *et al.* 2000). Ideally, the definitive diagnosis of chytridiomycosis requires a multidisciplinary approach involving data obtained using molecular, mycological, and histopathological techniques.

Until recently, amphibian skin-colonizing chytrid fungi were thought to be absent from Madagascar. This idea was supported by a series of surveys conducted across the island between 2005 and 2010 (Andreone *et al.* 2008a, b; Weldon *et al.* 2008; Crot-

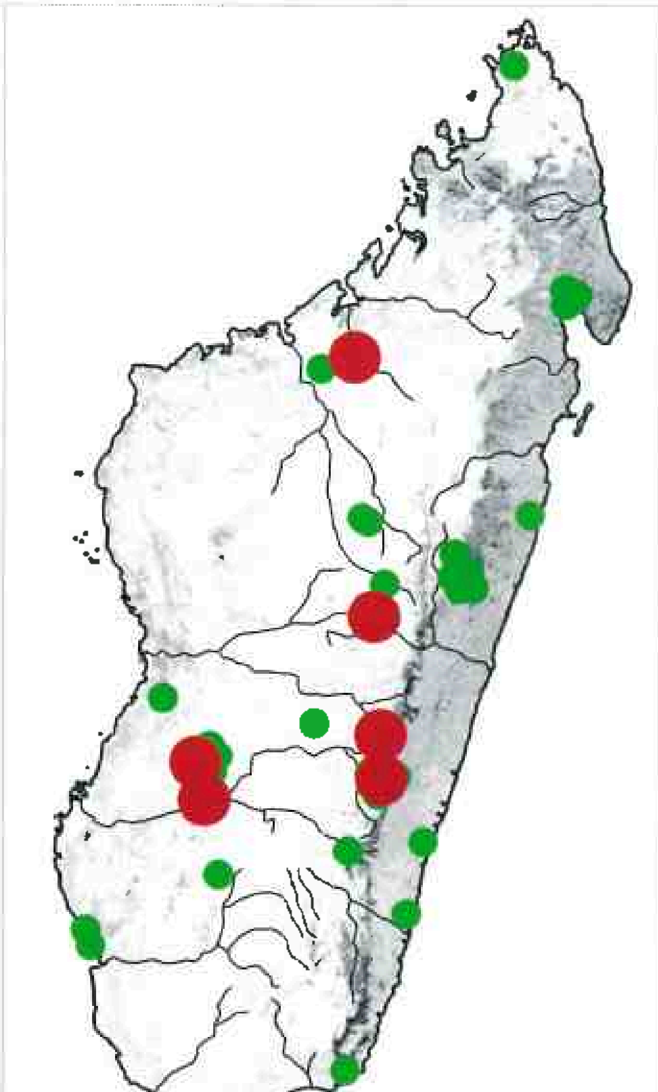

Fig. 4.9: Distribution of chytrid(s) detected in amphibians in Madagascar: the red dots represent the sites where chytrid was reported between 2010 and 2015, while the green dots show sites where it has not been detected.
(Based on data from Bletz *et al.* 2015a)

TINI *et al.* 2011a; VREDENBURG *et al.* 2012). The first *Bd*-oriented surveys in Madagascar were carried out in 2005 and 2006 covering sites from most biogeographic regions and elevational zones. Over 500 individuals belonging to almost 80 species were sampled and tested by a histological technique; all were negative (WELDON *et al.* 2008). A new effort took place between 2006 and 2007 covering 12 sites and screening 300 individuals (53 species), both using molecular and histological approaches, but again yielding no positive records of *Bd* (VREDENBURG *et al.* 2012). Finally, molecular screening at Itremo-Ambatofinandrahana (central Madagascar) in 2008 (CROTTINI *et al.* 2011a), Parc Ivoloina, Toamasina (eastern Madagascar) (CROTTINI *et al.* 2014b) and Ankaratra (central Madagascar) in 2010 (ANDREONE *et al.* 2014b), also failed to detect the presence of *Bd* (BLETZ *et al.* 2015a, b).

The presence of an amphibian chytrid in Madagascar was unexpectedly confirmed in 2010 after an expedition to the very remote area of the Makay Massif (southwestern Madagascar). Three individual frogs were molecularly diagnosed with low levels of chytrid infection (RABEMANANJARA *et al.* 2011; BLETZ *et al.* 2015a). In the following years, a chytrid was confirmed at the same place and detected with low prevalence at additional locations (Ankarafantsika and Antoetra), reaching a higher prevalence of infection in Ranomafana (up to 50%) and Ankaratra (up to 100%) (Fig. 4.9; BLETZ *et al.* 2015a). Later, *Bd* was detected in native amphibians commercially exported from Madagascar, but despite the sampling effort (565 frogs), its prevalence was only 0.53% (KOLBY 2014). The detection patterns in Madagascar seemed to follow trends similar to other tropical areas of the world (e.g., KRIGER & HERO 2007), where strong seasonality of the fungus may—at least partly—explain the overall low prevalences and lack of detectability in the field. Simultaneously, data suggested an association with mid-elevations, also reported in other studies (BLETZ *et al.* 2015a, b).

Suitability models suggested that Madagascar is particularly favourable to colonisation by *Bd* (RÖDDER *et al.* 2009; LÖTTERS *et al.* 2011). However, the origin of chytrids in the country and its current status still remain unclear. Accidental human-mediated introduction may have been a pathway (WOLLENBERG *et al.* 2010). Further possible modalities include the movement of infected animals (live or dead), contaminated water, and moist substrates. The arrival of a high-virulence lineage (such as *Bd*GPL: FARRER *et al.* 2011) and consequent exposure to naïve populations could have had catastrophic effects on the amphibian fauna. However, the

Fig. 4.10: Workshops and scientific meetings run in Madagascar to build capacity and promote amphibian conservation. (A) Participants of a 2010 training course at Parc Ivoloina in an exercise to discuss possible responses to chytrid emergency scenarios; (B) Working groups during a workshop on captive breeding and husbandry for frogs in Madagascar held in 2012; (C) Participants at the ACSAM2 meeting held in Centre ValBio, Ranomafana, in 2014.
(Photographs by D. EDMONDS [A] and F. ANDREONE [B, C])

detected burdens of infection have been low, and no mass mortality related to any chytrid infection has been noticed in Madagascar thus far (BLETZ *et al.* 2015a). This raises some possible scenarios: (1) the present chytrid is hypovirulent (likely not leading to die-offs); not excluding the possibility of (2) this being an endemic lineage or chytrid species that has largely evaded detection; (3) a combination of the two hypotheses, not being mutually exclusive, is also possible (BLETZ *et al.* 2015a). In any case, with the current state of knowledge, it remains unanswered as to whether emergence of chytridiomycosis in Madagascar will in fact lead to amphibian declines and/or extinctions (LÖTTERS *et al.* 2011).

Activities addressing the potential threat of *Bd* began proactively in October 2010 with the organization of a workshop on chytrid-prevention held at Parc Ivoloina (Fig. 4.10; GARCIA 2010; WELDON *et al.* 2013). To deal with the potential threat emerging from the presence of this pathogen in Madagascar, an "emergency unit" (the so-called Chytrid Emergency Cell, CEC) was officially put in place by the Ministère de l'Environnement et des Forêts (now Ministère de l'Environnement et du Développement Durable) on 5 April 2011. This body had the role of coordinating activities related to *Bd*. Further training opportunities were organised for students, researchers, and decision-makers to better prepare researchers and authorities for this issue. Much of this work has been carried out by the IUCN SSC Amphibian Specialist Group (ASG) of Madagascar, aiming to develop a national strategy to address the issue and raise awareness, although many other groups have contributed as well (ANDREONE *et al.* 2012).

The ASG and the CEC set up a National Monitoring Programme to detect *Bd* if and when it arrives in Madagascar in prioritised sites and to henceforth monitor trends in chytridiomycosis (WELDON *et al.* 2013). Supported by ASG, the CEC also has been working with the Malagasy government to implement quarantine measures related to commercial trade in aquarium fishes and plants to prevent any accidental introduction of *Bd* (ANDREONE *et al.* 2008a). In 2010, guidelines were published to enable an effective response to the threat of this disease, focusing on prevention and detection of *Bd* (RABIBISOA & RAHARIVOLOLONA 2010). Although an effective emergency plan is still lacking were there to be a case of massive die-offs, studies to prevent and mitigate the disastrous impact of a high virulence lineage of *Bd* are being carried out, aiming to understand the microbial ecology of amphibian skin and how this can be used as a defence mechanism against the pathogen (BLETZ *et al.* 2013) (Fig. 4.11).

Despite a global investment in developing and testing different approaches, all currently available strategies have shortcomings and are unlikely to yield the desired outcome of mitigation of the disease (GARNER *et al.* 2016). Augmentation of the amphibian skin microbiome with probiotics has been suggested as promising therapy, particularly for threatened species (e.g., the Golden Mantella, *Mantella aurantiaca*; BLETZ *et al.* 2013). This expanding research uses bacteria isolated from the skin of living amphibians that show the ability to inhibit *Bd* growth, thus, limiting infection or enhancing hosts' resistance. More recent research shows that a "bacterial consortium" would likely offer a more stable and effective approach as probiotics, rather than focusing on a single species or genus (ANTWIS *et al.* 2015). Yet, and despite the advances, this approach presents numerous challenges and issues that need to be overcome before being considered a viable strategy for mitigation (see GARNER *et al.* 2016 for more details).

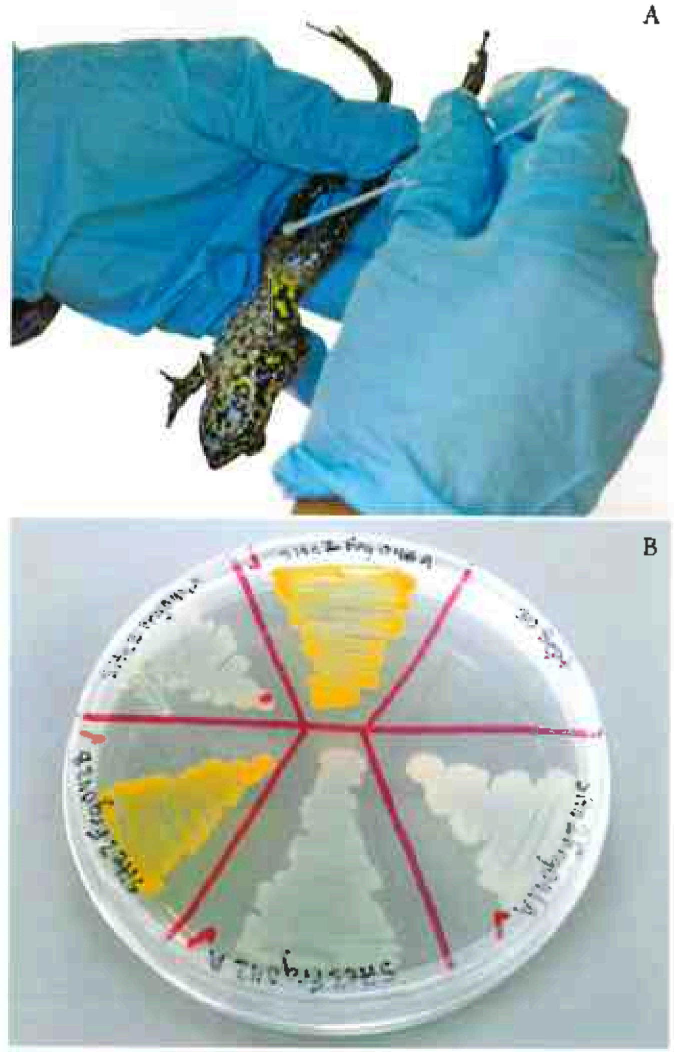

Fig. 4.11: The chytrid fungus as a threat for the batrachofauna of Madagascar. (A) Microbial swabbing of *Mantidactylus* sp. aff. *femoralis* in Ranomafana, to look for anti-*Bd* skin bacteria; (B) Six bacteria isolated from *Boophis madagascariensis* in Andasibe. (Photographs by B. GRATWICKE [A] and M. BLETZ [B])

In the meantime, other methods are being explored at the population and community level. These methods often involve environmental manipulation, given that a single strategy is unlikely to achieve mitigation of the disease. Despite the possible elimination of the pathogen from specific environments (BOSCH *et al.* 2015), most approaches rather focus on inhibiting growth of the chytrid and reducing the density of zoospores (GARNER *et al.* 2016). From biotic interventions, such as fostering the abundance of micro-predators that consume *Bd* zoospores (SCHMELLER *et al.* 2014), to physical interventions, e.g., manipulating temperature to limit growth of *Bd* (ROZNIK *et al.* 2015), or chemical treatment by increasing salinity (STOCKWELL *et al.* 2015); all these different avenues hold promise, yet have their limitations.

C. The international pet trade

The global demand for exotic pets is estimated to be worth billions of US dollars each year (BARBER-MEYER 2010). As the human population increases and as the economies of developing countries expand, demand for wildlife flourishes and hence so does the trade in wildlife. International travel and transport of goods are now commonplace, and they facilitate movement of wild animals through legal and illegal pathways (DUTTON *et al.* 2013). New media are also having a strong influence on the wildlife trade with increased online access to information driving demand for more exotic pets and products (Bush *et al.* 2014).

Wildlife trade can threaten wild populations through loss of species, introduction of invasive species, and disease (Mattioli *et al.* 2005; Andreone *et al.* 2013b; Carpenter *et al.* 2014). It can also have negative impacts on the welfare of animals during illegal capture, improper captive breeding, transport, sale, and subsequent use (Baker *et al.* 2013) and embraces wider societal issues, such as a zoonotic risk to human health (Macdonald & Laurenson 2006). On the other hand, wildlife trade can constitute an important revenue stream, particularly for people in biodiversity-rich but economically poor countries (Roe 2002; Dickson 2008; Carpenter & Robson 2008). Thus, a legal and sustainable trade has the potential to generate benefits in terms of livelihoods and the alleviation of poverty, and also create incentives for conservation (Hutton & Leader-Williams 2003). Moreover, there is a substantial legal trade in wildlife that is regulated through the Convention on International Trade in Endangered Species (CITES) via a series of trade-controls. There is growing interest in Madagascar's amphibian species within the international pet trade due to their unique and attractive nature and high levels of endemicity (Andreone *et al.* 2006). To date, only a few studies have investigated the range of species, numbers, and values of traded amphibians from Madagascar (Carpenter & Robson 2008; Rabemananjara *et al.* 2008a, b; Carpenter *et al.* 2014; Robinson *et al.* 2018a, b), with most focused on CITES-listed species. Data presented by Carpenter & Robson (2008), however, reported 91 species (both CITES and non-CITES) and over 221000 individuals being exported between 2000 and 2006, with estimates of the total value of the trade, at that time, varying from 590000 to 906750 USD (538000–826934 EUR). Carpenter (2003) and Rabemananjara *et al.* (2008a, b) reported on the trade structures, the most common being the three levels of participation in the trade (collector, intermediary, and exporter) and values at each stage for *Mantella* species. Carpenter *et al.* (2014) referred to 14 species of *Mantella* totaling 193600 individuals having been traded from 1976 to 2007. Efforts have been made to utilise amphibians sustainably to benefit conservation activities (e.g., Jenkins 1994; Carpenter *et al.* 2007; Carpenter & Robson 2008), in which case it is useful to review data on species, numbers, trade-structures and values (see also the chapter "Is a sustainable trade in Madagascar's frogs possible?").

Madagascar remains the second largest global exporter of live CITES-listed amphibians, after Nicaragua (UNEP-WCMC 2019a). Based on CITES export figures, over a five-year period, (2012 to 2016), Madagascar directly exported 28900 live, CITES-listed frogs belonging to nine species (UNEP-WCMC 2019b). All of the amphibians exported belonged to the genus *Mantella*, with the exception of the highly decorated Malagasy Rainbow Frog, *Scaphiophryne gottlebei*, from the Isalo area, for which 382 individuals were exported from 2012 to 2016. *Mantella baroni* was the most frequently exported species during this period, with over 11300 live individuals exported (UNEP-WCMC 2019b). This is in strong contrast to historical data, which showed *Mantella aurantiaca* dominating the trade (Carpenter *et al.* 2007; Rabemananjara *et al.* 2008a, b). *Mantella betsileo* was the second-most highly exported over the five-year period (10546 individuals exported), followed by *M. nigricans* (3970 individuals) and *M. aurantiaca* (1052 individuals). Historical data showed that after peaking at about 33300 individual frogs in 2001, exports in Madagascar's CITES-listed amphibians have decreased to about 6000 per year in 2011 (UNEP-WCMC 2019b). However, there are several non-CITES-listed species that also are shipped from Madagascar, especially in recent years, including species belonging to the following genera: *Boophis*, *Dyscophus*, *Gephyromantis*, *Guibemantis*, *Heterixalus*, *Mantidactylus*, *Platypelis*, and *Scaphiophryne* (Ministère de l'Environnement et du Développement Durable, unpublished data).

Various factors are likely to have influenced the amphibian trade from Madagascar over the years, including improved trade controls and the continued implementation of a quota system in-country (Rabemananjara *et al.* 2008a, b). For example, the quota for *Mantella aurantiaca* has gone through a series of revisions from 8000 individuals in 2001 to 280 individuals in 2015. Prior to the CITES Conference of the Parties (CoP) 17, held in South Africa in 2016, the tomato frog *Dyscophus antongilii* was Madagascar's sole frog listed on Appendix I of CITES and, therefore, wild-sourced individuals had not been permitted in commercial trade. However, Madagascar proposed the downlisting of *D. antongilii* to Appendix II, whilst simultaneously proposing the uplisting of the two other *Dyscophus* species (*D. guineti* and *D. insularis*). These proposals were accepted at CoP17 resulting in all the *Dyscophus* species (*D. antongili*, *D. guineti*, and *D. insularis*) being included on Appendix II. There were also successful proposals to list three additional *Scaphiophryne* species (*S. boribory*, *S. marmorata*, and *S. spinosa*) on CITES Appendix II alongside *S. gottlebei* (which was already in Appendix II). These listings were proposed to facilitate the management of trade, particularly given that species within the genera *Dyscophus* and *Scaphiophryne* were not only desirable in the international pet trade but whose identity could be mistaken due to their morphological similarity.

The Direction Générale des Forêts (within the Ministère de l'Environnement et du Développement Durable) is currently responsible for the trade in wildlife in Madagascar and constitutes the CITES Management Authority. The CITES Scientific Authority on Fauna is composed of a group of experts from various institutions and specialist groups who provide advice regarding export quotas and "non-detriment findings" (impact statements) for species in trade. Recent research has looked in detail at the chain in wildlife trade in Madagascar with a view to understanding the implications of the trade for conservation and for human livelihoods (Robinson *et al.* 2018a, b). In 2014, there were eleven licensed export facilities in Madagascar, ten of which were supplying frogs (and other wildlife) for the international pet trade. Most were located in and around the capital, Antananarivo. Annual export quotas were distributed between the licensed wildlife exporters. However, the exporter was required to obtain a collection-mandate from the CITES Management Authority prior to any collection from the wild, which specified the species to be collected, the quantity to be obtained, and the area from which the collection was to be taken. Additional requirements included charges levied against collections to be paid to the regional forestry department, and rebates to local communities in collection-areas, which varied geographically and were not always respected. At this time, all live amphibians in the commercial trade exported from Madagascar were sourced from the wild, with no captive-breeding facilities dedicated to this purpose in-country.

Exporters obtained animals from the the wild via a network of suppliers, including intermediaries and local collectors. The supply chain was somewhat flexible and in some cases exporters bypassed intermediaries and went straight to local collectors, whereas in other cases, one or more intermediaries made up the chain or helped others to supply orders (also see Carpenter 2003). The intermediaries also had to be in possession of the approved collection-mandate from the exporter. Animals were not permitted to be collected from protected areas, but were collected from a range of sites all over Madagascar, although it is unclear how strictly existing collection rules were obeyed. Orders for live herpetofauna usually were received between September and May, which coincides with the official collecting season for amphibians (beginning of February to the end of April) and the rainy season (summer in the southern hemisphere), when amphibians are most active. On occasion, orders are placed outside of this season, which could be more difficult to fulfill as some amphibians have short periods of activity. Following collection, animals usually were transported to the exporting facilities via "taxi-brousse" (mini-bus) or airplane, depending on the locality of collection. Once at the exporter's facility they spent from a few days to many weeks before being shipped, most often to the United States, Europe, or Japan (Robinson *et al.* 2018a).

During this research, a local collector reported receiving 200 MGA (Malagasy Ariary) [roughly corresponding to 0.07 USD/0.06 EUR] for each collected *Mantella madagascariensis* (J. Robinson, unpublished data). This value was supported by intermediaries, who claimed that they paid local collectors between 200 and 1000 MGA for a single *Mantella*. The collector's prices presented here are much higher than those reported by Rabemananjara *et al.* (2008a, b); in fact, for *M. madagascariensis* the value to the collector had increased more than three-fold since 2005. A three-fold increase also applied to the exporter, with them reporting to receive an average of 6.00 USD/5.5 EUR (equivalent to about 14000 MGA at the time of writing) for each single *Mantella* exported (J. Robinson, unpublished data). Despite this, research in the Moramanga district of Madagascar showed that local collectors receive a very small proportion (~1.4%) of the final export price of traded herpetofauna, and opportunities for a reduction in poverty or for incentives for sustainable management of the trade, appear to be limited as they currently stand (Robinson *et al.* 2018a, b). Whether a sustainable amphibian trade could help create incentives to conserve habitats from human disturbances, such as slash-and-burn agriculture or cattle grazing on Madagascar, is still not well understood. However, strategies to improve the sharing of benefits from the trade, such as promoting collective management of harvests and boosting capacity at the local-collector level, may enhance conservation and improve local livelihoods.

Although there are serious concerns regarding illegal trade in some Malagasy amphibians (Todd *et al.* 2011), the true number of frogs illegally exported from the country currently is poorly known. Rabemananjara *et al.* (2008a, b) suggested that illegal smuggling is unlikely to be high for species of low commercial value, such as *Mantella*, which is in stark contrast to the well documented smuggling of higher-valued species, such as Malagasy tortoises (O'Brien *et al.* 2003; Walker *et al.* 2004; Todd *et al.* 2011), which trade is prohibited by CITES Appendix I. Nevertheless, the pet trade is a dynamic process influenced by changing demand by consumers as well as by variances in international and local governance, and must, therefore, be constantly monitored. Whilst we have collated information on the dynamics of legal trade of amphibians from Madagascar, much work is still to be done in order to effectively monitor traded amphibian populations and ensure that their trade is sustainable amongst other considerable pressures on Madagascar's natural resources.

D. Is a sustainable trade in frogs possible?

Uncontrolled collection for either food or the pet trade can cause declines in amphibian populations and even local extirpations (Schlaepfer *et al.* 2005), but to date such events have not been recorded in Madagascar. Carpenter & Robson (2008) stated that the impact of collection is the highest for species from fragmented habitats and that have small populations with low fecundity rate and reproductive potential (e.g., *Mantella aurantiaca* and *M. cowanii*). Given that legal commercial trade in amphibians currently is being carried out in Madagascar, there is a need to develop quantitative methods to ensure its sustainability and provide relevant recommendations to CITES authorities, local collectors, and exporters.

A "sustainable quota" can be defined as the estimation of the maximum number of individuals that can be removed from wild populations and for which the probability of extinction does not increase over a long period of time (e.g., 100 years). To estimate sustainable quotas, many experts advocate the development of population-dynamic models (e.g., Taylor *et al.* 1987; Robinson & Redford 1991; Johnston *et al.* 2000; Marboutin *et al.* 2003; O'Neil *et al.* 2010; Sæther *et al.* 2010). However, these models need extensive long-term population metrics, such as population size, fecundity and survival rates, and sex ratio (Clark *et al.* 1991; Chapman *et al.* 2001; Ellner *et al.* 2002; Reed *et al.* 2002). Recent models have been developed on the basis of population viability analyses (PVA) and sensitivity analyses, and have been acknowledged for their transparency toward uncertainty and their broad range of application (Brook *et al.* 2002). Unfortunately, field data largely are missing for African amphibians, including traded species from Madagascar (except for *Mantella aurantiaca*). In a context of urgent decision-making, it is, therefore, necessary to use

Table 4.1: The five amphibian species commonly eaten in Madagascar. IUCN Red List status as assessed in 2017. The legal status refers to "Annexe du Décret No. 2006-400 du 13 juin 2006 portant classement des espèces de faune sauvages." Adapted from Jenkins *et al.* (2008).

Species	IUCN Red List	Legal status	Origin
Boophis goudoti	Least Concern	Category 3	Native species
Boehmantis microtympanum	Vulnerable	Category 1: Class I (protected species, no collection)	Native species
Mantidactylus grandidieri	Least Concern	Category 3: Game species (legally hunted within a defined season)	Native species
Mantidactylus guttulatus	Least Concern	Category 3	Native species
Hoplobatrachus tigerinus	Least Concern	Category 1: Class II (protected species, authorised collection permitted)	Introduced species

Fig. 4.12: The nine *Mantella* species taken into consideration by Tessa *et al.* (2009) for fecundity analysis. (A) *Mantella betsileo* (Isalo Massif); (B) *Mantella expectata* (Isalo Massif); (C) *Mantella viridis* (Antongombato); (D) *Mantella baroni* (Antoetra); (E) *Mantella cowanii* (Itremo); (F) *Mantella crocea* (Torotorofotsy); (G) *Mantella laevigata* (Tsararano); (H) *Mantella nigricans* (Betampona); (I) *Mantella pulchra* (Vohimana).

(Photographs by F. Andreone [A, D, E, G, I]; V. Mercurio [C]; D. Edmonds [F], and G. M. Rosa [B, H])

every available tool for the conservation of endangered systems. Here we provide for the first time our considerations and data on this aspect as applied to nine species of *Mantella* (Fig. 4.12).

Quantitative recommendations should be provided after estimating the effect of the removal of individuals on the probability of extirpation of wild populations, or extinction of entire wild species. This begs the question of whether there are sufficient monitoring programmes and demographic estimates to reliably model the target amphibian species in Madagascar. Table 4.2 reviews IUCN conservation status, the exportation quotas of 2013, and available published data on life-history traits for several species of the genus *Mantella*. The present data were obtained from published and unpublished information on preserved specimens housed in the herpetological collection of the Museo Regionale di Scienze Naturali (Torino, Italy). Breeding size was estimated from direct count of ovarian eggs (Tessa *et al.* 2009). To estimate the age of individuals, skeletochronological analyses were performed on bone samples (by counting the LAGs), enabling estimations of age-structure and age at sexual maturity. Sex ratio also was estimated from standardised monitoring of a single species (e.g., *M. aurantiaca*) (Randrianavelona *et al.* 2010a, b). However, due to potential behavioural differences between the sexes (e.g., males are more active than females), the sex ratio of individuals harvested by local collectors may be biased (Rabemananjara *et al.* 2008a, b).

Therefore, when integrating the sex ratio into Population Viability Analyses (PVA), the estimation of the impact of harvesting should be more accurate when using the proportion of males and females harvested by local collectors, rather than the true sex ratio of the population. Active field searches performed during recent years have allowed researchers to estimate the proportion of males and females harvested for seven species (Table 4.2). A first PVA computed using the software Vortex (Lacy *et al.* 2011) was performed to estimate the probability of extinction of a given population over a long period of time. A sensitivity analysis was then conducted to assess the degree to which the uncertainty of demographic estimates affected the results (N. Dubos, unpublished data). To predict the impact of collection in the wild, a given number of individuals removed each year was included. Datasets of age-structure for all *Mantella* species living in a similar habitat (e.g., rainforests, savannahs; Fig. 4.13) were pooled (Guarino *et al.* 2008). Assuming that mantellas reach the adult stage within one year and do not live more than three years, a simple three-stage matrix was used for juveniles and adults. Then, optimistic and pessimistic scenarios were built, based on sampling variation (Mills & Lindberg 2002) to rank the effect of uncertainty on each of the parameters. Juvenile survival, breeding size, and adult survival were the most sensitive life-history traits (e.g., the probability of extinction varied the most with these parameters). Hence, these deserve further investigation. A better accuracy in the sex ratio of harvested individuals and in estimates of population size also are needed. Finally, results suggested that the species from rainforests show a greater degree of variability (likely due to a higher ecological heterogeneity in rainforest habitats) than do those species from savannahs and dry forests; the latter are more homogeneous and ecologically more similar. The analysed rainforest species include several threatened species, such as *M. aurantiaca*, *M. cowanii*, and *M. milotympanum*. Using the findings it was possible to recommend prioritisation of future conservation and research efforts on rainforest species.

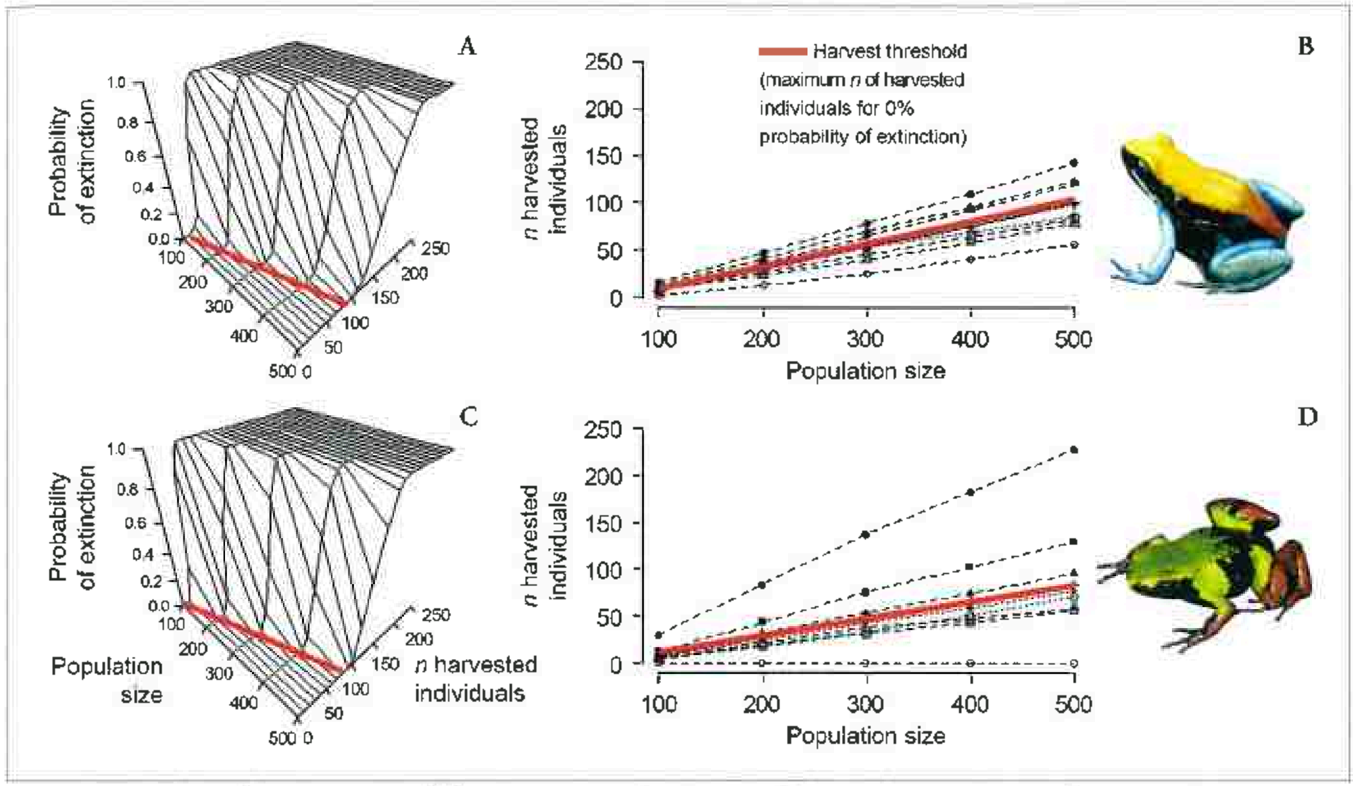

Fig. 4.13: Graphic representations for the test of sensitivity analysis applied to nine *Mantella* species. (A, B) Savannah/dry forest species (represented by *M. expectata*); (C, D) Rainforest species (represented by *M. nigricans*). A and C show base models; the red line represents the highest number individuals potentially collected when the probability of extinction remains null; B and D show the variation of this result while accounting for uncertainty in breeding size (circles), adult survival (squares) and the sex ratio of harvested individuals (triangles). Open and closed symbols are respectively pessimistic and optimistic bounds of 95% confidence intervals. For readability, we did not show variations in juvenile survival, as these outmatched every other parameter.

(Graphics by N. Dubos, *Mantella* photographs by F. Andreone)

Unfortunately, in a context of urgent decision making, the length of time it takes to collect new data and improve models to inform decisions about trade necessitates the immediate use of existing management tools, such as no-take zones or complete bans on trade for some species (e.g., *M. cowanii*). In the near future, monitoring programmes relating to the sustainable commercial trade of Malagasy amphibians should focus on (1) the identification of potential source sub-populations that can contribute greatly to population-recruitment and exclude others from harvest (e.g., the largest populations, see Piludu *et al.* 2015 for *M. aurantiaca*); and (2) development of demographic data, by performing detailed mark-recapture studies to provide robust estimates of survival and population sizes. The use of PVA based on reliable datasets may prevent Malagasy species from overexploitation for the pet and food trades, whilst also having the potential to benefit local economies.

E. The bushmeat trade

A further aspect related to the exploitation of frogs in Madagascar is collection for the bushmeat trade (Carpenter *et al.* 2014). In many parts of the world frogs are consumed as part of the local diet and are part of culinary traditions. This is the case in France, and it has been proposed that in Madagascar the trade in frogs for consumption by humans is a logical consequence of French colonisation. In Malagasy restaurants, and especially in those catering to foreign tourists, frog legs typically are available on the menu under the name "cuisses de nymphes." Frogs for the food trade are sourced from the wild. Only a few especially large anuran species that are considered suitable for consumption are collected. These include native species from rainforest habitats as well as *Hoplobatrachus tigerinus*, which became established after importation from Asia at the beginning of the 20th century (Guibé 1953; Vences *et al.* 2003a; Mohanty *et al.* 2021) (Fig. 4.14). Since *H. tigerinus* is an exotic species in Madagascar it is not subject to any particular protection, although it is included in CITES Appendix II due to the fact that in its native South-East Asia it has been subject to high levels of exploitation. Of much greater concern is the trade in native species of frogs. These include *Boehmantis microtympanum*, *Boophis goudoti*, *Mantidactylus grandidieri*, *M. guttulatus*, and *M. radaka* (Fig. 4.15) (Rancilhac *et al.* 2020). Of these four native species, one (*B. microtympanum*) is considered threatened and currently listed as Vulnerable on the IUCN Red List. Frogs typically are collected by hunters together with other aquatic and semi-aquatic organisms, such as crabs, eels, fish, and crayfish. It is important to be aware that under the names of *M. grandidieri* and *M. guttulatus* there are at least three additional candidate species (Rancilhac *et al.* 2020). This taxonomic fragmentation would likely result in the need for a re-evaluation of the Red List Assessment, and the collecting of these species for food may pose a more serious conservation problem than previously thought.

In Madagascar, frogs are not usually considered part of the local cuisine, nor are they regularly sold at markets. Rather, most frogs

Fig. 4.14: The Tiger Frog or Indian Bullfrog (*Hoplobatrachus tigerinus*), originally from Asia and nowadays acclimatised in Madagascar, is usually collected for human consumption. (A) An adult living individual captured to be sold in a local market; (B) Stall with skinned bullfrogs for sale in a local street market in Antananarivo. Due to this trade the species is now present in several areas of Madagascar, mostly in the NW. Apparently, although locally abundant (e.g., at Nosy Be), it does not seem to show invasive traits.
(Photographs by J. Robinson [A] and G. M. Rosa [B])

Fig. 4.15: A worker in Ambatolampy (Antananarivo Province) preparing frog legs of *Boophis goudoti* (locally known as "cuisses de nymphes"), collected on Ankaratra Massif. (Photograph by F. Andreone)

Table 4.2: Parameters used to establish the conservation status and viability of the *Mantella* species: IUCN status is according to the most recent assessment (2017) and exportation quotas are from 2013; Other data were extracted from Guarino *et al.* (2008, 2010), Rabemananjara *et al.* (2008a), Tessa *et al.* (2009), Randrianavelona *et al.* (2010a), and Andreone *et al.* (2011). Species marked with an asterisk are classified as "rainforest species;" the remaining ones are "savannah species." Numbers in parentheses refer to sample sizes. Abbreviations as follows: CR = Critically Endangered; EN = Endangered; LC = Least Concern; NE = Not Evaluated; NT = Near Threatened; VU = Vulnerable.

Mantella species	IUCN status	Exportation quota (2013)	Mean age at maturity	Brood size	Age structure (min–max)	Number of females–males randomly harvested	Minimal and maximal population size (number of sampling sessions)
*aurantiaca**	CR	550	–	–	0–2 (25)	–	75–201 (3)
*baroni**	LC	10 000	1.39 (28)	56.57 (7)	0–3 (24; 18)	9–15 (24)	49–108 (2)
*bernhardi**	VU	150	–	–	0–2 (32; 43)	–	41–316 (4)
betsileo	LC	6840	–	–	–	–	208–253 (2)
*cowanii**	EN	0	1.26 (26)	35.00 (4)	0–3 (26)	12–14 (26)	–
*crocea**	VU	0	–	–	–	–	35 (1)
ebenaui	LC	0	–	–	–	–	–
expectata	EN	250	1.24 (10)	68.36 (5)	0–3 (65)	7–10 (17)	–
*haraldmeieri**	EN	0	–	–	–	–	–
*laevigata**	LC	0	2.00 (10)	41.00 (5)	0–2 (10)	–	154–189 (2)
*madagascariensis**	VU	110	–	–	0–2 (10)	–	186 (1)
*manery**	VU	0	–	–	–	–	–
*milotympanum**	CR	0	1.21 (14)	61.25 (4)	0–4 (14)	0–14 (14)	62–283 (4)
*nigricans**	LC	2 000	1.20 (10)	43.14 (7)	0–4 (10)	5–5 (10)	–
*pulchra**	NT	472	1.56 (25)	48.00 (6)	0–4 (25)	12–13 (25)	98 (1)
sp. aff. *expectata*	NE	–	1.16 (19)	66.00 (4)	0–3 (15)	0–4 (15)	75–467 (4)
viridis	EN	0	1.10 (39)	117.900 (11)	0–3 (40)	–	–

are destined for restaurants, many of which cater to foreigners. So far, the impact of collection for food on wild amphibian populations is not known. One of the few studies on frogs in the food trade was carried out in the city of Moramanga by Jenkins *et al.* (2009). They found a single restaurant ordered on average 249 individual frogs per week. Should this be extrapolated to a larger scale, then the trade in native species of frogs for food could be quite significant and further studies are clearly needed to assess this trade as a potential threat. Jenkins *et al.* (2008) reviewed the demand, prices, and the Malagasy laws governing collection of species targeted for food. The large species collected for food were considered part of "game fauna" (Table 4.1). Given the numbers reported in the two studies, it seems likely that intense collecting could impact populations of *Mantidactylus* species and *Boehmantis microtympanum*. This is of concern, especially taking into consideration their low fecundity, likely slow growth, and delayed sexual maturity. Skeletochronological studies showed that sexual maturity in *B. microtympanum* is reached at three years of age, similar to that attributed to *Mantidactylus grandidieri* (Guarino *et al.* 1998, 2019).

F. Amphibians and climatic change

The current rate of climatic change, marked by an unprecedented increase in global temperature and large-scale shifts in weather patterns, is having adverse effects on species and ecosystems worldwide. While some species may expand their ranges, many others are being pushed towards higher elevations (Grimm *et al.* 2013). These elevational shifts are expected to impact species' phenology and may even lead to extinctions (Mayhew *et al.* 2007; Román-Palacios & Wiens 2020). Given their complex life history, amphibians are particularly vulnerable to the projected effects of climatic change. Because amphibian reproduction is closely associated with the presence of water, climatic changes that affect the hydroperiod pose a particularly menacing threat both to aquatic and terrestrially-breeding amphibians (Blaustein *et al.* 2001; Daszak *et al.* 2005). However, the considerable variation in predictions about climatic change for different geographic areas and habitats (e.g., Araújo *et al.* 2006; Alford *et al.* 2007; Laurance 2008), prevents having a single scenario on how amphibians are likely to respond.

Madagascar's imperiled biota is now experiencing the effects of this new threat of climatic change (Hannah *et al.* 2008). In Madagascar, particular attention has been given to montane habitats, which are expected to be more vulnerable to shifts in future climate due to rapid change in land-use, increasing population growth of humans, and changes in the climatic system (Raxworthy 2008). Montane amphibians often are rare and those that are local endemic species with very narrow geographic ranges and restricted movements, may not be able to shift their distributions to

Fig. 4.16: The invasive Asian Toad (*Duttaphrynus melanostictus*) introduced in Madagascar. (A) An adult individual from the Toamasina area; (B) Population well established among human settlements; (C) Survey of the species' breeding habitat. (Photographs by F. Andreone [A, B], and J. Reardon [C])

accommodate changes imposed by climatically modified habitats. Although the effects of climatic change on Malagasy amphibians have not been investigated in detail, relevant data from the Tsaratanana Massif (in the northern part of the island), revealed some clues. A study carried out between 1993 and 2003 in this area, particularly rich in endemics, provided evidence of a projected uphill displacement of species of 17 to 74 m per decade (Raxworthy *et al.* 2008). The phenological differences between these uplifts do not appear to be relevant, but the uphill changes are consistent with predictions based on meteorological warming. An analysis of an elevational shift in range projects total loss of habitat for three species below the "dangerous" warming threshold of 2 °C (Raxworthy & Nussbaum 1996a). A preliminary review for other major massifs in Madagascar points to a similar vulnerability to loss of habitat and likely extinctions on the ascending slopes. Additional elevational studies for these and other tropical montane assemblages have been recommended (Andreone & Randriamahazo 2008a, b; Andreone *et al.* 2014b).

Manipulation of hydroperiod has been cited often as a promising tool to mitigate the effects of climatic change (Shoo *et al.* 2011). Simple solutions could potentially be implemented in Madagascar such as irrigation systems, excavation of sites, or the management of vegetation. Nevertheless, the synergy of climatic change with other threats such as deforestation, or the difficult access to some of the most threatened areas in Madagascar, will also require the testing of other creative and challenging approaches to mitigation.

G. A toad invasion

The invasion of the Asian Toad, *Duttaphrynus melanostictus* in Toamasina on the east coast of Madagascar is an alarming threat, not only to other amphibian species but also to Madagascar's environment as a whole (Fig. 4.16). The toad is known to be invasive and has caused conservation issues in many other places in the world, such as Timor and Bali (Church 1960; Trainor 2009). In Madagascar, the introduced toad could lead to an ecological disaster, including the poisoning of vulnerable native predators (Crottini *et al.* 2014a; Kolby *et al.* 2014; Marshall *et al.* 2018).

The toad was first reported to the scientific community in March 2014 from an area near the city of Toamasina (Andreone *et al.* 2014a; Kolby *et al.* 2014). However, subsequent interviews with residents suggested that the toad most likely arrived prior to 2010 (Moore *et al.* 2015). Toamasina is Madagascar's second largest city and largest seaport, and it is suspected that the first toads arrived within a shipping container of imported material or goods. Notably, there was a surge in the amount of imported material to an otherwise rather rural location on the outskirts of Toamasina during the construction phase of a nickel and cobalt processing plant between 2007 and 2011. Analysis of mitochondrial DNA sequences were conducted to thoroughly investigate the geographic origin of this invasion, revealing that it was likely the result of a single introduction event with specimens in Madagascar identical (at the analysed mitochondrial marker) to a lineage of *D. melanostictus* distributed in Cambodia and southern Vietnam (Vences *et al.* 2017).

Two operative committees were created to coordinate activities related to the fight against the invasive toad. First, a national committee led by ASG Madagascar was put in charge of maintaining a relationship with the national government and communication between stakeholders. Simultaneously, the General Secretary of the Atsinanana Region took on the responsibility of supervising regional activities. In late 2014 a team of international experts on invasive species assessed the feasibility of eradication and recommended that efforts to eradicate this species proceed, although they warned that the likelihood of success was very low and that no eradication of an amphibian at such a large scale had been attempted before (McClelland *et al.* 2015).

Visual-encounter surveys conducted in 2014 as part of the eradication feasibility study showed that *D. melanostictus* already occupied an area of at least 108 km² to the South and South-West of Toamasina city centre (Moore *et al.* 2015). In Toamasina, the toad was found to be extremely abundant, with 30 or more adults observed in an hour of active searching (F. C. E. Rabemananjara, unpublished data). In September 2017 estimates showed the invaded area to have increased to at least 549 km² (Licata *et al.* 2019), and the toad was found to be widely distributed both in urban and rural areas. The most recent estimate of population size was 7.2 million toads (Licata *et al.* 2020), in comparison to the 3.77 million toads estimated from data collected in 2014 (McClelland *et al.* 2015; Reardon *et al.* 2018). Despite hopes for eradication in 2014, today the invasive population appears too large to be eradicated and instead there is now an emphasis only on control to limit or slow its spread.

Like most other bufonids, *D. melanostictus* secretes bufadienolides that are potent toxins (Ujvari *et al.* 2015). Across its native range, the coevolution of toxic toads with native fauna saw the emergence of numerous instances of resistance to bufadienolides (Ujvari *et al.* 2015). Unfortunately, in Madagascar a recent study revealed widespread vulnerability of potential predators to the bufotoxins of the introduced Asian Toad (Marshall *et al.* 2018). Additionally, the toad is a potential source of introduced pathogens and parasites of amphibians. Studies to investigate this more thoroughly are currently running, with special focus on highly virulent pathogens, such as the chytrid fungus and *Ranavirus* (G. M. Rosa, unpublished data).

Models of species' distributions suggest that the lowlands of the eastern and north-western coasts of Madagascar are most suitable for further invasion (Vences *et al.* 2017). Although there are no threatened or locally endemic amphibian species occurring in Toamasina city itself, the Parc Ivoloina and Betampona Strict Nature Reserve (respectively inhabited by 12 and 76 amphibian species, including several candidate species and species with restricted distributions) (Rosa *et al.* 2012; Crottini *et al.* 2014b), are in close proximity to Toamasina. Monitoring these sites and trial efforts to prevent colonization by the invasive toad hopefully will provide useful information to help implement control measures and limit the toad's spread in Madagascar (Shine 2018).

Fig. 4.17: Celebrations of some local festivals dedicated to the conservation of frogs. (A–C) The "Tomato Frog Festival" held in Maroantsetra in 2009; (D) One of the celebrations at the Ankaratra Massif and nearby sites. (Photographs by F. Andreone [A–C], and F. C. E. Rabemananjara [D])

VI. Conservation

A. Awareness and perception of amphibians by the public

Activities that increase the public's awareness of amphibians and to educate them about these fascinating animals are central to conservation wordwide. Such efforts are especially important for amphibians, which often are considered lesser fauna and not always deemed worthy of targeted conservation programmes. Madagascar is chronically affected by serious economic and political problems, and daily subsistence is the top priority for most people. The goal of improving the perception of amphibians and increasing knowledge of their value within Madagascar has been of high priority but often difficult to accomplish and requires further effort (Andreone *et al.* 2008a,b).

Since the launch of the Sahonagasy Action Plans and ACSAM workshops (Andreone & Randriamahazo 2008a, b; Andreone *et al.* 2016), one of the main achievements fostering awareness of the importance of amphibians has been the realisation of a number of booklets and materials for distribution in Madagascar (Andreone *et al.* 2007a, b, c, 2008b, c; Jovanovic *et al.* 2007a, b; Andreone 2019). These materials feature iconic species, such as those in the genus *Mantella*, and provide a more general overview of the threatened status of many amphibian species in Madagascar.

Furthermore, there have been a number of festivals and celebrations. Notably, in June 2009 a festival dedicated to the conservation of the Tomato Frog (*Dyscophus antongilii*) was held in the coastal town of Maroantsetra (Fig. 4.17). The event was attended by more than 800 participants and featured songs, dances, and speeches highlighting the importance of the Tomato Frog, which is endemic to the area around Maroantsetra. The Golden Mantella frog, *Mantella aurantiaca*, is also a flagship species used to increase awareness of the importance of amphibians and their environment at two annually held festivals: World Wetlands Day at the Torotorofotsy Ramsar Site and the Mangabe-Ranomena-Sasarotra celebration of biodiversity promoted by the NGO Madagasikara Voakajy.

While these festivals and publications have helped raise awareness of amphibians in Madagascar, they have only touched a small segment of the population. To be truly effective, frogs will need to be integrated more broadly as part of environmental education campaigns, or even included within the national science curriculum. However, it is interesting to note that the new 100 Ariary banknote of Madagascar now features Baron's Mantella, *Mantella baroni*, a significant step forward towards promoting awareness of amphibians in Madagascar and amphibians as iconic animals for the island.

B. Conservation actions for iconic species

Three of Madagascar's most iconic frog species have been used to launch focused conservation plans. For these species, attention has been given to forming new protected areas, with amphibians serving a flagship role. Here, we report on conservation plans that have targeted *Mantella aurantiaca*, *M. cowanii*, and *Dyscophus antongilii* (Fig. 4.18).

1. The Golden Mantella

The Critically Endangered frog *Mantella aurantiaca* is one of the better-known Malagasy species and serves as an ambassador for the amphibians of Madagascar. It has a spectacular colouration, from bright yellow to red, which makes it particularly popular within the international pet trade. Almost every terrarium hobbyist book features at least one photograph of this frog that consequently has been exported in high numbers and is currently kept by many zoological institutions and private breeders (Garcia *et al.* 2008). The species has a restricted distribution in east-central Madagascar in already highly fragmented habitat (Crottini *et al.* 2019), where its breeding ponds continue to be threatened by mining and by loss of forest (Bora *et al.* 2010; Randrianavelona *et al.* 2010a, b; Piludu *et al.* 2015). A species conservation strategy for *M. aurantiaca* was launched in February 2011 by the government of Madagascar that set out the key steps over the next five years to conserve this species in the wild.

Results from genetic analyses have demonstrated the existence of three sub-populations that serve as conservation units for *M. aurantiaca*. A northern lineage is found around the Torotorofotsy-Ambatovy area and two southern lineages (Sasarotra and Besariaka + Andranomandry, the latter in the southwest) are known from near Mangabe (Crottini *et al.* 2019). Recent surveys have identified 139 ephemeral ponds where the species occurs, 103 in the southern and 36 in the northern portion (Piludu *et al.* 2015). The NGO Madagasikara Voakajy initiated a survey to assess the frog populations and the habitat-qualities of individual ponds. A habitat-suitability index was generated and used to select suitable sites for reintroduction, with the aim of relocating populations from habitats impacted by the Ambatovy nickel and cobalt mining project.

The Ambatovy mine is one of the largest of its kind worldwide and to date is the greatest foreign financial investment in Madagascar. The mining project has impacted a number of important breeding ponds for *M. aurantiaca*, the footprint of the mine being centered within the last habitat remaining for the northern sub-population. To attempt to mitigate habitat damaged and destroyed on the mine's footprint, the Ambatovy project focused on recovery of the population, habitat-compensation, and the establishment of a captive survival-assurance colony. Results of these recently launched initiatives to offset biodiversity are still forthcoming.

With the loss of habitat being the greatest threat to the species, protecting what remains is key to ensuring a future for *M. aurantiaca*. Three main areas have been identified for protection and are in various stages of being developed: (1) Mangabe-Ranomena-Sasarotra, (2) Torotorofotsy Ramsar Site, and (3) the Forest Corridor Analamay-Mantadia. Mangabe-Ranomena-Sasarotra is the furthest along towards protection and supports most of the southern sub-populations of *M. aurantiaca*, which includes 79 ponds within a strict conservation zone, as well as others in an area for sustainable use and a buffer zone around the protected area. Mangabe-Ranomena-Sasarotra obtained the temporary status of "new protected area" in December 2010 and, as of this writing, ten local community groups (known as COBAs or Communautés Locales de Base) have been created to help manage *M. aurantiaca* habitat.

Farther north, the sub-population at Torotorofotsy wetland is monitored by the community groups of Association Mitsinjo and Taratra in collaboration with the NGO Asity, and at the Forest Corridor Analamay-Mantadia by Mamelontsoa, Telomira, and Fampana. Periodic visits to breeding sites for increasing public awareness and dissuading illegal mining activity are conducted by local government and monitoring agents several times per year.

Fig. 4.18: Threatened amphibian species with ongoing conservation projects. (A) Golden Mantella, *Mantella aurantiaca* is an Endangered species which is being affected by mining activity in the Andasibe area (Bekalala site); (B) Harlequin Mantella, *Mantella cowanii*, from a population close to Antoetra; (C) Tomato Frog, *Dyscophus antongilii* and its habitat around Antara on the East coast, where populations inhabit a non-urban habitat and breed in slow-moving waters.
(Photographs by F. Andreone)

To some extent this action has helped control illegal artisanal gold-mining, which is one of the major threats to the habitat of this species.

To help promote sustainable livelihoods for communities in the vicinity of *M. aurantiaca* habitat, four women's associations were established in 2010. Members were trained in sewing embroidery to sell at markets, and some of the resulting work has featured *M. aurantiaca* as a flagship species. In addition, local communities at Mangabe-Ranomena-Sasarotra and Torotorofotsy Ramsar Site have been trained in new agricultural techniques and methods for rearing livestock to provide alternatives to more harmful, but widely practiced, shifting agricultural methods that continue to threaten *M. aurantiaca*'s breeding ponds.

Although loss of habitat is the main threat facing *M. aurantiaca*, concern has also been raised regarding the collection of wild frogs for the pet trade. Accordingly, an already greatly reduced annual export quota of 550 individuals established for 2012 and 2013 under CITES, was lowered to 280 individuals in 2015–2019. Following monitoring in 2010, 2012, and 2013, three sites, represented by 11 ponds, were identified in Mangabe-Ranomena-Sasarotra for use for commercial collection.

The conservation strategy aimed at *M. aurantiaca* also has involved community outreach and awareness. Sessions have been conducted at schools around Mangabe that help highlight the ecological importance of the environment where *M. aurantiaca* is found and its unique endemism to the local area. An annual festival to celebrate the importance of conserving the forests around Mangabe-Ranomena-Sasarotra also takes place. This event is an occasion for the local community and the monitoring groups of which they are a part to share the results of their efforts towards the conservation of their local threatened species, which includes *M. aurantiaca*. Although there is still much to be done to assure a future for the Golden Mantella, the past decade of work has demonstrated substantial progress.

2. The Harlequin Mantella

The Harlequin Mantella, *Mantella cowanii* is among the most threatened amphibian species in Madagascar (Rabibisoa *et al.*

2013). Its distribution is restricted to the central highlands, and there are few known populations (Rabibisoa *et al.* 2009). These are mainly based around four areas—Antoetra, Itremo, Betafo, and Antakasina—which are all over 1400 m a.s.l. At these sites *M. cowanii* can be found within gallery forest and along humid rockwalls in otherwise degraded savannah.

The town of Antoetra was chosen as an area to dedicate to the conservation of *M. cowanii* (Rabibisoa 2008). One site, Fohisokina (also known as Vohisokina), has been set aside for protection and is currently managed by local authorities with the assistance of Conservation International and the NGO Man and the Environment. A second site, Soamazaka, is planned as an area for visiting researchers and tourists so as to limit the impact of visitors on the species.

To date, conservation activities around Antoetra include (1) initiatives to provide sustainable livelihoods, such as planting native trees for the production of essential oils (in particular Ravintsara, *Cinnamomum camphora*) and for use as fuel-wood, and (2) stricter conservation measures, such as the implementation of firebreaks to protect the last of the tiny remaining habitat where the frog occurs (Andreone *et al.* 2013c). A group called "Sahona Mena" was self-constituted by the community of Antoetra to help manage sites that support *M. cowanii*. This group patrols the territory and reports on actions that threaten two sites. However, further work is needed to assure the species' survival considering other recent threats, such as hybridization with *M. baroni* (Chiari *et al.* 2005) or potential impact from a chytrid fungus *Bd* (Bletz *et al.* 2015a).

In December 2018, a meeting-workshop was held in Ambositra to discuss and develop a new action plan for the species. Among the scheduled actions are an increase in ecological research, a biomolecular assessment of the known populations (including recently found populations in the Betafo region), development of local populations, and assessment of captive breeding. These actions were subsequently summarized in the *McAP*, the *Mantella cowanii* Action Plan 2021–2025 (Andreone *et al.* 2020).

3. *The Tomato Frog*

A third iconic frog species that has recently been involved in a conservation campaign is the Tomato Frog, *Dyscophus antongilii*. The Tomato Frog appears less in peril than the two *Mantella* species discussed previously, being currently assessed as Least Concern by the IUCN Red List. Its range is also larger than formerly believed, and it is present not only in the Maroantsetra and Makira area (North-East Madagascar) but also farther South, e.g., around the sites of Antara and Iampirano (Tessa *et al.* 2008). Still, the Maroantsetra population is notable since the species is synanthropic and can be found in ponds, roadside ditches, and residents' gardens. It serves as a true flagship species for amphibian conservation.

Such an iconic species occurring in an urban environment provides a unique opportunity for education and environmental outreach, and it has been featured widely around Maroantsetra in festivals and community events. Notably, in 2009 ASG Madagascar and the Madagascar Fauna and Flora Group organized a "Tomato Frog Festival" which was widely attended and reached many people (Fig. 4.17). Data collected during activities supported by the European Association of Zoos and Aquaria (EAZA) helped to reassess the species' status, which passed from former inclusion in CITES Appendix I to Appendix II.

During recent years, the Tomato Frog's population around Maroantsetra has appeared to have declined. The driver of this decline remains unknown, but it is suspected to be related to increased urbanisation and resulting loss of habitat. Its habitat and especially the aquatic areas needed for breeding have not been taken into consideration as development proceeds and as new roads and houses are built. For this reason, a small patch of land adjacent to one of the best-known breeding sites for the species was purchased using funds obtained from BIOPAT (Patrons for Biodiversity, *http://www.biopat.de*) and placed under management of the local NGO Antongil Conservation. Unfortunately, due to a series of difficulties associated with the lowering of the level of groundwater in Maroantsetra, the *Dyscophus* populations are still experiencing local decline.

C. *Ex situ* populations as a tool for conservation

When a species or population is in decline, securing captive-assurance colonies can serve as a rapid response, and in some situations may be the only option available to prevent imminent extinction (Gagliardo *et al.* 2008; Browne *et al.* 2011; Zippel *et al.* 2011). Such interventions hold populations of threatened species in captivity, maintaining a viable genetic representation which can provide animals for supplementation or reintroduction programmes, which have to follow very strict protocols to avoid doing harm when aiming to do good (e.g., importing diseases with the reintroduced animals).

The development of such programmes provides important opportunities to build capacity and expertise, to answer research questions that have implications for conservation, and to generate interest in, and raise funds for, amphibian conservation (Bloxam & Tonge 1995; Mendelson *et al.* 2007; Buley *et al.* 2008; Zippel *et al.* 2011; Preininger *et al.* 2012). However, such goals must be secondary to safeguarding against extinction, and *ex situ* conservation programmes should only be enacted following the guidelines provided by the IUCN (2014).

Given the goal of releasing captive-bred frogs back into natural habitats, conservation efforts must address and mitigate the causes of amphibian declines in addition to enacting breeding programmes (Griffiths & Pavajeau 2008; Harding *et al.* 2016). Other scenarios may involve translocation of populations to sites that were occupied in the past or to introduce species to new suitable sites. Yet, all of these interventions are shrouded with concerns, e.g., reducing the fitness of reintroduced animals and inbreeding depression (Smith *et al.* 2019). Moreover, *ex situ* programmes are expected to follow biosecurity measures so as to minimise the bidirectional risk of introducing pathogens (Green *et al.* 2009). This is particularly relevant when maintaining amphibians outside of their native range or in facilities with non-sympatric species (Tapley *et al.* 2015).

D. Malagasy frogs in captivity to date

Madagascar is home to many charismatic species of frogs familiar to zoological institutions. Well-known examples include those in the genera *Mantella*, *Dyscophus*, *Heterixalus*, and *Scaphiophryne*, most of which are attractively coloured and maintained informally in captivity for display. Some Malagasy species, such as the Golden Mantella, *Mantella aurantiaca*, have a history of being kept and bred in captivity dating from the early 1970's (Audy 1973; Mudrack 1974). Despite the interest, there is still a huge lack of knowledge and expertise on the requirements for captive husbandry for most of the island's amphibian species (Garcia *et al.* 2008; Griffiths & Pavajeau 2008), and the species currently

Fig. 4.19: Examples of zoological institutions committed to optimisation of husbandry protocols and techniques to successfully breed Malagasy amphibian species. (A) Exhibit of the False Tomato Frog, *Dyscophus guineti* at the Acquario di Genova (Genoa, Italy); (B) A breeding pair in amplexus; (C) Husbandry unit for breeding population of *Mantella laevigata* within "Masoala Regenwald" in Zoo Zürich (Switzerland). (Photographs by G.M. Rosa [A, B], and S. Furrer [C])

maintained represent only a tiny fraction of the amphibian species diversity found on the island. A survey of the international zoo community conducted in 2007 found merely 27 Malagasy frog species being maintained in captivity and of these barely half (14) had been bred in the past decade (Garcia *et al.* 2008). A search of the database six years later revealed no significant changes and the only improvement was an increase in the diversity of *Mantella* species that were being kept and bred. The lack of diversity represented in captivity hinders the ability of the *ex situ* conservation community to address the threats that Malagasy amphibians face through captive-breeding programmes. However, when compared to the amphibian species of the entire Afrotropical region, Lötters (2008) found that those from Madagascar already amounted to half of all species maintained by zoological institutions, and so comparatively, the scenario for Malagasy frogs may not be as dire as elsewhere.

1. *Amphibian husbandry outside Madagascar*

Outside Madagascar, many zoological institutions have contributed to captive-breeding programmes for Malagasy amphibians. The Acquario di Genova in Italy (Gili 2008) and Riga Zoo in Latvia have been developing husbandry techniques to successfully breed Tomato Frogs (*Dyscophus* spp.) (Fig. 4.19; Rosa *et al.* 2009). In Switzerland, Zoo Zürich has an entire building (greenhouse) devoted to the fauna and flora of Madagascar (the "Masoala-Halle") where some Malagasy frogs breed, such as the Climbing Mantella (*Mantella laevigata*; Fig. 4.1.C). These and numerous other projects with Malagasy species in Europe and North America have played a fundamental role in raising public awareness abroad about the diversity and threats facing amphibians in Madagascar; examples are the "Year of the Frog" and the "Madagascar" campaigns in 2007–2008.

Captive collections at zoos can contribute to understanding the ecology and behaviour of poorly known Malagasy species. By disseminating results to the *ex situ* conservation community, zoos can better contribute to helping conservationists and wildlife managers make informed decisions and provide a foundation on which to base future captive-breeding in Madagascar. The vision of locally staffed regional amphibian captive-breeding and research centres has been enhanced by a team of international conservation and policy authorities (Mendelson *et al.* 2006; Tapley *et al.* 2015). When developed within the native country of a species, captive-breeding programmes encourage autonomy of local institutions, reduce biosecurity risks, and instill a sense of pride within local stakeholders that contributes to a lasting impact upon conservation (Gagliardo *et al.* 2008; Tapley *et al.* 2015).

2. *Amphibian husbandry in Madagascar*

Historically, captive amphibians in Madagascar have been used for display at zoological parks such as the Parc Botanique et Zoologique de Tsimbazaza (Antananarivo), Croc-Farm (Antananarivo), or the Peyrieras Madagascar Exotique (Marozevo). Animals were typically sourced from the wild and often kept overstocked and poorly maintained (Fig. 4.20). After a general call for capacity-building of amphibian husbandry (Andreone *et al.* 2006; Furrer 2008; Mendelson & Moore 2008), the first steps were tak-

Fig. 4.20: In country facilities keeping Malagasy amphibian species. (A) False Tomato Frogs (*Dyscophus guineti*) sourced from the wild and maintained in large numbers, near Marozevo; (B) The "batrachorium" amphibian exhibits at the Parc Botanique et Zoologique de Tsimbazaza, in Antananarivo.
(Photographs by G. M. Rosa)

en to develop expertise in captive husbandry within Madagascar; these were supported later by an amphibian husbandry workshop (see below; Rakotonanahary *et al.* 2017). Several organisations in Madagascar are now putting effort into developing the infrastructure and capacity needed to manage captive amphibian populations (Edmonds *et al.* 2012, 2015; Dawson *et al.* 2014).

The Parc Ivoloina is a zoological and botanical garden managed by Madagascar Fauna and Flora Group (MFG) and located 12 km from the port city of Toamasina in eastern Madagascar. They developed an exhibit for the Tomato Frog (*D. antongilii*) in 2008. The project aimed both to expand expertise in amphibian husbandry among staff as well as to raise awareness of the plight of the Tomato Frog. A few years later, MFG also constructed a small centre to expand their amphibian husbandry, where they have maintained a group of reed frogs, *Heterixalus madagascariensis*, and work to culture live foods (Fig. 4.21; Edmonds 2013, 2014; Iambana 2015). This project seems to be suspended, at least for the moment.

In Andasibe, the community-run Association Mitsinjo has developed a breeding facility specifically for managing captive survival-assurance populations of its local species of frogs. Support to initiate the project was given by Amphibian Ark and the Association of Zoos and Aquariums (AZA), with the resulting building measuring 185 m² and consisting of three rooms: one for production of live food, one for quarantine, and one for maintaining captive frogs (Fig. 4.22; Edmonds *et al.* 2012). The project was officially launched in April 2011 through a contract of collaboration between Association Mitsinjo, ASG Madagascar, and the Direction Générale des Forêts. In this same month, the first frogs were collected and established at the facility, consisting of four locally common species to serve as practice for technicians while they developed expertise in husbandry.

During the six months it took to build the infrastructure in Andasibe, local invertebrates were collected, and trials were carried out to develop techniques for the production of live food prior to maintaining populations of frogs. Through this process, Association Mitsinjo and the Mention Zoologie et Biodiversité Animale at the University of Antananarivo (formerly Département de Biologie Animale) worked together to develop colonies of live invertebrates to use as food for future captive frogs. Today, Association Mitsinjo cultures five species of locally-sourced crickets, a fruit fly, cockroaches, and springtails.

Fig. 4.21: (A) Amphibian breeding facility realised at the Parc Ivoloina to build local capacity for husbandry; (B) Currently housing live food colonies and *Heterixalus madagascariensis*.
(Photographs by B. Iambana)

Fig. 4.22: Amphibian captive breeding facility in Andasibe managed by Association Mitsinjo. (A) Floor plan of the building; (B) Overview of the building; (C) Terraria setup on shelving and plumbed so waste water flows into a drain in the floor; (D) Crickets being bred for live food.
(Photographs by G. M. Rosa [B, D], and S. Sam[C])

In 2012, a training course focussing exclusively on the more technical side of the husbandry of captive amphibians, was supported by the EAZA (European Association of Zoos and Aquaria) and led collectively by the Durrell Wildlife Conservation Trust and the Chester Zoo; it was held in Andasibe under the coordination of the Association Mitsinjo. The course was composed of lectures, activities, and group-work, as well as of on-site training at the Andasibe breeding facility. Eight Malagasy institutions and NGO's participated in the training and developed further aptitude to manage local *ex situ* amphibian conservation centres and research facilities. Additional in-country building of capacity since then has consisted of exercises in amphibian-marking techniques carried out with staff from Chester Zoo, as well as veterinary support and screening of disease through the San Diego Zoo Institute for Conservation Research and the Woodland Park Zoo.

As of 2018, 14 species of frogs have been kept at the Mitsinjo amphibian breeding centre in Andasibe (Fig. 4.23). Eight of these have reproduced, several to the second or third generations. The Malagasy staff already are well versed in techniques to maintain various types of amphibians (and their food supply) in captivity. Technicians, who are local residents of Andasibe, and who have experience in caring for frogs that have a varied set of life-history traits, assist in carrying out investigations into the optimal requirements of species from different ecological guilds. Working with a diversity of species helps prepare for the emergence of threats, which may require rapid action to prevent extirpation or extinction.

To complement Association Mitsinjo's work and fulfill an objective within the national conservation strategy for the species (Randrianavelona *et al.* 2010a, b), a captive population of the Golden Mantella, *Mantella aurantiaca*, was also established at the facility (Fig. 4.24; Edmonds *et al.* 2015; Rakotonanahary *et al.* 2017). Offspring produced in captivity are used for reintroductions at created receptor sites to help mitigate the destruction of habitat on the footprint of the aforementioned Ambatovy nickel and cobalt mine.

3. Priorities for amphibian ex situ *conservation*

Lists of priority amphibian species have been developed for numerous countries and regions, including Madagascar, thereby providing direction for the network of stakeholders involved in *ex situ* amphibian conservation (Andreone *et al.* 2008a). Notably, it was stressed to call for the *ex situ* community to focus husbandry research on Malagasy species representative of various ecological guilds, especially with regard to those that may be able to serve as surrogates for threatened species (Andreone & Randriamahazo 2008a, b). The expectation is that surrogate species with similar ecological and life-history traits to those that are a high priority can serve as models to develop expertise in husbandry prior to establishing captive colonies of threatened species when needed (Buley *et al.* 2008).

Malagasy organisations, such as the Association Mitsinjo, have developed infrastructure for captive breeding programmes and

Fig. 4.23: Some of the frog species kept at the Association Mitsinjo captive breeding facility. (A) *Heterixalus betsileo*; (B) *Heterixalus punctatus*; (C) *Boophis pyrrhus*; (D) *Guibemantis pulcher*; (E) *Guibemantis* sp. aff. *albolineatus*; (F) *Blommersia blommersae*; (G) *Mantella aurantiaca*; (H) *Mantidactylus betsileanus*; (I) *Stumpffia* sp.
(Photographs by F. Andreone [B, C], D. Edmonds [A, E–I], and D. Vallan [D])

staff now have expertise in the husbandry of captive amphibians. However, there continues to be a lack of long-term sustainable support from conservation organizations and zoological parks outside of Madagascar to ensure these programmes continue in the future. Additionally, while training in the techniques of husbandry has been provided, the ambition to search for support to take on new captive-breeding projects of a significant magnitude continues to fall short within Madagascar.

To overcome these challenges requires a multitude of stakeholders to work together. Organisations in Madagascar will need external financing and lasting commitments from the international *ex situ* conservation community. Zoological institutions abroad that already maintain amphibian species from Madagascar in captivity should consider becoming involved in the effort. Malagasy staff from various organisations also will need to partner together, allowing the technical aspects of amphibian captive husbandry to be shared through training exchanges and additional capacity-building workshops. Fortunately, authorities in Madagascar are on board to develop further capacity for captive breeding, and with the New Sahonagasy Action Plan (see below) ratified by the Malagasy state there is an existing framework for appropriate actions.

There is also a need to increase the available information on captive husbandry for Malagasy amphibian species currently held by zoological institutions. Individual zookeepers, technicians, students, and breeders should make an effort to conduct scientific investigations into the species of frogs from Madagascar they already maintain, and then disseminate this information through peer-reviewed publications. Far too often only anecdotal reports of captive husbandry exist, or valuable behavioural observations are left to hearsay, and while this is better than nothing, ideally the community of amphibian breeders can work together to test some of the assumptions made about the frogs they keep, especially for species from Madagascar for which little information is available otherwise.

While it may be intimidating to confront the difference between what resources are available in Madagascar and what is needed to enact further *ex situ* programmes, the developments during the past decade are encouraging. Mitsinjo's in-country facility is now operational, although still in its formative years. Care should be taken that these, and future, *ex situ* programmes align with *in situ* conservation action, and that prospective captive-breeding projects in Madagascar have clearly defined objectives. The harmony of parallel *ex situ* and *in situ* conservation actions will be based on stakeholders planning conservation strategies together, maintaining communication, and implementing adaptive management practices. Ideally, an *ex situ* national coordinator for amphibian conservation should be appointed to facilitate these goals.

International stakeholders can contribute to the captive-breeding effort in Madagascar by making the lasting commitments of support needed to further these projects, as well as by sharing information garnered through studies of captive husbandry. So far, despite the alarming threats the frogs of Madagascar face, no modern

extinctions have been detected (Andreone *et al.* 2008a). This provides hope that there may still be time left to further prepare the infrastructure, knowledge, and capacity for priority species in time to be able to rapidly implement programmes for captive breeding.

E. The ACSAM Initiative and the Sahonagasy Action Plans

In 2006, the "A Conservation Strategy for the Amphibians of Madagascar" (ACSAM) meeting was held in Antananarivo and led by ASG Madagascar. The meeting resulted in several publications, including an important monograph and a book of contributions, as well as the first Sahonagasy Action Plan (Andreone & Randriamahazo 2008a, b).

The implementation of the Sahonagasy Action Plan was estimated to cost almost 1.8 million EUR over a five-year period, but only a fraction of these funds eventually were raised (Andreone *et al.* 2012). The conservation actions launched as part of the 2008 Sahonagasy Action Plan soon faded into the background as the 2009 political crisis led to the suspension of donor activity from many of the traditional funding sources for the conservation of biodiversity. Only in 2014 did the democratic election of a new president take place, helping renew partnerships with international aid. During this gap period many problems arose for wildlife and the environment, among which was the rampant illegal logging of Malagasy hardwoods, especially rosewood, from protected areas, notably in the North-East around the Masoala Peninsula and at Marojejy (Schuurman & Lowry 2009; Barrett *et al.* 2010). The illegal logging from protected areas was also linked to the inability of Malagasy authorities to enforce the laws managing the use of natural resources.

In November 2014, a second amphibian conservation workshop (ACSAM2) was held at Centre ValBio in Ranomafana (Rosa *et al.* 2015; Andreone *et al.* 2016; Fig. 4.10C). More than 70 herpetologists, conservationists, and politicians participated. Among the main topics discussed at ACSAM2, two issues emerged as new potential threats: the detection of a chytrid fungus (Bletz *et al.* 2015a, b) and the introduction of the Asian Common Toad (Crottini *et al.* 2014a). Additional topics included long-term population monitoring, captive breeding, standardisation of field protocols, and a review of progress since the first ACSAM. The ACSAM2 meeting resulted in the publication of the New Sahonagasy Action Plan (NSAP), which is now ratified by the Malagasy government and sets priorities for amphibian conservation for the five-year period of 2016–2020.

Fig. 4.24: Captive Golden Mantellas (*Mantella aurantiaca*) in the Mitsinjo breeding facility in Andasibe. (A) Population in the quarantine-restricted area; (B) Frogs in a terrarium.
(Photographs by G.M. Rosa [A], and D. Edmonds [B])

The NSAP has six main themes/topics: (1) Coordination of Research and Conservation, (2) Monitoring Madagascar's Amphibians and their Environment, (3) Emerging Infectious Diseases, (4) Site-Management, (5) Harvesting and Trade, and (6) Captive Breeding and Zoo Actions. Within each theme, participants of ACSAM2 identified specific conservation actions that were needed, their priority, the timeframe of their activity, indicators of success, and the responsible institutions. The new plan provided clear direction for amphibian research and conservation in Madagascar, and with support from funding agencies and continued political stability there is real potential to see a positive outcome for the frogs of the island.

F. Where will amphibian conservation go in Madagascar?

As we have shown, the conservation of Madagascar's amphibians is a task to which many herpetologists and naturalists have devoted (and are still devoting) a great amount of time and passion. This is especially true when considering the work conducted over the past decade, coordinated in large part by the IUCN SSC Amphibian Specialist Group. Several areas around the world that support high levels of biodiversity fall in countries that are characterised by serious socioeconomic problems and instability. Madagascar supports a very high number of amphibian species (likely more than 500; Perl *et al.* 2014), but at the same time continues in a critical socioeconomic situation. We strongly reaffirm our conviction that the promotion of amphibian conservation throughout Madagascar is extremely important because amphibians make up a spectacular component of the island's unique biodiversity, and like the renowned lemurs, we hope that amphibians can serve as a new flagship for the island's conservation. Biodiversity is probably the only long-lasting resource of Madagascar, and we believe that its management can play a crucial role in the economic development of the country. The publication of two action plans (Andreone

& Randriamahazo 2008a, b; Andreone *et al.* 2016) is an opportunity to drive nature conservation in Madagascar by taking into consideration the need for a global approach to biodiversity. Madagascar's high amphibian species diversity, together with old threats (e.g., deforestation) and novel ones (e.g., chytridiomycosis; introduction of an invasive toad), make a clear case for the importance of conservation. Conserving Madagascar's amphibians means working for the love of its nature, wildlife, and people, and believing in providing a future for the island's unique frogs for future generations.

VII. Acknowledgements

We thank the following people for their help during many years of field and laboratory work, discussions, friendship, and companionship: K.A. Andreone, S.C. Andreone, R.L. Andriamiarisoa, B. Andriamihaja, A. Angulo, O. Arnoult, C. Avesani Zaborra, M. Bauert, O. Behra, P. Eusebio Bergò, S. Bin, P. Bishop, M. Bletz, A. Bollen, Y. Chiari, V.C. Clark, J. Copsey, N. Cox, D. Church, J. Dawson, G. Deltour, R. Dolch, C. Domergue, E.J. Edwards, S. Faravelli, M. Fisher, K. Freeman, S. Furrer, C. Gibault, F. Glaw, J. Glos, S.M. Goodman, B. Gratwicke, R.A. Griffiths, F.M. Guarino, R. Harris, N. Heard, B. Iambana, R. Jenkins, J. Köhler, J.W. Lewis, R. Lewis, O. Marquis, F. Mattioli, V. Mercurio, C. Misandeau, M. Moore, R. Moore, S.H. Ndriantsoa, J. Noël, G. Odierna, I. Porton, S. Rabesihanaka, H. Rabetaliana, N.H. Rabibisoa, J.C. Rakotoarisoa, A. Rakotoarison, T.F. Rakotonanahary, F. Rakotondraparany, H. Randriamahazo, J.E. Randrianirina, A.P. Raselimanana, C.J. Raxworthy, A. Rübel, A. Sabin, D. Salvi, S. Sam, A. Sarovy, E. Scanarini, M.D. Scherz, D. Schuurman, M.O. Sohantenaina, S.N. Stuart, G. Tessa, M. Vences, C. Weldon, S. Wolf, L. Woolaver, and P. Wright. We also thank the Mention Zoologie et Biodiversité Animale at the University of Antananarivo, the Parc Botanique et Zoologique de Tsimbazaza, and ICTE/MICET for their precious assistance in various administrative and logistical aspects. In particular, we thank the Madagascar National Parks, the Ministère de l'Environnement et du Développement Durable, and the Diréction des Aires Protégées, des Ressources Naturelles renouvelables et des Ecosystèmes for the much-needed research authorisations. The field and laboratory work have been supported by several institutions and organisations, that we thank here: IUCN SSC Amphibian Specialist Group, Amphibian Survival Alliance, Andrew Sabin Family Foundation, Association Vahatra, Madagasikara Voakajy, Bioparco ZOOM, BIOPAT, Critical Ecosystem Partnership Fund, Conservation International, Deutsche Gesellschaft für Internationale Zusammenarbeit, European Association of Zoos and Aquaria, Gondwana Conservation and Research, John D. and Catherine T. MacArthur Foundation, Madagascar Fauna and Flora Group, Association Mitsinjo, Mohamed bin Zayed Species Conservation Fund, Nando Peretti Foundation, Parco Natura Viva, Regione Piemonte, Reptiland, Rufford Small Grants for Nature Conservation, UIZA, Van Thienhoven Foundation, WAZA, Wildcare Institute, Wildlife Conservation Society, WWF Madagascar et Océan Indien Occidental, Zoo Project, Zoo de Thoiry, and Zoo Zürich. Finally, F. Andreone thanks M.-O. Rödel for having invited him to coordinate the redaction of this chapter.

VIII. References

Alford R., Bradfield K. & Richards S. 2007. Global warming and amphibian losses. Nature **447**: E3–E4.

Ali J.R. & Aitchison J.C. 2008. Gondwana to Asia: plate tectonics, paleogeography and the biological connectivity of the Indian subcontinent from the Middle Jurassic through latest Eocene (166–35 Ma). Earth-Science Reviews 88: 145–166.

Allnutt T.F., Asner G.P., Golde C.D. & Powell G.V.N. 2013. Mapping recent deforestation and forest disturbance in northeastern Madagascar. Tropical Conservation Science 6: 1–15.

AmphibiaWeb 2021. *https://amphibiaweb.org*. University of California, Berkeley (accessed on the 10th March 2021).

Anderson A., Clark G., Haberle S., Higham T., Nowak-Kemp M., Prendergast A., Radimilahy C., Rakotozafy L.M., Ramilisonina, Schwenninger J.-L., Virah-Sawmy M. & Camens A. 2018. New evidence of megafaunal bone damage indicates late colonization of Madagascar. PLoS ONE 13: e0204368.

Andreone F. 1991. Conservation aspects of the herpetofauna of Malagasy rainforests. Zoological Society La Torbiera Scientific Reports 1: 1–45.

Andreone F. 1994. The amphibians of Ranomafana rain forest, Madagascar – preliminary community analysis and conservation considerations. Oryx 28: 207–214.

Andreone F. 2003a. Un'arca nell'Oceano Indiano? La biodiversità in Madagascar fra conservazione, ricerca scientifica e sviluppo. Berenice 27: 140–156.

Andreone F. 2003b. The herpetological diversity of Madagascar: from field surveys to conservation. *In*: Anonymous (ed.) Toward the integration of biodiversity studies. Kyoto, 26–27 March 2003.

Andreone F. 2013. Oltre 20 anni di survey erpetologiche e di conservazione della biodiversità in Madagascar del Museo Regionale di Scienze Naturali (Torino). Museologia Scientifica 9: 51–56.

Andreone F. 2015. Malagasy rainbow frog. *In*: Hegan A. (ed.) No more endlings: saving species one story at a time. Purple Elephant, New York, pp. 189–196.

Andreone F. 2019. In Madagascar. Fra le rane e altri animali. Fiorina Edizioni, Varzi.

Andreone F. & Luiselli L. 2000. Are there shared patterns of specific diversity, abundance, and guild structure in snake communities of tropical forests of Madagascar and continental Africa? Terre et Vie (Revue d'Écologie) 55: 215–239.

Andreone F. & Randriamahazo H. 1997. Ecological and taxonomic observations on the amphibians and reptiles of the Andohahela low altitude rainforest, S. Madagascar. Revue Française d'Aquariologie 3/4: 95–128.

Andreone F. & Randriamahazo H. 2008a. Sahonagasy Action Plan. Conservation strategies for the amphibians of Madagascar/Stratégies de conservation pour les amphibiens de Madagascar. Museo Regionale di Scienze Naturali, Conservation International, IUCN/SSC Amphibian Specialist Group, Torino.

Andreone F. & Randriamahazo H. 2008b. Essay 5.2. The endemic and threatened amphibians of Madagascar. *In*: Stuart S., Hoffmann M., Chanson J., Cox N., Berridge R., Ramani P. & Young B. (eds) Threatened amphibians of the world. Lynx Editions, Barcelona, pp. 59–60.

Andreone F., Randrianirina J.E., Jenkins P.D. & Aprea G. 2000. Species diversity of Amphibia, Reptilia and Lipotyphla at Ambolokopatrika, a rainforest between Anjanaharibe-Sud and Marojejy massifs, NE Madagascar. Biodiversity and Conservation 9: 1587–1622.

Andreone F., Behler J., Bloxam Q., Cadle J., Kuchling G., Rabemananjara F.C., Rabesihanaka S., Rabibisoa N., Rakotoarimanana J., Rakotomalala D., Rakotomavo E., Ramanamankjato J.-B., Ramilison O., Randriamahazo H., Randrianirina J., Raselimanana A.P., Ravolonaivo R., Raxworthy C., Razafindrasoa R. & Raxandrimamilafiniarivo 2001. Rapport du groupe reptiles et amphibiens. *In*: AAVV (eds) Evaluation et plans de gestion pour la conservation (CAMP) de la faune de Madagascar: lémuriens, autres mammifères, reptiles et amphibiens, poissons d'eau douce. Madagascar Fauna Group, Mantasoa 20–25 May 2001.

Andreone F., Cadle J.E., Cox N., Glaw F., Nussbaum R.A., Raxworthy C.J., Stuart S.N., Vallan D. & Vences M. 2005. Species review of amphibian extinction risks in Madagascar: conclusions from the Global Amphibian Assessment. Conservation Biology 19: 1790–1802.

Andreone F., Mercurio V. & Mattioli F. 2006. Between environmental degradation and international pet trade: conservation strategies for the threatened amphibians of Madagascar. Natura – Società italiana Scienze Naturali e deMuseo civico di Storia naturale in Milano 95: 81–96.

Andreone F., Bungard M. & Freeman K. 2007a. Amphibiens menacés de Madagascar. Museo Regionale di Scienze Naturali, Torino.

Andreone F., Bungard M. & Freeman K. 2007b. Anfibi minacciati del Madagascar. Museo Regionale di Scienze Naturali, Torino.

Andreone F., Bungard M. & Freeman K. 2007c. Threatened amphibians of Madagascar. Museo Regionale di Scienze Naturali, Torino.

Andreone F., Bungard M. & Freeman K. 2008a. Ireo sahona tandindomin-doza eto Madagasikara. Museo Regionale di Scienze Naturali, Torino.

Andreone F., Carpenter A.I., Cox N., du Preez L., Freeman K., Furrer S., Garcia G., Glaw F., Glos J., Knox D., Köhler J., Mendelson J.R. III, Mercurio V., Mittermeier R.A., Moore R.D., Rabibisoa N.H.C., Randriamahazo H., Randrianasolo H., Raminosoa N.R., Ramilijaona O.R., Raxworthy C.J., Vallan D., Vences M., Vieites D.R. & Weldon C. 2008b. The challenge of conserving amphibian megadiversity in Madagascar. PLoS Biology 6: e118.

Andreone F., Cox N., Glaw F., Köhler J., Rabibisoa N.H.C., Randriamahazo H., Randrianasolo H., Raxworthy C.J., Stuart S.N., Vallan D. & Vences M. 2008c. Update of the global amphibian assessment for Madagascar in light of new species discoveries, nomenclature changes, and new field information. *In*: Andreone F. (ed.) A conservation strategy for the amphibians of Madagascar, Monografie 45. Museo Regionale di Scienze Naturali, Torino, pp. 419–438.

Andreone F., Rosa G.M., Noël J., Crottini A., Vences M. & Raxworthy C.J. 2010. Living within fallen palm leaves: the discovery of an unknown *Blommersia* (Mantellidae: Anura) reveals a new reproductive strategy in the amphibians of Madagascar. Naturwissenschaften 97: 525–543.

Andreone F., Giacoma C., Guarino F.M., Mercurio V. & Tessa G. 2011. Age profile in nine *Mantella* poison frogs from Madagascar, as revealed by skeletochronological analyses. Alytes 27: 73–84.

Andreone F., Carpenter A.I., Copsey J., Crottini A., Garcia G., Jenkins R.K.B., Köhler J., Rabibisoa N.H.C., Randriamahazo H. & Raxworthy C.J. 2012. Saving the diverse Malagasy amphibian fauna: where are we four years after implementation of the Sahonagasy Action Plan? Alytes 29: 44–58.

Andreone F., Eusebio Bergò P., Mercurio V. & Rosa G. 2013a. Spatial ecology of *Scaphiophryne gottlebei* in the Isalo canyons, Madagascar. Herpetologica 69: 11–21.

Andreone F., Loarie S.R., Pala R., Luiselli L.M. & Carpenter A.I. 2013b. Trade and exploitation of amphibians and reptiles: a conservation overview. Atti dell'Accademia delle Scienze di Torino. Classe di Scienze Fisiche, Matematiche e Naturali **146**: 85–93.

Andreone F., Rabemananjara, F.C.E., Rabibisoa N., Rahantalisoa H. & Rakotondrasoa J.M. 2013c. Awareness and citizen-based initiatives in Madagascar boost the conservation of its endemic amphibians. FrogLog **107**: 38–40.

Andreone F., Cadle J.E., Crottini A., Dawson J., Larney E., Rabemamanjara F.C.E., Rabesihanaka S., Rabibisoa N., Rabsomanitrandrasana E., Rakotonanahary T. & Rosa G.M. 2014a. A new meeting for amphibian conservation in Madagascar: ACSAM2. FrogLog 111: 4–5.

Andreone F., Crottini A., Rabemananjara F.C.E., Randrianirina J.E., Razafindrabe T. & Tessa G. 2014b. Age structure, population estimate and *Bd*-status of two Critically Endangered frogs from the Ankaratra Massif (Madagascar), *Boophis williamsi* and *Mantidactylus pauliani* (Amphibia: Mantellidae). *In*: Capula M. & Corti C. (eds) Scripta Herpetologica – Studies on amphibians and reptiles in honour of Benedetto Lanza. Edizioni Belvedere, Latina, pp. 17–29.

Andreone F., Rabibisoa N., Randrianantoandro C., Crottini A., Edmonds D., Kraus F., Lewis J.P., Moore M., Rabemananjara F.C.E., Rabemanantsoa J.C. & Vences M. 2014c. Madagascar: Risk review is under way for invasive toad. Nature 512: 253.

Andreone F., Rosa G.M. & Raselimanana A.P. 2014d. Les amphibiens de l'Ouest et du Sud de Madagascar. Vahatra, Antananarivo.

Andreone F., Crottini A. & Randriamahazo H. 2015. L'isola delle rane: Strategie di conservazione per gli anfibi del Madagascar. Le Scienze (Italian edition of Scientific American) 559: 62–67.

Andreone F., Dawson J., Rabemananjara F.C.E., Rabibisoa N.H.C. & Rakotonanahary T. 2016. New Sahonagasy Action Plan 2016–2020/Nouveau Plan d'Action Sahonagasy 2016–2020. Museo Regionale di Scienze Naturali, Torino.

Andreone F., Crottini A., Rosa G.M., Rakotoarison A., Scherz M. & Raselimanana A. 2018. Les amphibiens du Nord de Madagascar. Vahatra, Antananarivo.

Andreone F., Andriantsimanarilafy R.R., Crottini A., Edmonds D., Garcia G., Hansen-Hendrikx C.M., Rakotoarison A. & Razafimanahaka J.R. 2020. *Mantella cowanii* Action Plan. 2021–2025. Museo Regionale di Scienze Naturali and Amphibian Survival Alliance, Torino.

Andriamialisoa F. & Langrand O. 2003. The history of zoological exploration of Madagascar. *In*: Goodman S.M. & Benstead J.P. (eds) The natural history of Madagascar. The University of Chicago Press, Chicago and London, pp. 1–15.

Antwis R.E., Preziosi R.F., Harrison X.A. & Garner T.W.J. 2015. Amphibian symbiotic bacteria do not show universal ability to inhibit growth of the global pandemic lineage of *Batrachochytrium dendrobatidis*. Applied and Environmental Microbiology 18: 3706–3711.

Araújo M.B., Thuiller W. & Pearson R.G. 2006. Climate warming and the decline of amphibians and reptiles in Europe. Journal of Biogeography 33: 1712–1728.

Audy F. 1973. *Mantella aurantiaca*. Aquarama: Revue Aquariophile Trimestrielle 7: 56–57.

Baker S.E., Cain R., van Kesteren F., Zommers Z.A., D'Cruze N. & Macdonald D.W. 2013. Rough trade: animal welfare in the global wildlife trade. BioScience 63: 928–938.

Barber-Meyer S.M. 2010. Dealing with the clandestine nature of wildlife-trade market surveys. Conservation Biology **24**: 918–923.

Barrett M.A., Brown J.L., Morikawa M.K., Labat, J.-N. & Yoder A.D. 2010. CITES designation for Endangered rosewood in Madagascar. Science 328: 1109–1110.

Berger L., Speare R., Daszak, P., Green D.E., Cunningham A.A., Goggin C.L., Ron Slocombe R., Ragan M.A., Hyatt A.D., McDonald K.R., Hines H.B., Lips K.R., Marantelli G. & Parkes H. 1998. Chytridiomycosis causes amphibian mortality associated with population declines in the rainforests of Australia and Central America. Proceedings of the National Academy of Sciences USA 95: 9031–9036.

Berger L., Speare R. & Hyatt A.D. 2000. Chytrid fungi and amphibian declines: Overview, implications and future directions. *In*: Campbell A. (ed.) Declines and disappearances of Australian frogs. Environmental Australia, Canberra, Australia: Environmental Australia, pp. 21–31.

Blaustein A.R., Belden L.K., Olson D.H., Green D.M., Root T.L. & Kiesecker J.M. 2001. Amphibian breeding and climate change. Conservation Biology 15: 1804–1809.

Bletz M.C., Loudon A.H., Becker M.H., Bell S.C., Woodhams D.C., Minbiole K.P.C. & Harris R.N. 2013. Mitigating amphibian chytridiomycosis with bioaugmentation: characteristics of effective probiotics and strategies for their selection and use. Ecology Letters 16: 807–820.

Bletz M. C., Rosa G. M., Andreone F., Courtois E. A., Schmeller D. S., Rabibisoa N. H. C., Rabemananjara F. C. E., Raharivololoniaina L., Vences M., Weldon C., Edmonds D., Raxworthy C. J., Harris R. N., Fisher M. C. & Crottini A. 2015a. Widespread presence of the pathogenic fungus *Batrachochytrium dendrobatidis* in wild amphibian communities in Madagascar. Scientific Reports 5: 8633.

Bletz M. C., Rosa G. M., Andreone F., Courtois E. A., Schmeller D. S., Rabibisoa N. H. C., Rabemananjara F. C. E., Raharivololoniaina L., Vences M., Weldon C., Edmonds D., Raxworthy C. J., Harris R. N., Fisher M. C. & Crottini A. 2015b. Consistency of published results on the pathogen *Batrachochytrium dendrobatidis* in Madagascar: formal comment on Kolby *et al.* Rapid response to evaluate the presence of amphibian chytrid fungus (*Batrachochytrium dendrobatidis*) and *Ranavirus* in wild amphibian populations in Madagascar. PLoS ONE 10: e0135900.

Blommers-Schlösser R. M. A. 1979a. Biosystematics of the Malagasy frogs. I. Mantellinae (Ranidae). Beaufortia 29: 1–77.

Blommers-Schlösser R. M. A. 1979b. Biosystematics of the Malagasy frogs. II. The genus *Boophis* (Racophoridae). Bijdragen tot de Dierkunde 49: 261–312.

Blommers-Schlösser R. M. A. 1981. On endemic Malagasy frogs (Ranidae, Rhacophoridae, and Hyperolidae). Monitore Zoologico Italiano 12 (Suppl. XV): 217–224.

Blommers-Schlösser R. M. A. & Blanc C. P. 1991. Amphibiens (première partie). Faune de Madagascar 75: 1–379.

Blommers-Schlösser R. M. A. & Blanc C. P. 1993. Amphibiens (deuxième partie). Faune de Madagascar 75: 385–530.

Bloxam Q. M. C. & Tonge S. J. 1995. Amphibians: suitable candidates for breeding-release programmes. Biodiversity and Conservation 4: 636–644.

Boettger O. 1881. Die Reptilien und Amphibien von Madagascar. Dritter Nachtrag. Abhandlung der Senckenbergischen Naturforschenden Gesellschaft 12: 435–558.

Bora P., Randrianantoandro J. C., Randrianavelona R., Hantalalaina E. F., Andriantsimanarilafy R. R., Rakotondravony D., Ramilijaona O. R., Vences M., Jenkins R. K. B., Glaw F. & Köhler J. 2010. Amphibians and reptiles of the Tsingy de Bemaraha Plateau, Western Madagascar: Checklist, biogeography and conservation. Herpetological Conservation and Biology 5: 111–125.

Bosch J., Sanchez-Tomé E., Fernández-Loras A., Oliver J. A., Fisher M. C & Garner T. W. J. 2015. Successful elimination of a lethal wildlife infectious disease in nature. Biological Letters 11: 20150874.

Boulenger G. A. 1888. Descriptions of new reptiles and batrachians from Madagascar. Annals and Magazine of Natural History, series 6: 101–107.

Boulenger G. A. 1889. Descriptions of new reptiles and batrachians from Madagascar. Annals and Magazine of Natural History, series 6: 244–248.

Brook B. W., Burgman M. A., Akçakaya H. R., O'Grady J. J. & Frankham R. 2002. Critiques of PVA ask the wrong questions: throwing the heuristic baby out with the numerical bath water. Conservation Biology 16: 262–263.

Brooks T. M., Mittermeier R. A., da Fonseca G. A. B., Gerlach J., Hoffmann, M., Lamoreux J. F., Mittermeier C. G., Pilgrim J. D. & Rodrigues A. S. L. 2006. Global biodiversity conservation priorities. Science 313: 58–61.

Brown J. L., Cameron A., Yoder A. D. & Vences M. 2014. A necessarily complex model to explain the biogeography of the amphibians and reptiles of Madagascar. Nature Communications 5: e5046.

Brown J. L., Sillero N., Glaw F., Bora P., Vieites D. R. & Vences M. 2016. Spatial biodiversity patterns of Madagascar's amphibians and reptiles. PLoS ONE 11: e0144076.

Browne R. K., Wolfram K., Garcia G., Bagaturov M. F. & Pereboom Z. J. J. M. 2011. Zoo based amphibian research and conservation breeding programs. Amphibian and Reptile Conservation 5: 1–14.

Buley K., Furrer S. C., Garcia G., Gibson R. C., Gili C., Mattioli F. & Andreone F. 2008. Captive breeding and zoo actions. *In*: Andreone F. & Randriamahazo H. (eds) Sahonagasy Action Plan: Conservation programs for the amphibians of Madagascar. Museo Regionale di Scienze Naturali, Conservation International, IUCN/SSC Amphibian Specialist Group, Torino, pp. 67–75.

Burney D. A. 1987. Late Holocene vegetational change in central Madagascar. Quaternary Research 28: 130–143.

Bush E. R., Baker S. E. & MacDonald D. W. 2014. Global trade in exotic pets 2006–2012. Conservation Biology 28: 663–676.

Carpenter A. I. 2003. The ecology and exploitation of chameleons in Madagascar. PhD thesis, University of East Anglia.

Carpenter A. I., Dublin H., Lau M., Syed G., McKay J. E. & Moore R. D. 2007. Over-harvesting. *In*: Gascon C., Collins J., Moore R. D., Church D. R., McKay J. E. & Mendelson J. R. (eds) Amphibian Conservation Action Plan. IUCN/SSC Amphibian Specialist Group, Gland and Cambridge, pp. 26–31.

Carpenter A. I. & Robson O. 2008. Madagascan amphibians as a wildlife resource and their potential as a conservation tool: Species and numbers exported, revenue generation and bio-economic models to explore conservation benefits. *In*: Andreone F. (ed.) A conservation strategy for the amphibians of Madagascar, Monografie 45. Museo Regionale di Scienze Naturali, Torino, pp. 357–376.

Carpenter A. I., Andreone F., Moore R. & Griffiths R. 2014. A review of the international trade in amphibians: the types, levels and dynamics of trade in CITES-listed species. Oryx 48: 565–574.

Catenazzi A., Lehr E., Rodriguez L. O. & Vredenburg V. T. 2011. *Batrachochytrium dendrobatidis* and the collapse of anuran species richness and abundance in the upper Manu National Park, southeastern Peru. Conservation Biology 25: 382–391.

Chapman A. P., Brook B. W., Clutton-Brock T. H., Grenfell B. T. & Frankham R. 2001. Population viability analysis on cycling population: a cautionary tale. Biological Conservation 97: 61–69.

Chiari Y., Andreone F., Vences M. & Meyer A. 2005. Genetic variation of an endangered Malagasy frog, *Mantella cowani*, and its phylogeographic relationships to the widespread *M. baroni*. Conservation Genetics 6: 1041–1047.

Church G. 1960. The invasion of Bali by *Bufo melanostictus*. Herpetologica 16: 15–21.

Clark T. W., Backhouse G. N. & Lacy R. C. 1991. Report of a workshop on population viability assessment as a tool for a threatened species management and conservation. Australian Zoologist 27: 28–35.

Cocca W., Rosa G. M., Andreone F., Aprea G., Bergò P. E., Mattioli F., Mercurio V., Randrianirina J. E., Rosado D., Vences M. & Crottini A. 2018. The herpetofauna (Amphibia, Crocodylia, Squamata, Testudines) of the Isalo Massif, Southwest Madagascar: combining morphological, molecular and museum data. Salamandra 54: 178–200.

Cocca W., Andreone F., Belluardo F., Rosa G. M., Randrianirina J. E., Glaw F. & Crottini A. 2020. Resolving a taxonomic and nomenclatural puzzle in mantellid frogs: synonymization of *Gephyromantis azzurrae* with *G. corvus*, and description of *Gephyromantis kintana* sp. nov. from the Isalo Massif, western Madagascar. ZooKeys 951: 133–157.

Corson C. 2014. Conservation politics in Madagascar, The expansion of protected areas. *In*: Scales I. R. (ed.) Conservation and environmental management in Madagascar. Routledge, London and New York, pp. 193–215.

Crottini A., Chiari Y., Mercurio V., Meyer A., Vences M. & Andreone F. 2008. 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). Organisms Diversity & Evolution 8: 368–377.

Crottini A., Barbuto M., Casiraghi M. & Andreone F. 2011a. A rapid amphibian survey at Itremo-Ambatofinandrahana, central Madagascar, with confirmed absence of chytrid fungus and recommendations for future monitoring activities. North-Western Journal of Zoology 7: 346–351.

Crottini A., Glaw F., Casiraghi M., Jenkins R. K. B., Mercurio V., Randrianantoandro J. C., Randrianirina J. E. & Andreone F. 2011b. A new *Gephyromantis* (*Phylacomantis*) frog species from the pinnacle karst of Bemaraha, western Madagascar. ZooKeys 81: 51–71.

Crottini A., Madsen O., Poux C., Strauss A., Vieites D. R. & Vences M. 2012. Vertebrate time-tree elucidates the biogeographic pattern of a major biotic change around the K–T boundary in Madagascar. Proceedings of the National Academy of Sciences USA 109: 5358–5363.

Crottini A., Andreone F., Edmonds D., Hansen C. M., Lewis J. P., Rabemanantsoa J. C., Moore M., Kraus F., Vences M., Rabemananjara F. C. E. & Randrianantoandro C. 2014a. A new challenge for amphibian conservation in Madagascar: the invasion of *Duttaphrynus melanostictus* in Toamasina province. FrogLog 111: 46–47.

Crottini A., Bollen A., Weldon C., Dalton D. L., Kotzé A., Noël J., Iambana B. & Andreone F. 2014b. Amphibian survey and current absence of *Batrachochytrium dendrobatidis* (*Bd*) in Ivoloina Park, Toamasina (eastern Madagascar). African Journal of Herpetology 63: 1–9.

Crottini A., Orozco-terWengel P., Rabemananjara F. C. E., Hauswaldt J. S. & Vences M. 2019. Mitochondrial introgression, color pattern variation, and severe demographic bottlenecks in three species of Malagasy poison frogs, genus *Mantella*. Genes 10: 317.

Crottini A., Rosa G. M., Penny S. G., Cocca W., Holderied M. W., Rakotozafy L. M. S. & Andreone F. 2020. A new stump-toed frog from the transitional forests of NW Madagascar (Anura: Microhylidae: Cophylinae: *Stumpffia*). ZooKeys 933: 139–164.

Crowley B. E., Godfrey L. R., Bankoff R. J., Perry G. H., Culleton B. J., Kennett D. J., Sutherland M. R., Samonds K. E. & Burney D. A. 2017. Island-wide aridity did not trigger recent megafaunal extinctions in Madagascar. Ecography 40: 901–912.

Cushman S. A. 2006. Effects of habitat loss and fragmentation on amphibians: A review and prospectus. Biological Conservation 128: 231–240.

D'Cruze N. & Kumar S. 2011. Effects of anthropogenic activities on lizard communities in northern Madagascar. Animal Conservation 14: 542–552.

Daszak P., Scott D. E., Kilpatrick A. M., Faggioni C., Gibbons J. W. & Porter D. 2005. Amphibian population declines at Savannah River site are linked to climate, not chytridiomycosis. Ecology 86: 3232–3237.

Dawson J., Edmonds D., Freeman K., Iambana B., Moore M. & Rakotoarisoa J. C. 2014. Working together to develop Madagascar's amphibian captive breeding capacity. FrogLog 22: 61–62.

De Wit, M. J. 2013. Madagascar: heads it's a continent, tails it's an island. Annual Review of Earth and Planetary Sciences 31: 213–248.

Dickson B. 2008. CITES and the livelihoods of the poor. Oryx 42: 548–553.

Dixo M. & Metzger P. J. 2010. The matrix-tolerance hypothesis: an empirical test with frogs in the Atlantic Forest. Biodiversity and Conservation 19: 3059–3071.

Douglass K., Hixon S., Wright H. T., Godfrey L. R., Crowley B. E., Manjakahery B. E., Rasolondrainy T., Crossland Z. & Radimilahy C. 2019. A critical review of radiocarbon dates clarifies the human settlement of Madagascar. Quaternary Science Reviews 221: 105878.

Dubos N., Morel L., Crottini A., Freeman K., Honoré L., Noël L., Porton I., Rendrirendry G., Rosa G. M. & Andreone F. 2020. High interannual variability of a climate-driven amphibian community in a seasonal rainforest. Biodiversity and Conservation 29: 893–912.

Duffus A. L. J. & Cunningham A. A. 2010. Major disease threats to European amphibians. Herpetological Journal 20: 117–127.

Dufils J. M. 2003. Remaining forest cover. *In*: Goodman S. M. & Benstead J. P. (eds) The natural history of Madagascar. The University of Chicago Press, Chicago and London, pp. 88–96.

Dutton A. J., Gratwicke B., Hepburn C., Herrera E. A. & Wunder S. 2013. Tackling unsustainable wildlife trade. *In*: Macdonald D. W. & Willis K. J. (eds) Key topics in conservation biology. Wiley-Blackwell, New York, pp. 74–92.

Edmonds D. 2013. Breeding golden mantellas in Madagascar. Amphibian Ark Newsletter 22: 13–14.

Edmonds D. 2014. Taking the first steps together at Parc Ivoloina. Amphibian Ark Newsletter 29: 9–10.

Edmonds D., Rakotoarisoa J. C., Dolch R., Pramuk J., Gagliardo R., Andreone F., Rabibisoa N., Rabemananjara F., Rabesihanaka S. & Robsomanitrandrasana E. 2012. Building capacity to implement conservation breeding programs for frogs in Madagascar: Results from year one of Mitsinjo's amphibian husbandry research and captive breeding facility. Amphibian and Reptile Conservation 5: 57–69.

Edmonds D., Rakotoarisoa J. C., Rasoanantenaina S., Sam S. S., Soamiarimampionona J., Tsimialomanana E., Dolch Y. R., Rabemananjara F., Rabibisoa N. & Robsomanitrandrasana E. 2015. Captive husbandry, reproduction and fecundity of the golden mantella (*Mantella aurantiaca*) at the Mitsinjo breeding facility in Madagascar. Salamandra 51: 315–325.

Ellner S. P., Fieberg J., Ludwig D. & Wilcox C. 2002. Precision of population viability analysis. Conservation Biology 16: 258–261.

Evans M. V., Garchitorena A. V., Rakotonanahary R. J. L., Drake J. M., Andriamihaja B., Rajaonarifara E., Ngonghala C. N., Roche B., Bonds M. H. & Rakotonirina J. 2020. Reconciling model predictions with low reported cases of COVID-19 in Sub-Saharan Africa: Insights from Madagascar. Global Health Action 13: 1816044.

Farrer R. A., Weinert L. A., Bielby J., Garner T. W. J., Balloux F., Clare F., Bosch J., Cunningham A. A., Weldon C., Du Preez L. H., Anderson L., Pond S. L. K., Shahar-Golan R., Henk D. A. & Fisher M. C. 2011. Multiple emergences of genetically diverse amphibian-infecting chytrids include a globalized hypervirulent recombinant lineage. Proceedings of the National Academy of Sciences USA 108: 18732–18736.

Fisher M. C., Garner T. W. J. & Walker S. F. 2009. The global emergence of *Batrachochytrium dendrobatidis* and amphibian chytridiomycosis in space, time and host. Annual Review of Microbiology 63: 291–310.

Friedberg S. 2019. Demand for charcoal threatens the forest of Madagascar's last hunter-gatherers. *https://news.mongabay.com/2019/10/demand-for-charcoal-threatens-the-forest-of-madagascars-last-hunter-gatherers/* (accessed on the 1st October 2020).

Gade D. W. 1996. Deforestation and its effects in highland Madagascar. Mountain Research and Development 16: 101–116.

Gagliardo R., Crump P., Griffith E., Mendelson J. III, Ross H. & Zippel K. 2008. The principles of rapid response for amphibian conservation, using the programmes in Panama as an example. International Zoo Yearbook 42: 125–135.

Ganzhorn J. U., Wilmé L. & Mercier J.-L. 2014. Explaining Madagascar's biodiversity. *In*: Scales I. R. (ed.) Conservation and environmental management in Madagascar. Earthscan, Oxon, New York, pp 17–43.

Garcia G. 2010. Preparations for the battle against chytrid: building capacity for chytrid detection in Madagascar. Amphibian Ark Newsletter 13: 17–18.

Garcia G., Bock L., Earle S., Berridge R. & Copsey J. 2008. Captive breeding as a tool for the conservation of Malagasy amphibians: how ready are we to respond to the need? *In*: Andreone F. (ed.) A conservation strategy for the amphibians of Madagascar, Monografie 45. Museo Regionale di Scienze Naturali, Torino, pp. 321–342.

Garner T. W. J., Schmidt B. R., Martel A., Pasmans F., Muths E., Cunningham A. A., Weldon C., Fisher M. C. & Bosch J. 2016. Mitigating amphibian chytridiomycoses in nature. Philosophical Transactions of the Royal Society B, 371: 20160207.

Gascon C., Collins J. P., Moore R. D., Church D. R., McKay J. E. & Mendelson J. R. III. 2007. Amphibian Conservation Action Plan. IUCN/SSC Amphibian Specialist Group, Gland and Cambridge.

Gascon C., Collins J., Church D., Moore R. D., Andreone F., Bishop P., Biju S. D., Bolanos F., Feng X., Pipeng L., Zhang L., Shi H., Lötters S., Mitchell P. N., Mora-Benavides J. M., Garcia Moreno J., Randriamahazo H., Reardon J. T., Molina C., Ron S., Rowley J. J. L., Silvano D., Valdijo P. & Verdade V. K. 2012. Scaling a global plan into regional strategies for amphibian conservation. Alytes 29: 15–27.

Gehring P.-S., Pabijan M., Randrianirina J. E., Glaw F. & Vences M. 2012. The influence of riverine barriers on phylogeographic patterns of Malagasy reed frogs (*Heterixalus*). Molecular Phylogenetics and Evolution 64: 618–632.

Gehring P.-S., Ratsoavina F. M. & Vences M. 2010. Filling the gaps – amphibian and reptile records from lowland rainforests in eastern Madagascar. Salamandra 46: 214–234.

Gili C. 2008. Conservation activities on Malagasy amphibians at Acquario di Genova. *In*: Andreone F. (ed.) A conservation strategy for the amphibians of Madagascar, Monografie 45. Museo Regionale di Scienze Naturali, Torino, pp. 309–320.

Glaw F. & Vences M. 1994. A field guide to the amphibians and reptiles of Madagascar, 2nd edition. Vences and Glaw Verlag GbR, Cologne.

Glaw F. & Vences M. 2003. Introduction to amphibians. *In*: Goodman S. M. & Benstead J. P. (eds) The natural history of Madagascar. The University of Chicago Press, Chicago and London, pp. 883–898.

Glaw F. & Vences M. 2006. Phylogeny and genus-level classification of mantellid frogs. Organisms Diversity and Evolution 6: 236–253.

Glaw F. & Vences M. 2007a. A field guide to the amphibians and reptiles of Madagascar, 3rd edition. Vences and Glaw Verlag, Cologne.

Glaw F. & Vences M. 2007b. Ny Toro-Hai Momba ny Amphibia sy ny Reptlia an'i Madagasikara. Vences and Glaw Verlag, Cologne.

Glaw F., Köhler J., de la Riva I., Vieites D. R. & Vences M. 2010. Integrative taxonomy of Malagasy treefrogs: combination of molecular genetics, bioacoustics and comparative morphology reveals twelve additional species of *Boophis*. Zootaxa 2383: 1–82.

Glaw F., Hawlitschek O., Glaw K. & Vences M. 2019. Integrative evidence confirms new endemic island frogs and transmarine dispersal of amphibians between Madagascar and Mayotte (Comoros archipelago). The Science of Nature 106: 19.

Glos J., Dausmann K. H. && Linsenmair K. E. 2007a. Mixed-species social aggregations in Madagascan tadpoles – determinants and species composition. Journal of Natural History 41: 1965–1977.

Glos J., Erdmann G., Dausmann K. H. & Linsenmair K. E. 2007b. A comparative study of predator-induced social aggregation of tadpoles in two anuran species from western Madagascar. Herpetological Journal 17: 261–268.

González-Hernández M., Denoël M., Duffus A. J., Garner T. W., Cunningham A. A. & Acevedo-Whitehouse K. 2010. Dermocystid infection and associated skin lesions in free-living palmate newts (*Lissotriton helveticus*) from Southern France. Parasitology International 59: 344–350.

Green D. E. Gray M. J. & Miller D. L. 2009. Disease monitoring and biosecurity. Forestry, wildlife, and fisheries publications and other works. Available at *http://trace.tennessee.edu/utk_forepubs/2*.

Griffiths R. A. & Pavajeau L. 2008. Captive breeding, reintroduction, and the conservation of amphibians. Conservation Biology 22: 852–861.

Grimm N. B, Chapin F. S., Bierwagen B., Gonzalez P., Groffman P. M., Luo Y., Melton F., Nadelhoffer K., Pairis A., Raymond P. A., Schimel J. & Williamson C. E. 2013. The impacts of climate change on ecosystem structure and function. Frontiers in Ecology and the Environment 11: 474–482.

Grosjean S., Strauss A., Glos J., Randrianiaina R. D., Ohler A. & Vences M. 2011. Morphological and ecological uniformity in the funnel-mouthed tadpoles of Malagasy litter frogs, subgenus *Chonomantis*. Zoological Journal of the Linnean Society 162: 149–183.

Guarino F. M., Andreone F. & Angelini F. 1998. Growth and longevity by skeletochronological analysis in *Mantidactylus microtympanum*, a rain-forest anuran of southern Madagascar. Copeia 1998: 194–198.

Guarino F. M., Sacco M., Tessa G. & Andreone F. 2008. Short life span of two charismatic species: age-structure in Critically Endangered *M. cowanii* and in the syntopic *M. baroni*. *In*: Andreone F. (ed.) A conservation strategy for the amphibians of Madagascar, Monografie 45. Museo Regionale di Scienze Naturali, Torino, pp. 265–276.

Guarino F. M., Tessa G., Mercurio M. & Andreone F. 2010. Rapid sexual maturity and short life span in the blue-legged frog and the rainbow frog from the arid Isalo Massif, southern-central Madagascar. Zoology 113: 378–384.

Guarino F. M., Crottini A., Mezzasalma M., Randrianirina J. E. & Andreone F. 2019. A skeletochronological estimate of age and growth in a large riparian frog from Madagascar (Anura: Mantellidae. Herpetozoa 32: 39–44.

Guibé J. 1953. Au sujet de l'introduction de *Rana tigerina* Daudin à Madagascar. Le Naturaliste Malgache 5: 241–242.

Guibé J. 1978. Les batraciens de Madagascar. Bonner Zoologische Monographien 11: 1–140.

Hannah L., Dave R., Lowry II P. P., Andelman S., Andrianarisata M., Andriamaro L., Cameron A., Hijmans R., Kremen C., MacKinnon J., Randrianasolo H. H., Andriambolonera S., Razafimpahanana A., Randriamahazo H., Randrianarisoa J., Razafinjatovo P., Raxworthy C., Schatz G. E., Tadross M. & Wilmé L. 2008. Climate change adaptation for conservation in Madagascar. Biology Letters 4: 590–594.

Harding G., Griffiths R. A. & Pavajeau L. 2016. Developments in amphibian captive breeding and reintroduction programs. Conservation Biology 30: 340–349.

Harper G. J., Steininger M. K., Tucker C. J., Juhn D. & Hawkins F. 2007. Fifty years of deforestation and forest fragmentation in Madagascar. Environmental Conservation 34: 1–9.

Heinermann J., Rodríguez A., Segev O., Edmonds D., Dolch R. & Vences M. 2015. Year-round activity patterns in a hyperdiverse community of rainforest amphibians in Madagascar. Journal of Natural History 49: 2213–2231.

Hillers A., Veith M. & Rödel M.-O. 2008. Effects of forest fragmentation and habitat degradation on West African leaf-litter frogs. Conservation Biology 22: 762–772.

Hirschfeld M. & Rödel M.-O. 2017. What makes a successful species? Traits facilitating survival in altered tropical forests. BMC Ecology 17: 25.

Humbert H. 1927. Principaux aspects de la végétation à Madagascar. La destruction d'une flore insulaire par le feu. Mémoires de l'Academie Malgache, Antananarivo.

Humbert H. & Cours Darne G. 1965. Notice de la Carte Madagascar. Section Scientifique et Technique de l'Institut Français de Pondichéry.

Hutter C., Lambert S. M., Andriampenomanana Z. F., Glaw F. & Vences M. 2018. Molecular phylogeny and diversification of Malagasy bright-eyed tree frogs (Mantellidae: *Boophis*). Molecular Phylogenetics and Evolution 127: 568–578.

Hutton J. M. & Leader-Williams N. 2003. Sustainable use and incentive-driven conservation: realigning human and conservation interests. Oryx 37: 215–226.

Iambana B. 2015. Amphibian conservation center at Parc Ivoloina, Toamasina, Madagascar. Amphibian Ark Newsletter 31: 11–12.

Innes J. L. 2010. Madagascar rosewood, illegal logging and the tropical timber trade. Madagascar Conservation and Development 5: 6–10.

International Monetary Fund 2019. GDP per capita, current prices. *https://www. imf. org/external/datamapper/NGDPDPC@WEO/OEMDC/ADVEC/WEOWORLD*

Irwin M. T., Wright P. C., Birkinshaw C., Fisher B. L., Gardner C. J., Glos J., Goodman S. M., Loiselle P., Rabeson P., Raharison J. L., Raherilalao M. J., Rakotondravony D., Raselimanana A., Ratsimbazafy J., Sparks J. S., Wilmé L. & Ganzhorn J. U. 2010. Patterns of species change in anthropogenically disturbed forests of Madagascar. Biological Conservation 143: 2351–2362.

IUCN 2012. IUCN Red List categories and criteria: Version 3.1. Second edition. IUCN, Gland, and Cambridge.

IUCN 2014. Guidelines on the use of *ex situ* management for species conservation, Version 2.0. IUCN Species Survival Commission, Gland.

IUCN 2019. IUCN Red List of Threatened Species. *www.iucnredlist.org* (accessed on the 15th December 2019).

Jarosz L. 1993. Defining and explaining tropical deforestation shifting cultivation and population growth in colonial Madagascar (1896–1940). Economic Geography 69: 366–379.

Jenkins M. 1994. A review of the national level reforms necessary to improve control of the export trade in Madagascar's wild animals and plants and their products. Contract No. LAG 4200-1-01-3056-D011, USAID-Madagascar.

Jenkins R. K. B., Andrianasolonjatovo M. N., Freeman K., Rabearivelo A., Rampilimanana R. L. & Randrianavelona R. 2008. The exploitation of amphibians for food in Madagascar. *In*: Andreone F. (ed.) A conservation strategy for the amphibians of Madagascar, Monografie 45. Museo Regionale di Scienze Naturali, Torino, pp. 343–356.

Jenkins R. K. B., Rabearivelo A., Tak Chan C., Mine Andre W., Randrianavelona R. & Randrianantoandro J. C. 2009. The harvest of endemic amphibians for food in eastern Madagascar. Tropical Conservation Science 2: 25–33.

Jenkins R. K. B., Tognelli M. F., Bowles P., Cox N., Brown J. L., Chan L., Andreone F., Andriamazava A., Andriantsimanarilafy R. R., Anjeriniaina M., Bora P., Brady L. D., Hantalalaina E. F., Glaw F., Griffiths R. A., Hilton-Taylor C., Hoffmann M., Katariya V., Rabibisoa N. H., Rafanomezantsoa J., Rakotomalala D., Rakotondravony H., Rakotondrazafy N. A., Ralambonirainy J., Ramanamanjato J. B., Randriamahazo H., Randrianantoandro J. C., Randrianasolo H. H., Randrianirina J. E., Randrianizahana H., Raselimanana A. P., Rasolohery A., Ratsoavina F. M., Raxworthy C. J., Robsomanitrandrasana E., Rollande F., van Dijk P. P., Yoder A. D. & Vences M. 2014. Extinction risks and the conservation of Madagascar's reptiles. PLoS ONE 9: e100173.

Johnston D. W., Meisenheimer P. & Lavigne D. M. 2000. An evaluation of management objectives for Canada's commercial harp seal hunt. Conservation Biology 14: 729–737.

Jovanovic O., Rabemananjara F., Ramilijaona O., Andreone F., Glaw F. & Vences M. 2007a. Frogs of Madagascar, genus *Mantella*. Tropical Pocket Guide Series. Conservation International, Bogotà.

Jovanovic O., Rabemananjara F., Ramilijaona O., Andreone F., Glaw F. & Vences M. 2007b. Grenouilles de Madagascar du genre Mantella. Tropical Pocket Guide Series. Conservation International, Bogotà.

Kilpatrick A. M., Briggs C. J. & Daszak P. 2010. The ecology and impact of chytridiomycosis: an emerging disease of amphibians. Trends in Ecology & Evolution 25: 109–118.

Knapp R. A. & Morgan J. A. T. 2006. Tadpole mouthpart depigmentation as an accurate indicator of chytridiomycosis, an emerging disease of amphibians. Copeia 2006: 188–197.

Kolby J. E. 2014. Presence of the amphibian chytrid fungus *Batrachochytrium dendrobatidis* in native amphibians exported from Madagascar. PLoS ONE 9: e89660.

Kolby J. E., Kraus F., Rabemananjara F. C. E., Rabesihanaka S., Rabibisoa N., Rafanomezantsoa J., Randrianantoandro C., Randrianiana R. D., Raxworthy C. J., Razafimahatratra B. & Robsomanitrandrasana E. 2014. Stop Madagascar's toad invasion now. Nature 509: 563.

Kremen C., Cameron A., Moilanen A., Phillips S. J., Thomas C. D., Beentje H., Dransfield J., Fisher B. L., Glaw F., Good T. C., Harper G. J., Hijmans R. J., Lees D. C., Louis Jr. E., Nussbaum R. A., Raxworthy C. J., Razafimpahanana A., Schatz G. E., Vences M., Vieites D. R. & Zjhra M. L. 2008. Aligning conservation priorities across taxa in Madagascar with high-resolution planning tools. Science 320: 222–226.

Kriger K. M. & Hero J. M. 2007. Large-scale seasonal variation in the prevalence and severity of chytridiomycosis. Journal of Zoology 271: 352–359.

Kull C. A. 2000. Deforestation, erosion, and fire: degradation myths in the environmental history of Madagascar. Environment and History 6: 423–450.

Lacy R. C., Borbat M. & Pollak J. P. 2011. VORTEX: A stochastic simulation of the extinction process. Version 9.99b. Chicago Zoological Society, Brookfield.

Lam B., Noël J., Crottini A., Andreone F. & Rosa G. M. 2020. Report of agonistic interaction in Malagasy frogs of the genus *Gephyromantis* (Anura, Mantellidae). Arxius de Miscellània Zoològica 18: 27–32.

La Marca E., Lips K. R., Lötters S., Puschendorf R., Ibáñez R., Rueda-Almonacid J. V., Schulte R., Marty C., Castro F., Manzanilla-Puppo J., Garcia-Pérez J. E., Bolaños F., Chaves G., Pounds J. A., Toral E. & Young B. E. 2005. Catastrophic population declines and extinction in Neotropical harlequin frogs (Bufonidae: *Atelopus*). Biotropica 37: 190–201.

Laurance W. F. 2008. Global warming and amphibian extinctions in eastern Australia. Australian Ecology 33: 1–9.

Lehtinen R. M. & Ramanamanjato J.-B. 2006. Effects of rainforest fragmentation and correlates of local extinction in a herpetofauna from Madagascar. Applied Herpetology 3: 95–110.

Lehtinen R. M., Ramanamanjato J. B. & Raveloarison J. G. 2003. Edge effects and extinction proneness in a herpetofauna from Madagascar. Biodiversity and Conservation 12: 1357–1370.

Lehtinen R. M., Glaw F. & Vences M. 2011. Two new plant-breeding frog species (Anura: Mantellidae, *Guibemantis*) from southeastern Madagascar.Herpetological Journal 21: 95–112.

Licata F., Andreone F., Freeman K., Rabesihanaka S., Robsomanitrandrasana E., Reardon J. T. & Crottini A. 2020. Chapter 21. The Asian toad (*Duttaphrynus melanostictus*) in Madagascar: A report of an ongoing invasion. *In*: Angelici F. M. & Rossi L. (eds) Problematic wildlife II. New conservation and management challenges in the human–wildlife interactions. Springer, Berlin, Germany, pp. 617–638.

Licata F., Ficetola G. F., Freeman K., Mahasoa R. H., Ravololonarivo V., Fidy J. F. S. N., Koto-Jean A. B., Rasoanomenjanahary E. N., Andreone F. & Crottini A. 2019.Abundance, distribution and spread of the invasive Asian toad *Duttaphrynus melanostictus* in eastern Madagascar. Biological Invasions 21: 1615–1626.

Lips K. R., Brem F., Brenes R., Reeve J. D., Alford R. A., Voyles J., Carey C., Livo L., Pessier A. P. & Collins J. P. 2006. Emerging infectious disease and the loss of biodiversity in a Neotropical amphibian community. Proceedings of the National Academy of Sciences USA 103: 3165–3170.

Longcore J. E., Pessier A. P. & Nichols D. K. 1999. *Batrachochytrium dendrobatidis* gen. et sp. nov., a chytrid pathogenic to amphibians. Mycologia 91: 219–227.

Lötters S. 2008. Afrotropical amphibians in zoos and aquariums: will they be on the ark? International Zoo Yearbook 42: 136–142.

Lötters S., Rödder D., Kielgast J. & Glaw F. 2011. Hotspots, conservation, and diseases: Madagascar's megadiverse amphibians and the potential impact of chytridiomycosis. *In*: Zachos F. E. & Habel J. C.

(eds) Biodiversity hotspots: Distribution and protection of conservation priority areas. Springer Berlin Heidelberg, pp. 255–274.

Macdonald D.W. & Laurenson K. 2006. Infectious disease: inextricable linkages between human and ecosystem health. Biological Conservation 131: 143–150.

Marantelli G., Berger L., Speare R. & Keegan L. 2004. Distribution of the amphibian chytrid *Batrachochytrium dendrobatidis* and keratin during tadpole development. Pacific Conservation Biology 10: 173–179.

Marboutin E., Bray Y., Péroux R., Mauvy B. & Lartiges A. 2003. Population dynamics in European hare: breeding parameters and sustainable harvest rates. Journal of Applied Ecology 40: 580–591.

Marshall B.M., Casewell N.R., Vences M., Glaw F., Andreone F., Rakotoarison A., Zancolli G., Woog F. & Wüster W. 2018. Widespread vulnerability of Malagasy predators to the toxins of an introduced toad. Current Biology 28: R654–R655.

Martel A., Adriaensen C., Bogaerts S., Ducatelle R., Favoreel H., Crameri S., Hyatt A.D., Haesebrouck F. & Pasmans F. 2012a. Novel Chlamydiaceae disease in captive salamanders. Emerging Infectious Diseases 18: 1020–1022.

Martel A., Adriaensen C., Sharifian-Fard M., Vandewoestyne M., Deforce D., Favoreel H., Bergen K., Spitzen-van der Sluijs A., Devisscher S., Adriaens T., Louette G., Baert K., Hyatt A., Crameri S., Haesebrouck F. & Pasmans F. 2012b. The novel "Candidatus Amphibiichlamydia ranarum" is highly prevalent in invasive exotic bullfrogs (*Lithobates catesbeianus*). Environmental Microbiology Reports 5: 105–108.

Martel A., Spitzen-van der Sluijs A., Blooi M., Bert W., Ducatelle R., Fisher M.C., Woeltjes A., Bosman W., Chiers K., Bossuyt F. & Pasmans F. 2013. *Batrachochytrium salamandrivorans* sp. nov. causes lethal chytridiomycosis in amphibians. Proceedings of the National Academy of Sciences USA 110: 15325–15329.

Mattioli F., Gili C. & Andreone F. 2005. Economics of captive breeding applied to the conservation of selected amphibian and reptile species from Madagascar. Natura 95: 67–80.

Mayhew P.J., Jenkins G.B. & Benton T.G. 2007. A long-term association between global temperature and biodiversity, origination and extinction in the fossil record. Proceedings of the Royal Society B, 275: 47–53.

McClelland P., Reardon J.T., Kraus F., Raxworthy C.J. & Randrianantoandro C. 2015. Asian toad eradication feasibility report for Madagascar. Te Anau.

Mendelson J.R. III & Moore R. 2008. Amphibian conservation at the global, regional, and national level. *In*: Andreone F. (ed.) A conservation strategy for the amphibians of Madagascar, Monografie 45. Museo Regionale di Scienze Naturali, Torino, pp. 15–20.

Mendelson J.R. III, Gagliardo R., Andreone F., Buley K.R., Coloma L., Garcia G., Gibson R., Lacy R., Lau M.W., Murphy J., Pethiyagoda R., Pelican K., Pukazhenthi B.S., Rabb G., Raffaelli J., Weissgold B., Wildt D. & Feng X. 2007. Captive programs. *In*: Gascon C., Collins J.P., Moore R.D., Church D.R., McKay J.E. & Mendelson J.R. III (eds) Amphibian Conservation Action Plan. IUCN/SSC Amphibian Specialist Group, Gland and Cambridge, pp. 36–37.

Mendelson J.R. III, Lips K.R., Gagliardo R.W., Rabb G.B., Collins J.P., Diffendorfer J.E., Daszak P., Ibáñez D.R., Zippel K.C., Lawson D.P., Wright K.M., Stuart S.N., Gascon C., da Silva H.R., Burrowes P.A., Joglar R.L., La Marca E., Lötters S., du Preez L.H., Weldon C., Hyatt A., Rodriguez-Mahecha J.V., Hunt S., Robertson H., Lock B., Raxworthy C.J., Frost D.R., Lacy R.C., Alford R.A., Campbell J.A., Parra-Olea G., Bolaños F., Calvo Domingo J.J., Halliday T., Murphy J.B., Wake M.H., Coloma L.A., Kuzmin S.L., Price M.S., Howell K.M., Lau M., Pethiyagoda R., Boone M., Lannoo M.J., Blaustein A.R., Dobson A., Griffiths R.A., Crump M.L., Wake D.B. & Brodie Jr. E.D. 2006. Confronting amphibian declines and extinctions. Science 313: 48–48.

Mercurio V. & Andreone F. 2006. The tadpoles of *Scaphiophryne gottlebei* (Microhylidae, Scaphiophryninae) and *Mantella expectata* (Mantellidae, Mantellinae) from Isalo Massif, central-southern Madagascar. Alytes 23: 81–95.

Mercurio V., Aprea G., Crottini A., Mattioli F., Randrianirina J.E., Razafindrabe T.J. & Andreone F. 2008. The amphibians of Isalo Massif, southern-central Madagascar: high frog diversity in an apparently hostile dry habitat. *In*: Andreone F. (ed.) A conservation strategy for the amphibians of Madagascar, Monografie 45. Museo Regionale di Scienze Naturali, Torino, pp. 143–196.

Mills L.S. & Lindberg M.S. 2002. Sensitivity analysis to evaluate the consequences of conservation actions. Population viability analysis. The University of Chicago Press, Chicago and London.

Mitchell P. 2019. Settling Madagascar: when did people first colonize the world's largest island? The Journal of Island and Coastal Archaeology 15: 576–595.

Mittermeier R.A., Louis E.E., Richardson M., Schwitzer C., Langrand O., Rylands A.B., Hawkins F., Rajaobelina S., Ratsimbazafy J., Rasoloarison R., Roos C., Kappeler P.M. & MacKinnon J. 2010. Lemurs of Madagascar. Conservation International, Bogotà.

Moat J. & Smith P. 2007. Atlas of the vegetation of Madagascar / Atlas de la végétation de Madagascar. Kew Publishing, Royal Botanical Gardens, Kew.

Mohanty N.P., Crottini A., Garcia R.A. & Measey J. 2021. Non-native populations and global invasion potential of the Indian bullfrog *Hoplobatrachus tigerinus*: a synthesis for risk-analysis. Biological Invasions 23: 69–91.

Moore M., Francois J. & Edmonds D. 2015. The new toad in town: distribution of *Duttaphrynus melanostictus* in the Toamasina area of eastern Madagascar. Tropical Conservation Science 8: 440–455.

Mudrack W. 1974. Haltung und zucht des Goldfröschchens, *Mantella aurantiaca* Mocquard, 1900. Das Aquarium 8: 160–161.

Murcia C. 1995. Edge effects in fragmented forests: implications for conservation. Trends in Ecology and Evolution 10: 58–62.

Myers N., Mittermeier R.A., Mittermeier C.G., da Fonseca G.A.B. & Kent J. 2000. Biodiversity hotspots for conservation priorities. Nature 403: 853–858.

Ndriantsoa, S.H., Riemann J.C., Raminosoa N., Rödel M.-O. & Glos J.S. 2017. Amphibian diversity in the matrix of a fragmented landscape around Ranomafana in Madagascar depends on matrix quality. Tropical Conservation Science 10: 1–16.

Neudert R., Ganzhorn J. & Watzold F. 2017. Global benefits and local costs – The dilemma of tropical forest conservation: A review of the situation in Madagascar. Environmental Conservation 44: 82–96.

Nimpa M.M., Andrianirinarison J.C., Sodjinou V.D., Douba A., Masembe Y.V., Randriatsarafara F., Ramamonjisoa C.B., Rafalimanantsoa A.S., Razafindratsimandresy R., Ndiaye C.F. & Rakotonirina J. 2020. Measles outbreak in 2018–2019, Madagascar: epidemiology and public health implications. The Pan African Medical Journal 35: 84.

Nowack C., Peram P.S., Wenzel S., Rakotoarison A., Glaw F., Poth D., Schulz S. & Vences M. 2017. Volatile compound secretion coincides with modifications of the olfactory organ in mantellid frogs. Journal of Zoology 303: 72–81.

Nussbaum R.A., Raxworthy C.J., Raselimanana A.P. & Ramanamanjato J.B. 1999. Amphibians and reptiles of the Réserve Naturelle Intégrale d'Andohahela, Madagascar. *In*: Goodman S.M. (ed.) A floral and faunal inventory of the Réserve Naturelle Intégrale d'Andohahela, Madagascar: with reference to elevational variation. Fieldiana: Zoology, New Series 94: 155–175.

O'Brien S., Emahalala E.R., Beard V., Rakotondrainy R.M., Reid A., Raharisoa V. & Coulson T. 2003. Decline of the Madagascar radiated tortoise *Geochelone radiata* due to overexploitation. Oryx 37: 338–343.

Ofori-Boateng C., Oduro W., Hillers A., Norris K., Oppong S.K., Adum G.B. & Rödel M.-O. 2013. Differences in the effects of selective logging on amphibian assemblages in three West African forest types. Biotropica 45: 94–101.

O'Neil M.F., Campbell A.B., Brown I.W. & Johnstone R. 2010. Using catch rate data for simple cost-effective quota setting in the Australian spanner crab (*Ranina ranina*) fishery. ICES Journal of Marine Science 67: 1538–1552.

Orozco-Terwengel P., Andreone F., Louis Jr. E. & Vences M. 2013. Mitochondrial introgressive hybridization following a demographic expansion in the tomato frogs of Madagascar, genus *Dyscophus*. Molecular Ecology 22: 6074–6090.

Penny S.G., Crottini A., Andreone F., Bellati A., Rakotozafy L.M.S., Holderied M.W., Schwitzer C. & Rosa G.M. 2017. Combining old and new evidence to increase the known biodiversity value of the Sahamalaza Peninsula, Northwest Madagascar. Contributions to Zoology 86: 273–296.

Perl R.G.B., Nagy Z.T., Sonet G., Glaw F. & Wollenberg K.C. 2014. DNA barcoding Madagascar's amphibian fauna. Amphibia-Reptilia 35: 197–206.

Piludu N., Dubos N., Razafimanahaka J.H., Razafindraibe, P., Randrianantoandro J.R. & Jenkins R.K.B. 2015. Distribution, threats and conservation of a Critically Endangered amphibian (*Mantella aurantiaca*) in Eastern Madagascar. Herpetology Notes 8: 119–123.

Poth D., Wollenberg K.C., Vences M. & Schulz S. 2012. Volatile amphibian pheromones: macrolides of mantellid frogs from Madagascar. Angewandte Chemie International Edition 51: 2187–2190.

Preininger D., Weissenbacher A., Wampula T. & Hödl W. 2012. The conservation breeding of two foot-flagging frog species from Borneo, *Staurois parvus* and *Staurois guttatus*. Amphibian and Reptile Conservation 5: 45–56 (e51).

Quéméré E., Amelot X., Pierson J., Crouau-Roy B. & Chikhi L. 2012. Genetic data suggest a natural prehuman origin of open habitats in northern Madagascar and question the deforestation narrative in this region. Proceedings of the National Academy of Sciences USA 109: 13028–13033.

Rabemananjara F.C.E., Bora P., Razafindrabe T., Randriamitso E., Ramilijaona O.R., Raminosoa N.R., Rakotondravony D., Vieites D.R. & Vences M. 2008a. Rapid assessments of population sizes in ten species of Malagasy poison frogs, genus *Mantella*. *In*: Andreone F. (ed.) A conservation strategy for the amphibians of Madagascar, Monografie 45. Museo Regionale di Scienze Naturali, Torino, pp. 253–254.

Rabemananjara F.C.E., Raminosoa N.R., Ramilijaona O.R., Rakotondravony D., Andreone F., Bora P., Carpenter A.I., Glaw F., Razafindrabe T., Vallan D., Vieites D.R. & Vences M. 2008b. Malagasy poison frogs in the pet trade: A survey of levels of exploitation of species in the genus *Mantella*. *In*: Andreone F. (ed.) A conservation strategy for the amphibians of Madagascar, Monografie 45. Museo Regionale di Scienze Naturali, Torino, pp. 357–376.

Rabemananjara F., Andreone F. & Rabibisoa N. 2011. Madagascar and chytrid news: needed an urgent action and close collaboration between stakeholders. FrogLog 97: 33–33.

Rabibisoa N. 2008. *Mantella cowanii* Action Plan. Conservation International, Antananarivo.

Rabibisoa N. & Raharivololona L. 2010. Plan stratégique de prévention et de lutte contre l'introduction du chytride à Madagascar. Conservation International & Amphibian Specialist Group, Antananarivo.

Rabibisoa N., Randrianasolo H., Anjeriniaina M., MacKinnon J., Andriamamonjisoa A., Ramandibison, Randrianantoandro C. & Andreone F. 2009. New findings of harlequin mantella improve the conservation of Madagascar's most threatened frog. FrogLog 92: 5–8.

Rabibisoa N.H., Anjeriniaina M., Rakotoniaina V., Randrianasolo H., Rabemananjara F.E.C. & Andreone F. 2013. The harlequin mantella *Mantella cowanii* in Antoetra Region, High Plateau of Madagascar: new steps in conservation. FrogLog 107: 50–51.

Rakotoarison, A., Scherz M.D., Glaw F., Köhler J., Andreone F., Franzen M., Glos J., Hawlitschek O., Jono T., Mori A., Ndriantsoa S.H., Rasoamampionona R.N., Riemann J.C., Rödel M.-O., Rosa G.M., Vieites D.R., Crottini A. & Vences M. 2017. Describing the smaller majority: integrative taxonomy reveals twenty-six new species of tiny microhylid frogs (genus *Stumpffia*) from Madagascar. Vertebrate Zoology 67: 271–398.

Rakotonanahary T.F., Dawson J., Andreone F., Rakotoarisoa J.C. & Edmonds D. 2017. Amphibian captive breeding programs for Madagascar: where we are now and the road ahead. FrogLog 25: 37–39.

Ramasindrazana B., Parany M.N.J., Rasoamalala F., Rasoanoro M., Rahajandraibe S., Vogler A.J., Sahl J.W., Andrianaivoarimanana V., Rajerison M. & Wagner D.M. 2020. Local-scale genotype diversity of *Yersinia pestis*: a case study from Ambohitromby, Ankazobe District (2003–2016), Madagascar. Research Square.

Rancilhac L., Bruy T., Scherz M.D., Almeida Pereira E., Preick M., Straube N., Lyra M., Ohler A., Streicher J.W., Andreone F., Crottini A., Hutter C., Randrianantoandro C., Rakotoarison A., Glaw F., Hofreiter M. & Vences M. 2020. Targeted enrichment DNA sequencing from historical type material enables a partial revision of the Madagascar giant stream frogs (genus *Mantidactylus*). Journal of Natural History 54: 87–118.

Randrianavelona R., Rakotonoely H., Ratsimbazafy J. & Jenkins R.K.B. 2010a. Conservation assessment of the critically endangered frog *Mantella aurantiaca* in Madagascar. African Journal of Herpetology 59: 65–78.

Randrianavelona R., Randrianantoandro J.C., Rabibisoa N., Randrianasolo H., Rabesihanaka S., Randriamahaleo S. & Jenkins R.K.B. 2010b. Stratégie de conservation de l'éspèce *Mantella aurantiaca* (grenouille dorée) 2011–2015. Ministère de l'Environnement et des Forêts. Antananarivo.

Randrianiaina R.D., Raharivololoniaina L., Preuss C., Strauss A., Glaw F., Teschke M., Glos J., Raminosoa N. & Vences M. 2009. Descriptions of the tadpoles of seven species of Malagasy treefrogs, genus *Boophis*. Zootaxa **2021**: 23–41.

Randrianiaina R.D., Strauss A., Glos J., Glaw F. & Vences M. 2011a. Diversity, external morphology and "reverse taxonomy" in the specialized tadpoles of Malagasy river bank frogs of the subgenus *Ochthomantis* (genus *Mantidactylus*). Contributions to Zoology 80: 17–65.

Randrianiaina R.D., Wollenberg K.C., Rasolonjatovo Hiobiarilanto T., Strauss A., Glos J. & Vences M. 2011b. Nidicolous tadpoles rather than direct development in Malagasy frogs of the genus *Gephyromantis*. Journal of Natural History 45: 2871–2900.

Randrianiaina R.D., Strauss A., Glos J. & Vences M. 2012. Diversity of strongly rheophilous tadpoles of Malagasy tree frogs, genus *Boophis* (Anura, Mantellidae), and identification of new candidate species via larval DNA sequence and morphology. ZooKeys 178: 59–124.

Raxworthy C.J. 2008. Global warming and extinction risks for amphibians in Madagascar: a preliminary assessent of upslope displacement. *In*: Andreone F. (ed.) A conservation strategy for the amphibians of Madagascar, Monografie 45. Museo Regionale di Scienze Naturali, Torino, pp. 67–84.

Raxworthy C.J. & Nussbaum R.A. 1996a. Montane amphibian and reptile communities in Madagascar. Conservation Biology 10: 750–756.

Raxworthy C.J. & Nussbaum R.A. 1996b. Amphibians and reptiles of the Rèserve Naturelle Intégrale d'Andringitra, Madagascar: a study of the elevational distribution and local endemicity. *In*: Goodman S.M. (ed.) A floral and faunal inventory of the eastern slopes of the Réserve Naturelle Intégrale d'Andringitra, Madagascar: with reference to elevational variation, Fieldiana: Zoology, New Series 85: 158–171.

Raxworthy C.J., Andreone F., Nussbaum R.A., Rabibisoa N. & Randriamahazo H. 1998. Amphibians and reptiles of the Anjanaharibe-Sud Massif, Madagascar: Elevational distribution and regional endemicity. *In*: Goodman S.M. (ed.) A floral and faunal inventory of the Réserve Spéciale d'Anjanaharibe-Sud, Madagascar: with reference to elevational variation, Fieldiana: Zoology, New Series **90**: 79–93.

Raxworthy C. J., Pearson R. G., Rabibisoa N., Rakotondrazafy A. M., Ramanamanjato J. B., Raselimanana A. P., Wu S., Nussbaum R. A. & Stone D. A. 2008. Extinction vulnerability of tropical montane endemism from warming and upslope displacement: a preliminary appraisal for the highest massif in Madagascar. Global Climate Change **14**: 1–18.

Reardon J.T., Kraus F., Moore M., Rabenantenaina L., Rabinivo A., Rakotoarisoa N. H. & Randrianasolo H. H. 2018. Testing tools for eradicating the invasive toad *Duttaphrynus melanostictus* in Madagascar. Conservation Evidence **15**: 12–19.

Reed J. M., Mills L. S., Dunning J. B., Menges E. S., McKelvey K. S., Frye R., Beissinger S. R., Anstett M. C. & Miller P. 2002. Emerging issues in population viability analysis. Conservation Biology **16**: 7–19.

Reeve E., Ndriantsoa S. H., Strauss A., Randrianiaina R. D., Rasolonjatovo Hiobiarilanto T., Glaw F., Glos J. & Vences M. 2011. Acoustic underwater signals with a probable function during competitive feeding in a tadpole. Naturwissenschaften **98**: 135–143.

Rege J. E. O. & Tawah C. L. 1999.The state of African cattle genetic resources II. Geographical distribution, characteristics and uses of present-day breeds and strains. FAO/UNEP Animal Genetic Resources Information Bulletin **26**: 1–26.

Retallick R. W. R., McCallum H. & Speare R. 2004. Endemic infection of the amphibian chytrid fungus in a frog community post-decline. PLoS Biology **2**: e351.

Riemann J. C., Ndriantsoa S. H., Raminosoa N. R., Rödel M.-O. & Glos J. 2015. The value of forest fragments for maintaining amphibian diversity in Madagascar. Biological Conservation **191**: 707–715.

Riemann J. C., Ndriantsoa S. H., Rödel M.-O. & Glos J. 2017. Functional diversity in a fragmented landscape – habitat alterations affect functional trait composition of frog assemblages in Madagascar. Global Ecology and Conservation **10**: 173–183.

Robinson J. E., Fraser I. M., John F. A. S., Randrianantoandro J. C., Andriantsimanarilafy R. R., Razafimanahaka J. H., Griffiths R. A. & Roberts D. L. 2018a. Wildlife supply chains in Madagascar from local collection to global export. Biological Conservation **226**: 144–152.

Robinson J. E., Griffiths R. A., Fraser I. M., Raharimalala J., Roberts D. L. & St John F. A. 2018b. Supplying the wildlife trade as a livelihood strategy in a biodiversity hotspot. Ecology and Society **23**: 13.

Robinson, J. G. & Redford, K. H. 1991. Sustainable harvest of neo-tropical mammals. *In*: Robinson J. G. & Redford K. H. (eds) Neo-tropical wildlife use and conservation. The Chicago University Press, pp. 415–429.

Rocha R., Borda E., Andreone F. & Rosa G. M. 2012. First reports of leech parasitism in Malagasy anurans. Comparative Parasitology **79**: 352–356.

Rödder D., Kielgast J., Bielby J., Schmidtlein S., Bosch J., Garner T. W. J., Veith M., Walker S., Fisher M. C. & Lötters S. 2009. Global amphibian extinction risk assessment for the panzootic chytrid fungus. Diversity **1**: 52–66.

Roe D. 2002. Making a killing or making a living: wildlife trade, trade controls, and rural livelihoods. Biodiversity and Livelihoods 6. IIED and TRAFFIC, London and Cambridge.

Román-Palacios C. & Wiens J. J. 2020.Recent responses to climate change reveal the drivers of species extinction and survival. Proceedings of the National Academy of Sciences USA **117**: 4211–4217.

Rosa G. M., Andreone F., Crottini A., Hauswaldt J. S., Noël J., Rabibisoa N. H., Randriambahiniarime M. O., Rebelo R. & Raxworthy C. J. 2012. The amphibians of the relict Betampona low-elevation rainforest, eastern Madagascar: an application of the integrative taxonomy approach to biodiversity assessments. Biodiversity and Conservation **21**: 1531–1559.

Rosa G. M., Anza I., Moreira P. L., Conde J., Martins F., Fisher M. C. & Bosch J. 2013. Evidence of chytrid-mediated population declines in common midwife toad in Serra da Estrela, Portugal. Animal Conservation **16**: 306–315.

Rosa G. M., Cadle J. E., Crottini A., Dawson J., Edmonds D., Fisher M. C., Garcia G., Glaw F., Glos J., Harris R. N., Köhler J., Rabemananjara F., Rabesihanaka S., Rabibisoa N., Randrianantoandro J.C., Raselimanana A.P., Raxworthy C.J., Razafindraibe H., Vallan D., Vences M., Weldon C., Wright P. C. & Andreone F. 2015. ACSAM2, A conservation strategy for the amphibians of Madagascar 2: abstract book. Museo Regionale di Scienze Naturali, Torino.

Rosa G.M., Mattioli F., Dunce I. & Zwartepoorte H. 2009. AARK *ex situ* management guidelines: *Dyscophus antongilii* and *D. guineti*. AARK / EAZA.

Rosa G. M., Mercurio V., Crottini A. & Andreone F. 2011. Explosion into the canyon: an insight into the breeding aggregation of *Scaphiophryne gottlebei* Busse & Böhme, 1992. North-Western Journal of Zoology **7**: 329–333.

Rosa G. M., Sabino-Pinto J., Laurentino T. G., Martel A., Pasmans F., Rebelo R., Griffiths R. A., Stöhr A. C., Marschang R. E., Price S. J., Garner T. W. J. & Bosch J. 2017. Impact of asynchronous emergence of two lethal pathogens on amphibian assemblages. Scientific Reports **7**: 43260.

Roznik E. A., Sapsford D. A., Pike L., Schwarzkopf L. & Alford R. A. 2015. Natural disturbance reduces disease risk in endangered rainforest frog populations. Scientific Reports **5**: 13472.

Sæther B. E., Engen S., Odden J., Linnell J. D. C., Grotan V. & Andrèn H. 2010. Sustainable harvest strategies for age-structured Eurasian lynx populations: The use of reproductive value. Biological Conservation **143**: 1970–1979.

Scheele B. C., Pasmans F., Skerratt L.F., Berger L., Martel A., Beukema W., Acevedo A. A., Burrowes P. A., Carvalho T., Catenazzi A., De La Riva I., Fisher M. C., Flechas S. V., Foster C. N., Frías-Álvarez P., Garner T. W. J., Gratwicke B., Guayasamin J. M., Hirschfeld M., Kolby J. E., Kosch T. A., La Marca E., Lindenmayer D. B., Lips K. R., Longo A. V., Maneyro R., McDonald C. A., Mendelson III J., Palacios-Rodriguez P., Parra-Olea G., Richards-Zawacki C. L., Rödel M.-O., Rovito S. M., Soto-Azat C., Toledo L. F., Voyles J., Weldon C., Whitfield S. M., Wilkinson M., Zamudio K. R. & Canessa S. 2019. Amphibian fungal panzootic causes catastrophic and ongoing loss of biodiversity. Science **363**: 1459–1463.

Scherz M. D., Vences M., Rakotoarison A., Andreone F., Köhler J., Glaw F. & Crottini A. 2016. Reconciling molecular phylogeny, morphological divergence and classification of Madagascan narrow-mouthed frogs (Amphibia: Microhylidae). Molecular Phylogenetics and Evolution **100**: 372–381.

Scherz M. D., Vences M., Rakotoarison A., Andreone F., Köhler J., Glaw F. & Crottini A. 2017. Lumping or splitting in the Cophylinae (Anura: Microhylidae) and the need for a parsimony of taxonomic changes: a response to Peloso *et al.* (2017). Salamandra **53**: 479–483.

Schlaepfer M.A., Hoover C. & Dodd K. Jr. 2005. Challenger in evaluating the impact of the trade in amphibians and reptiles on wild populations. BioScience **55**: 256–254.

Schmeller D. S., Blooi M., Martel A., Garner T. W., Fisher M. C., Azemar F., Clare F. C., Leclerc C., Jäger L., Guevara-Nieto M., Loyau A. & Pasmans F. 2014. Microscopic aquatic predators strongly affect infection dynamics of a globally emerged pathogen. Current Biology **24**: 176–180.

Schmidt H., Strauss A., Glaw F., Teschke M. & Vences M. 2009. Description of tadpoles of five frog species in the subgenus *Brygoomantis* from Madagascar (Mantellidae: *Mantidactylus*). Zootaxa **1988**: 48–60.

Schuurman D. & Lowry P. P. II. 2009. The Madagascar rosewood massacre. Madagascar Conservation & Development **4**: 98–102.

Searle C. L., Gervasi S. S., Hua J., Hammond J. I., Relyea R. A., Olson D. H. & Blaustein A. R. 2011. Differential host susceptibility to *Batrachochytrium dendrobatidis*, an emerging amphibian pathogen. Conservation Biology **25**: 965–974.

Segev O., Andreone F., Pala R., Tessa G. & Vences M. 2012. Reproductive phenology of the tomato frog, *Dyscophus antongili*, in an urban pond of Madagascar's east coast. Acta Herpetologica **7**: 331–340.

Shine R. 2018. Cane toad wars. University of California Press, Oakland.

Shinya T., Hyojung L., Fuminari M., Hin C. Y., Sung-mok J., Akhmetzhanov A. R. & Hiroshi N. 2017. Dynamics of the pneumonic plague epidemic in Madagascar, August to October 2017. Euro Surveillance 22. *https://doi.org/10.2807/1560-7917*.

Shoo L. P., Olson D. H., McMenamin S. K., Murray K. A., Van Sluys M., Donnelly M. A., Stratford D., Terhivuo J., Merino-Viteri A., Herbert S. M., Bishop P. J., Corn P. S., Dovey L., Griffiths R. A., Lowe K., Mahony M., McCallum H., Shuker J. D., Simpkins C., Skerratt L. F., Williams S. E. & Hero J.-M. 2011. Engineering a future for amphibians under climate change. Journal of Applied Ecology **48**: 487–492.

Skerratt L. F., Berger L., Speare R., Cashins S., McDonald K. R., Phillott A. D., Hines H. B. & Kenyon N. 2007. Spread of chytridiomycosis has caused the rapid global decline and extinction of frogs. EcoHealth **4**: 125–134.

Solofondranohatra C. L.,Vorontsova M. S., Hackel J., Besnard G., Cable S., Williams J., Jeannoda V. & Lehmann C. E. R. 2018. Grass functional traits differentiate forestand savanna in the Madagascar Central highlands. Frontiers in Ecology and Evolution **6**: 184.

Smith R. K., Meredith H. & Sutherland W. J. 2019. Amphibian conservation. *In*: Sutherland W. J., Dicks L. V., Ockendon N., Petrovan S. O. & Smith R. K.(eds) What works in conservation 2019. Open Book Publishers,Cambridge, pp. 9–65.

Starnberger I., Poth D., Peram P. S., Schulz S., Vences M., Knudsen J., Barej M. F., Rödel M.-O., Walzl M. & Hödl W. 2013. Take time to smell the frogs: vocal sac glands of reed frogs (Anura: Hyperoliidae) contain species-specific chemical cocktails. Biological Journal of the Linnean Society **110**: 828–838.

Stockwell M.P., Storrie L. J., Pollard C. J., Clulow J. & Mahoney M. J. 2015. Effects of pond salinization on survival rate of amphibian hosts infected with the chytrid fungus. Conservation Biology **29**: 391–399.

Strauss A., Reeve E., Randrianiaina R.-D., Vences M. & Glos J. 2010. The world's richest tadpole communities show functional redundancy and low functional diversity: ecological data on Madagascar's stream-dwelling amphibian larvae. BMC Ecology **10**: 12.

Strauss A., Randrianiaina R.-D., Vences M. & Glos J. 2013. Species distribution and assembly patterns of frog larvae in rainforest streams of Madagascar. Hydrobiologia **702**: 27–43.

Stuart S. N., Chanson J. S., Cox N. A., Young B. E., Rodrigues A. S. L., Fischman D. L. & Waller R. W. 2004. Status and trends of amphibian declines and extinctions worldwide. Science **306**: 1783–1786.

Styger E., Rakotondramasy H. M., Pfeffer M. J., Fernandes E. C. M. & Bates D. M. 2007. Influence of slash-and-burn farming practices on fallow succession and land degradation in the rainforest region of Madagascar. Agriculture, Ecosystems and Environment **119**: 257–269.

Tapley B., Bradfield K.S., Michaels C. & Bungard M. 2015. Amphibians and conservation breeding programmes: do all threatened amphibians belong on the ark? Biodiversity and Conservation **24**: 2625–2646.

Taylor M., Demaster D., Bunnel F. & Schweinsburg R. E. 1987. Modeling the sustainable harvest of female polar bears. Journal of Wildlife Management **51**: 811–820.

Tessa G., Crottini A., Giacoma C., Guarino F. M., Randrianirina J. E. & Andreone F. 2017. Comparative longevity and age at sexual maturity in twelve rainforest frogs of the genera *Boophis*, *Gephyromantis*, and *Mantidactylus* (Anura: Mantellidae) from Madagascar. Phyllomedusa **16**: 13–21.

Tessa G., Guarino F. M., Giacoma C., Mattioli F. & Andreone F. 2008. Longevity and body size in three populations of *Dyscophus antongilii* (Microhylidae, Dyscophinae), the tomato frog from north-eastern Madagascar. Acta Herpetologica **2**: 139–146.

Tessa G., Mattioli F., Mercurio V. & Andreone F. 2009. Egg number and fecundity traits in nine species of *Mantella* poison frogs from arid grasslands and rainforests of Madagascar (Anura: Mantellidae). Madagascar Conservation and Development **4**: 113–119.

Tessa G., Guarino F. M., Randrianirina J. E. & Andreone F. 2011. The age structure in the false tomato frog *Dyscophus guineti* from eastern Madagascar, compared to the closely related *D. antongilii* (Anura, Microhylidae). African Journal of Herpetology **60**: 84–88.

Todd M. 2011. Trade in Madagascar's endemic reptiles and amphibians in Thailand. TRAFFIC Southeast Asia, Petaling Jaya, Selangor.

Trainor C. R. 2009. Survey of a population of black-spined toad *Bufo melanostictus* in Timor-Leste: confirming identity, distribution, abundance and impacts of an invasive and toxic toad. Report by Charles Darwin University to AusAID.

Tyson P. 2000. The eighth continent. Life, death, and discovery in the lost world of Madagascar. Harper Collins, New York.

Uetz P., Freed P. & Hošek J. 2020. The Reptile Database. *http://www.reptile-database.org* (accessed on the 30th September 2020).

Ujvari B., Casewell N. R., Sunagar K., Arbuckle K., Wüster W., Lo N., Denis O. M., Beckmann C., King G. F., Deplazes E. & Madsen T. 2015. Widespread convergence in toxin resistance by predictable molecular evolution. Proceedings of the National Academy of Sciences USA **112**: 11911–11916.

UNEP-WCMC 2019a. CITES trade data dashboards: global trade in amphibians, UNEP-World Conservation Monitoring Centre. *http://dashboards.cites.org/* (accessed on the 10th April 2019).

UNEP-WCMC 2019b. CITES Trade Database, UNEP-World Conservation Monitoring Centre. *http://www.unep-wcmc-apps.org/citestrade/* (accessed on the 10th April 2019).

UNSD 2014. World Statistics Pocketbook 2014 edition. United Nations, New York.

Vallan D. 2000. Influence of forest fragmentation on amphibian populations in Ambohitantely, highland Madagascar. Biological Conservation **96**: 31–43.

Vallan D. 2002. Effects of anthropogenic environmental changes on amphibian diversity in the rainforests of eastern Madagascar. Journal of Tropical Ecology **18**: 725–742.

Vallan D. 2003. Consequences of forest fragmentation on the herpetofauna of the nature reserve of Ambohitantely. *In*: Goodman S. M. & Benstead P. (eds) The natural history of Madagascar. The University of Chicago Press, Chicago and London, pp. 899–907.

Vallan D., Raherisoa V. H., Andreone F. & Dolch R. 2004. Does selective wood exploitation affect amphibian diversity? The case of An'Ala, a tropical rainforest in eastern Madagascar. Oryx **38**: 410–417.

Van der Meijden A., Vences M., Hoegg S., Boistel R., Channing A. & Meyer A. 2007. Nuclear gene phylogeny of narrow-mouthed toads (Family Microhylidae) and a discussion of competing hypotheses concerning their biogeographical origins. Molecular Phylogenetics and Evolution **44**: 1017–1030.

Vences M., Andreone F., Glaw F., Raminosoa N., Randrianirina J. E. & Vieites D. R. 2002. Amphibians and reptiles of the Ankaratra Massif: reproductive diversity, biogeography and conservation of a montane fauna in Madagascar. Italian Journal of Zoology **69**: 263–284.

Vences M., Raselimanana A. P. & Glaw F. 2003a. Ranidae: *Hoplobatrachus*, Indian tiger frog. *In*: Goodman S. M. & Benstead J. P. (eds) The natural history of Madagascar. The University of Chicago Press, Chicago and London, pp. 926–927.

Vences M., Vieites D. R., Glaw F., Brinkmann H., Kosuch J., Veith M. & Meyer A. 2003b. Multiple overseas dispersal in amphibians. Proceedings of the Royal Society B, 270: 2435–2442.
Vences M., Kosuch J., Rödel M.-O., Lötters S., Channing A., Glaw F. & Böhme W. 2004. Phylogeography of *Ptychadena mascareniensis* suggests transoceanic dispersal in a widespread African-Malagasy frog lineage. Journal of Biogeography 31: 593–601.
Vences M., Chiari Y., Teschke M., Randrianiaina R.-D., Raharivololoniaina L., Bora P., Vieites D. R. & Glaw F. 2008a. Which frogs are out there? A preliminary evaluation of survey techniques and identification reliability of Malagasy amphibians. *In*: Andreone F. (ed.) A conservation strategy for the amphibians of Madagascar. Monografie 45. Museo Regionale di Scienze Naturali, Torino, pp. 233–253.
Vences M., Jovanovic O. & Glaw F. 2008b. Historical analysis of amphibian studies in Madagascar: an example for increasing research intensity and international collaboration. *In*: Andreone F. (ed.) A conservation strategy for the amphibians of Madagascar. Monografie 45. Museo Regionale di Scienze Naturali, Torino, pp. 47–58.
Vences M., Wollenberg K. C., Vieites D. R. & Lees D. C. 2009. Madagascar as a model region of species diversification. Trends in Ecology and Evolution 24: 456–465.
Vences M., Köhler J., Crottini A. & Glaw F. 2010a. High mitochondrial sequence divergence meets morphological and bioacoustic conservatism: *Boophis quasiboehmei* sp. nov., a new cryptic treefrog species from south-eastern Madagascar. Bonn zoological Bulletin 57: 241–255.
Vences M., Köhler J., Pabijan M. & Glaw F. 2010b. Two syntopic and microendemic new frogs of the genus *Blommersia* from the east coast of Madagascar. African Journal of Herpetology 59: 133–156.
Vences M., Brown J. L., Lathrop A., Rosa G. M., Cameron A., Crottini A., Dolch R., Edmonds D., Freeman K. L. M., Glaw F., Grismer L. L., Litvinchuk S., Milne M. G., Moore M., Solofo J. F., Noël J., Nguyen T. Q., Ohler A., Randrianantoandro C., Raselimanana A. P., van Leeuwen P., Guinevere O. W. W., Ziegler T., Andreone F. & Murphy R. W. 2017. Tracing a toad invasion: lack of mitochondrial DNA variation, haplotype origins, and potential distribution of introduced *Duttaphrynus melanostictus* in Madagascar. Amphibia-Reptilia 38: 197–207.
Vieites D. R., Wollenberg K. C., Andreone F., Köhler J., Glaw F. & Vences M. 2009. Vast underestimation of Madagascar's biodiversity evidenced by an integrative amphibian inventory. Proceedings of the National Academy of Sciences USA 106: 8267–8272.
Vieilledent G., Grinand C., Rakotomalala F. A., Ranaivosoa R., Rakotoarijaona J. R., Allnutt T. F. & Achard F. 2018. Combining global tree cover loss data with historical national forest cover maps to look at six decades of deforestation and forest fragmentation in Madagascar. Biological Conservation 222: 189–197.
Virah-Sawmy M., Gardner C. J. & Ratsifandrihamanana A. N. 2014. The Durban Vision in practice. Experience in the participatory governance of Madagascar's new protected areas. *In*: Scales I. R. (ed.) Conservation and environmental management in Madagascar. Routledge, London and New York, pp. 193–215.
Vollset S. E., Goren E., Yuan C.-W., Cao J., Smith A. E., Hsiao T., Bisignano C., Azhar G. S., Castro E., Chalek J., Dolgert A. J., Frank T., Fukutaki K., Hay S. I., Lozano R., Mokdad A. H., Nandakumar V., Pierce M., Pletcher M., Robalik T., Steuben K. M., Wunrow K. Y., Zlavog B. S. & Murray C. J. L. 2020. Fertility, mortality, migration, and population scenarios for 195 countries and territories from 2017 to 2100: a forecasting analysis for the Global Burden of Disease Study. The Lancet 396(10258): 1285–1306.
Vredenburg V. T., du Preez L., Raharivololoniaina L., Vieites D. R., Vences M. & Weldon C. 2012. A molecular survey across Madagascar does not yield positive records of the amphibian chytrid fungus *Batrachochytrium dendrobatidis*. Herpetology Notes 5: 507–517.
Walker R. C. J., Rix C. E. & Woods-Ballard A. J. 2004. The export of the endangered Madagascar spider tortoise (*Pyxis arachnoides*) to support the exotic pet trade. Herpetological Bulletin 90: 2–9.
Weldon C., Du Preez L. & Vences M. 2008. Lack of detection of the amphibian chytrid fungus (*Batrachochytrium dendrobatidis*) in Madagascar. *In*: Andreone F. (ed.) A conservation strategy for the amphibians of Madagascar. Monografie 45. Museo Regionale di Scienze Naturali, Torino, pp. 95–106.
Weldon C., Crottini A., Bollen A., Rabemananjara F. C. E., Copsey J., Garcia G. & Andreone F. 2013. Pre-emptive National Monitoring Plan for detecting the amphibian chytrid fungus in Madagascar. EcoHealth 10: 234–240.
Wilmé L., Goodman S.M. & Ganzhorn J. U. 2006. Biogeographic evolution of Madagascar's microendemic biota. Science 312: 1063–1065.
Wollenberg K. C., Glaw F., Meyer A. & Vences M. 2007. Molecular phylogeny of Malagasy reed frogs, *Heterixalus*, and the relative performance of bioacoustics and color-patterns for resolving their systematics. Molecular Phylogenetics and Evolution 45: 14–22.
Wollenberg K. C., Vieites D. R., Van der Meijden A., Glaw F., Cannatella D. C. & Vences M. 2008. Patterns of endemism and species richness in Malagasy cophyline frogs support a key role of mountainous areas for speciation. Evolution 62: 1890–1907.
Wollenberg K. C., Jenkins R. K. B, Randrianavelona R., Ralisata M., Rampilamanana R., Ramanandraibe A., Ravoahangimalala O. R. & Vences M. 2010. Raises awareness of amphibian chytridiomycosis will not alienate ecotourists visiting Madagascar. EcoHealth 7: 248–251.
Wollenberg K. C., Vieites D. R., Glaw F. & Vences M. 2011. Speciation in little: the role of range and body size in the diversification of Malagasy mantellid frogs. BMC Evolutionary Biology 11: 217.
Wren S., Angulo A., Meredith H., Kielgast J., Dos Santos M. & Bishop P. 2015. Amphibian Conservation Action Plan. IUCN SSC Amphibian Specialist Group. *https://www.iucn-amphibians.org/resources/acap/*
Young B. E., Stuart S. N., Chanson J. S., Cox N. A. & Boucher T. M. 2004. Disappearing jewels: the status of New World amphibians. NatureServe, Arlington.
Zimkus B. M., Lawson L. P., Barej M. F., Barratt C. D., Channing A., Dash K. M., Dehling J. M., Du Preez L., Gehring P., Greenbaum E., Gvoždík V., Harvey J., Kielgast J., Kusamba C., Nagy Z. T., Pabijan M., Penner J., Rödel M.-O., Vences M. & Lötters S. 2017. Leapfrogging into new territory: How Mascarene ridged frogs diversified across Africa and Madagascar to maintain their ecological niche. Molecular Phylogenetics and Evolution 106: 254–269.
Zippel K., Johnson K., Gagliardo R., Gibson R., McFadden M., Browne R., Martinez C. & Townsend E. 2011. The Amphibian Ark: a global community for *ex situ* conservation of amphibians that cannot currently be safeguarded *in situ*. Herpetological Conservation and Biology 6: 340–352.

Chapter 5.

The Status of Amphibian Decline and Conservation on the Islands of the Western Indian Ocean

(Seychelles, Mascarenes, Comoros)

Oliver Hawlitschek

Harold Heatwole · Mark-Oliver Rödel (Editors)

Status and Threats of Afrotropical Amphibians

Amphibian Biology, Volume 11, Part 7

Status of Conservation and Decline of Amphibians: Eastern Hemisphere

Edition Chimaira

Due to their physiology, morphology and complex life cycles, amphibian species are often highly habitat-specific and particularly threatened by environmental changes. Currently more than one third of all species is believed to be threatened. The worldwide decline of amphibians therefore has become a symbol for the Global Biodiversity Crisis.

Whereas in recent years many studies have reported the threat status of amphibians in the Northern Hemisphere, Latin America and Australia, very little information was available for Africa, in particular for sub-Saharan Africa.

This book illustrates the beauty of Afrotropical amphibians as well as their habitats and threats, summarizing our previous knowledge and presenting new facts concerning the status, threats and potential future of amphibians in all sub-Saharan countries, Madagascar and western Indian Ocean islands.

It will serve as a guideline for conservationists, decision makers and researchers, and due to its lavishly illustrated layout, will also be attractive to everybody interested in African amphibians in particular and amphibian biology and conservation in general.

9 783899 373103