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The amphibians and reptiles of Nosy Be (NW Madagascar) and nearby islands: a case study of diversity and conservation of an insular fauna

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Surveys of the amphibians and reptiles on Nosy Be (an island off north-west Madagascar) and nearby islands were undertaken between 1991 and 2001 and are discussed here in view of biodiversity considerations and conservation efforts. Since Nosy Be is the type locality of several amphibian and reptile taxa, their exact status is of crucial importance for the nomenclatural stability of many groups of the Madagascan herpetofauna. A total of 20 amphibian and 61 reptile species (excluding marine reptiles) was confirmed for this archipelago. Other species (*Mantidactylus horridus*, *Androngo elongatus*, *Typhlops madagascariensis*, *T. reuteri*, *Micropisthodon ochraceus* and *Pararhadinea melanogaster*) were not found during these inventories, but are quoted in the literature or housed in herpetological collections, and are considered as likely to be present at Nosy Be. A further 18 taxa are tentatively excluded from its fauna, due to biogeographic incongruence and/or lack of reliable voucher specimens. Few taxa are so far only known from the island; they may represent endemics or may have been overlooked on the adjacent mainland. They are respectively *Stumpffia pygmaea*, *Mabuya lavarambo*, *Lygodactylus h. heterurus*, *Lycodryas granuliceps* and *Typhlops reuteri*. *Heterixalus tricolor* too is likely to be present on Nosy Be only, but the difference with respect to taxa present on the mainland needs to be confirmed. Several species are known from nearby islands and islets surveyed (11 amphibians and 26 reptiles). A few of them (*Heterixalus* '*variabilis*', *Kinixys belliana*, *Furcifer*

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oustaleti, *Mabuya comorensis*, *Paracontias milloti*) are present on some of these islands but have not yet been found on Nosy Be. Much of the field research was conducted at Lokobe, a strict nature reserve still characterized by good forest coverage (typical of the Sambirano Domain), and an important area of biodiversity. With 15 amphibian and 45 reptile species, Lokobe hosts 81% of the overall Nosy Be herpetofauna: of the species found during our surveys, only *Heterixalus tricolor*, *Hoplobatrachus tigerinus*, *Gehyra mutilata*, *Phelsuma dubia* and *Crocodylus niloticus* were only found outside the reserve. In view of this, the protection of Lokobe should be assured and reinforced. Except for Lokobe, habitats on Nosy Be are largely anthropogenic, and have a lower species diversity, especially where there is intensive agriculture. At other sites (e.g. ylang-ylang and coffee plantations) and in forested bands along roads, species diversity is still high: careful management of these anthropogenic habitats might also assure the survivorship and conservation of a diverse herpetofauna outside the protected area.

KEYWORDS: Amphibia, Reptilia, Madagascar, Nosy Be, Lokobe Reserve, Sambirano, Island, Biodiversity, Conservation.

Introduction

The high degree of diversity and endemicity of animals and plants of Madagascar is well known (Myers *et al.*, 2000; Ganzhorn *et al.*, 2001): the comprehension that understanding of biogeographic patterns is crucial to assess conservation priorities has led to a renewed interest in faunal and floral inventories (Anonymous, 2001). Most recent surveys were carried out in protected areas on the mainland (e.g. Raxworthy and Nussbaum, 1995; Raselimanana *et al.*, 1998; Rexworthy *et al.*, 1998), while few data are available for non-protected and secondary habitats in Madagascar (e.g. Andreone *et al.*, 2000), and little is known of the herpetofauna of the Malagasy offshore islands. In general, the analysis of biodiversity on islands is noteworthy, because they may be important centres of endemicity and their study aids in understanding historical patterns of animal and plant distribution and dispersal. Moreover, the island's limited size may accelerate extinction. This situation has been documented for lemurs and birds, as pointed out by Goodman (1993), where human disturbance and intensive hunting has caused the extinction of a bird [the snail-eating coua, *Coua delalandei* (Temminck)], and the disappearance of native lemurs at Sainte Marie (off the eastern coast of Madagascar).

However, only limited data are available about the composition, richness and conservation of amphibian and reptile communities of the Malagasy offshore islands. Due to its historical importance as a trade centre, and its recent access and tourist facilities, the island of Nosy Be (also known as Nossi Be, Nossi-Bé or Nossi Bé)—located in north-west Madagascar—has been for long one of the main zoological collecting localities on Madagascar and is one of the best known islands, also from a geographical point of view (Battistini, 1960). Regarding the herpetofauna, it is worth mentioning as an example, the many contributions by Boettger (1877, 1878, 1879, 1880a,b, 1881a,b,c, 1882, 1893, 1894, 1898, 1913), who described several taxa, based upon materials from Nosy Be.

Recently we had the opportunity to survey Nosy Be, including the Réserve Naturelle Intégrale de Lokobe (RNI 6), which occurs on Nosy Be. In this context, we also examined the preserved specimens housed in the major herpetological collections and analysed the pertinent literature with the purpose of providing an exhaustive list of the non-marine herpetofauna.

Materials and methods

Geographic context

Nosy Be, located in the north-west (coordinates: 47°15′E and 13°20′S), is the largest off-shore island of Madagascar, with a total surface area of about 25,200 ha, and a maximum altitude of 430 m (Nicoll and Langrand, 1989; Projet ZICOMA, 1999). Together with several satellite islands it is included within the Sambirano Domain, which is characterized by a vegetation similar in many aspects to that of the eastern rainforest (Humbert, 1955). At Nosy Be, the annual mean rainfall is 2250 mm, the maximum being in January (462 mm), and the minimum in July (37 mm) (Battistini, 1960). The mean yearly temperature is 26°C, with a maximum of 34.8°C and a minimum of 15°C.

Nosy Be falls within the Faritany (Province) of Antsiranana (Diégo Suarez). Its distance from the nearest mainland sites (e.g. Ankify to the south, Ambato to the east) is about 12–12.5 km (figure 1). There are several other islands and islets near Nosy Be, one of the largest being Nosy Komba, located almost midway between Nosy Be and the mainland. Some other islands (e.g. Nosy Faly, Nosy Mamoko) are very near the mainland, and are likely to have originated by a recent separation from the mainland by rising sea levels (R. Battistini, pers. comm.). For ease we here refer to these small islands and islets as 'nearby islands' or 'satellite islands'.

Nosy Be is an important centre for tourism and agriculture. For this reason, this island has several roads and is largely deforested for conversion into coffee plantations, ricefields, ylang-ylang (*Cananga odorata* Hook.), and sugar cane fields, for the production of essential oils and alcoholic beverages. A portion of the original Sambirano forest (of about 740 ha) still persists at Lokobe, a protected area located in the south-eastern part of the island (13°25′S and 48°20′E). Lokobe is currently managed as a 'Réserve Naturelle Intégrale' (RNI = Strict Nature Reserve), although its upgrading to 'Parc National' (National Park) is under consideration (Anonymous, 2001).

The satellite islands for which we summarize herpetological information are grouped as follows [latitude/longitude (approximate surface extension), according to Battistini (1960), Cooke (1996) and Projet ZICOMA (1999)]:

(1) *Islands close to Nosy Be*: (a) Nosy Fanihy (48°11′S/13°10′E; 7.9 ha); (b) Nosy Komba (also named Nosy Ambato or Nosy Ambariobato) (48°19′–48°21′S/13°26′–13°28′E, 2200 ha); (c) Nosy Sakatia (48°10′S/13°18′E; 500 ha); (d) Nosy Tanikely (48°14′–48°15′S/13°28′–13°29′E; 30 ha); (e) Nosy Ambariobe (48°22′S/13°26′E; 0.5 ha).

(2) *Islands close to the mainland in the Sambirano region*: (f) Nosy Faly (48°27′–48°30′S/13°19′–13°23′E; 1400 ha); (g) Nosy Mamoko (48°10′S/13°43′E; 64 ha).

(3) *Island group located 40–60 km north-east of Nosy Be*: (h) Nosy Mitsio (48°36′S/12°54′E; 2700 ha).

The data presented here (for both Nosy Be and satellite islands) were taken from: (i) analysis of literature; (ii) analysis of preserved specimens housed in some

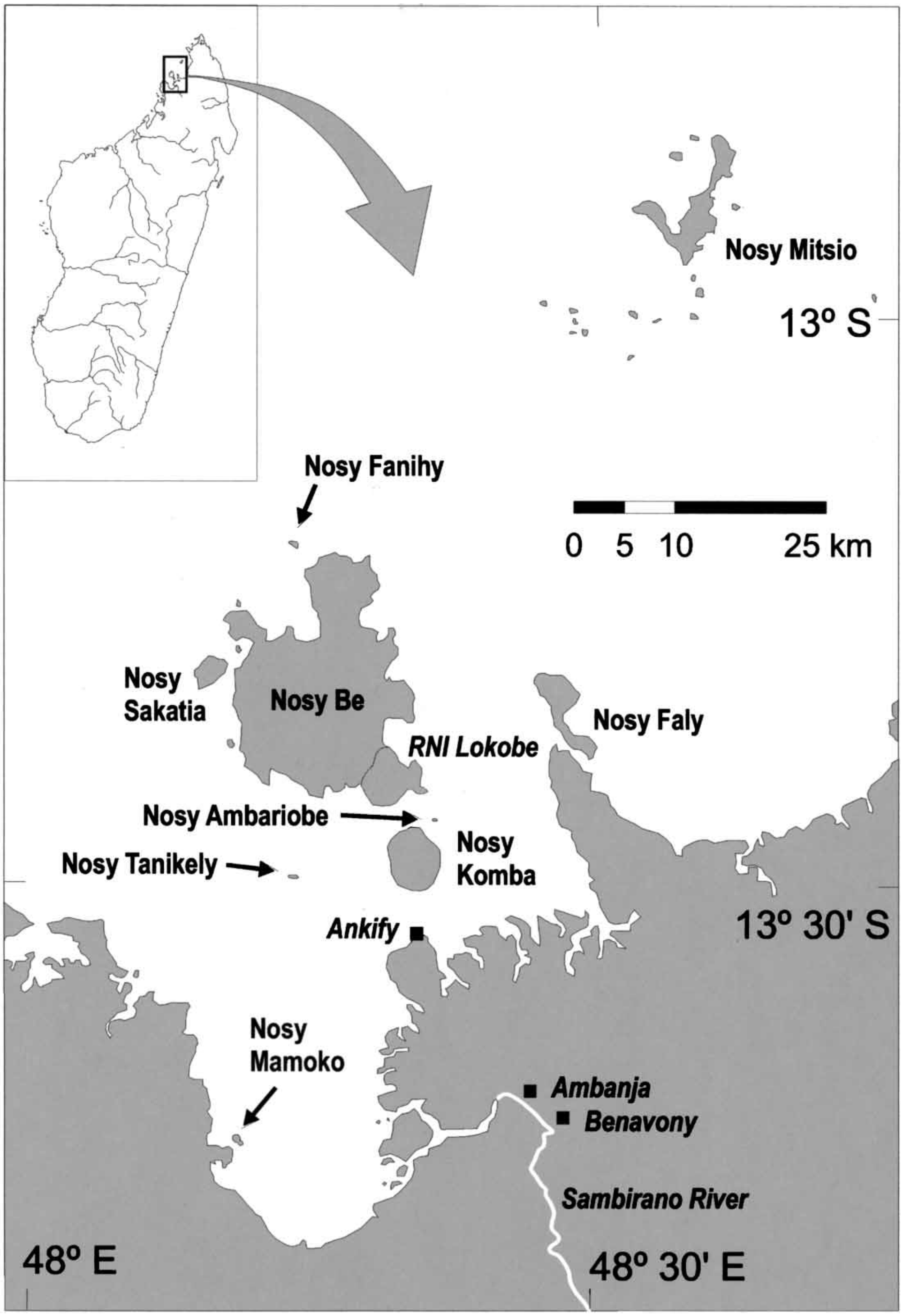

FIG. 1. Location of Nosy Be and of the Réserve Naturelle Integrale (RNI) de Lokobe, and nearby islands. Map source: GIS Service of WWF-Antananarivo, based upon FTM (Foiben-Taosarintanin'i Madagascar/Institut Géographique et Hydrographique National) maps.

natural history museum collections; (iii) field research. We excluded from our analysis the marine species (sea snakes and sea turtles). For comparison, we also discussed species known from Ambanja (13°40′S, 48°27′E) and Benavony Forest (13°41′S, 48°28′E) on the mainland adjacent to Nosy Be, and from Sahamalaza Peninsula (14°04′–14°37′S/47°52′–48°04′E; see Andreone *et al.*, 2001).

Study teams and periods

The field research was conducted by different teams at different times, as follows:

(1) 1991 (28 March–2 April)—F. Glaw and M. Vences surveyed Nosy Be. F. Glaw and J. Müller made additional surveys during 16 January–2 February 1992, 5–15 and 19–25 February 1992. A short trip to Nosy Komba was carried out between 2 and 4 February 1992.
(2) 1993—A team led by C. J. Raxworthy, which included I. Constable, R. A. Nussbaum, J.-B. Ramanamanjato, A. P. Raselimanana, A. Razafimanantsoa, and A. Razafimanantsoa, worked on a one-month survey at RNI de Lokobe. The main campsite was placed next to Ampasindava (48°19′E, 13°25′S, 0–430 m), 30 September–31 October 1993; a 'satellite' campsite next to the Andranomainty River (48°20′E, 13°25′S, 0–300 m) was utilized on 24–26 October 1993. Nineteen Earthwatch volunteers joined the team between 3–28 October (see *Acknowledgements*).
(3) 1994 (6–7 March)—F. Glaw, N. Rabibisoa and O. Ramilison surveyed the degraded area and streams along the street from Hellville (Andoany) to the island's airport (Fascéne).
(4) 1999 (4–18 February)—F. Andreone and J. E. Randrianirina made a survey at Antsaharavy (Madirotelo campsite, RNI de Lokobe; 13°24.73′S, 48°20.19′E). In addition, they visited the Ambariobe Islet on 14 February 1999.
(5) 2000 (7–11 March)—F. Glaw, M. Vences and K. Schmidt visited several non-protected areas, as well as Nosy Sakatia and Nosy Fanihy and the forested buffer zone around Lokobe. M. Vences surveyed Nosy Faly on a short visit on 26 February 2000.
(6) 2000 (11–19 March)—F. Andreone and J. E. Randrianirina conducted a study on the ecology of *Furcifer pardalis* around the town of Andoany (Hellville). On this occasion they made further observations on the herpetofauna inhabiting the altered areas along roads.
(7) 2001 (26–28 January)—F. Andreone, F. Mattioli, J. E. Randrianirina and M. Vences briefly visited Nosy Be, to check the presence of some species in altered areas.

Search methods

Three methods were used to search for the amphibians and reptiles: (1) opportunistic searching, conducted in most of the natural habitats; night searches were made with the aid of headlamps and flashlights; (2) location of frogs by searching for calling males; (3) pitfall trapping associated with drift fences (used in 1993 and 1999). The pitfalls consisted of plastic buckets (about 280 mm deep, 220–290 mm internal diameter), sunk in the ground at 10 m intervals along a plastic drift fence. Small holes were punched in the bottom to allow water to drain; each fence (0.5 m high and 100 m long) was stapled to wooden stakes; its bottom was buried in the ground using forest litter and positioned to run across or beside each pitfall trap. A pitfall was positioned at both ends of the drift fence. The pitfalls were checked each morning and evening. In 1993 four lines were used, and placed in the following forest types: ridge (along the crest of a ridge), slope/ridge and slope/valley (on a gradient, intermediate between ridge top and valley bottom), and valley (within 20 m of a stream in a valley bottom). In 1999 two lines were placed in slope/valley and slope forest.

Representative individuals of almost all the taxa were photographed to document their live coloration. As a further aid to taxonomic identification, advertisement calls of frogs were recorded when possible, and compared to an existing vocalization database. Voucher specimens were anaesthetized in ether or chlorobutanol, fixed in 10% buffered formalin or 90% ethanol, and transported in 65–75% ethanol.

Collected material was deposited at the Museo Regionale di Scienze Naturali, Torino (Italy, temporary numeration: MRSN-FAZC, MRSN-FN, MRSN-RJS; definitive numeration: MRSN), the Parc Botanique et Zoologique de Tsimbazaza, Antananarivo (Madagascar, PBZT-FAZC, PBZT-RJS), the Université d'Antananarivo, Departément de Biologie Animale (Madagascar, UADBA), University of Michigan, Museum of Zoology (USA, UMMZ), the Zoologisches Forschungsinstitut und Museum A. Koenig, Bonn (Germany, ZFMK), and the Zoologische Staatssammlung München (Germany, ZSM). Other acronyms used in this paper are CAS (California Academy of Sciences, San Francisco, USA), referring to some analysed specimens, and ZMH (Zoologisches Institut und Zoologisches Museum der Universität Hamburg, Germany). A list of the examined specimens is provided in *Appendix I*. Additional specimens deposited at UADBA in 1993 were not examined by us.

Some taxa were cited in the past for Nosy Be, but were not found during our surveys. Therefore, we checked for their presence in the relevant herpetological collections, which are mainly the Muséum national d'Histoire naturelle de Paris (MNHN) and the Zoölogisch Museum Amsterdam (ZMA).

Results

The results of our surveys, and the analysis of the literature and museum collections are presented in tables 1–3. The species accumulation curves for the two standardized surveys (1993 and 1999) are given in figure 2. We have drawn separately the amphibian and reptile curves in accordance with Andreone and Randrianirina (2000). In table 4 we provide a list of all the taxa described based on material from Nosy Be and nearby islands.

In total, 18 species of amphibians and 57 species of reptiles are currently known for the Island of Nosy Be (table 1). At RNI de Lokobe, we found 15 amphibians and 45 reptiles. Two further species, *Typhlops madagascariensis* and *T. reuteri*, were not found by us during our surveys at Lokobe, but are described from specimens coming just from this protected forest (V. Wallach, pers. comm.).

Several other species recorded on Nosy Be were not found during our surveys. Some of these species (*Mantidactylus horridus*, *Androngo elongatus*, *Ramphotyphlops braminus*, *Typhlops madagascariensis*, *T. reuteri*, *Micropisthodon ochraceus*, *Pararhadinaea melanogaster*, *Pelusios castanoides*) are represented by museum specimens and therefore considered as present on Nosy Be, and consequently included in table 2. Other taxa, due to absence of field observations and reliable museum vouchers, are currently excluded from the herpetofauna of Nosy Be and nearby islands. These are: *Hyperolius nossibeensis*, *Heterixalus betsileo*, *Aglyptodactylus madagascariensis*, *Mantella baroni*, *Mantidactylus betsileanus*, *M. femoralis*, *Brookesia superciliaris*, *Calumma brevicornis*, *C. gallus*, *C. parsoni*, *Zonosaurus brygooi*, *Z. laticaudatus*, *Ithycyphus perineti*, *Liophidium rhodogaster*, *Lycodryas arctifasciatus*, *L. gaimardi* and *Mimophis mahfalensis*. Detailed justifications for these decisions are given in *Appendix II*.

The overall number of species, comprising the herpetofauna of Nosy Be and nearby islands, is 20 amphibians and 61 reptiles. One introduced species (*Mabuya comorensis*) is present only at Nosy Tanikely, while the skink *Paracontias milloti* is so far known only for Nosy Mamoko.

The results of the pitfall trapping at RNI de Lokobe (table 2) indicate that during the extensive 1993 survey the four pitfall lines captured 46 amphibians (represented by *Rhombophryne testudo* and by two *Stumpffia* species) and 45 reptiles (13 species) over a total of 968 trap days. The overall mean daily pitfall capture rate was 4.75% for amphibians and 4.65% for reptiles. The lines that provided the highest number of captures were, respectively, the fourth (valley) and third (slope/valley) for amphibians (with 31 and eight specimens), and the second (slope/ridge) and third (slope/valley) for reptiles (with 15 and 14 specimens, respectively). During the 1999 survey, six specimens of amphibians were captured during 154 trap days (3.90% of trapping success) and three reptiles were caught over the same study period (1.95%).

Discussion

Sampling methods

The pitfall traps set during the 1993 inventory did not capture any amphibian species not found with other methods, with the exception of *Rhombophryne testudo* (table 2). However, this species was found by opportunistic searching as part of other surveys. In this study, pitfalls were not essential for obtaining information on the presence of anurans, as no species undetected by direct observation were captured with pitfalls. By contrast, the trapping system is extremely useful for detecting secretive terrestrial and/or burrowing reptiles: skinks and typhlopid snakes are difficult to find during the day by direct observation, and the use of drift fences and pitfall traps revealed species not otherwise observed. Pitfall trapping during the 1993 survey at Nosy Be captured a new *Amphiglossus* species and *Typhlops mucronatus*, both of which were not otherwise observed. Bioacoustic searching yielded two frog species (*Boophis jaegeri*, *Platypelis occultans*) which were missed with other methods.

The species accumulation curves for amphibians (figure 2) show that the increase in previously unrecorded species is rather similar throughout both the 1993 and 1999 surveys. The saturation point is reached for both amphibians and reptiles in 1993, suggesting that the one month survey was sufficient to give a good estimate of local species diversity. Most likely, only a few more species could have been detected with a longer survey. This might be achieved by surveying different habitats and looking in degraded and manmade environments. In fact, some species (e.g. *Heterixalus tricolor*, *Ptychadena mascareniensis*, *Hoplobatrachus tigerinus*, *Boophis tephraeomystax*, *Furcifer pardalis*) are uncommon in forest habitats, and are mainly found in some anthropogenic sites such as ricefields, swamps and fields.

The total number of reptile species found on Nosy Be is considerably higher than that of amphibians (about four times). This might be explained when it is

Table 1. List of amphibians and reptiles of Nosy Be Island based upon bibliography, museum collections and recent survey work.

		Literature/ Museum	Survey	RNI de Lokobe 1992	RNI de Lokobe 1993	RNI de Lokobe 1999	Unprotected areas
	HYPEROLIIDAE						
1	*Heterixalus tricolor*	+	+	–	–	–	+
	RANIDAE						
2	*Hoplobatrachus tigerinus*[a]	+	+	–	–	–	+
3	*Ptychadena mascareniensis*	+	+	–	+	–	+
	MANTELLIDAE[b]						
4	*Boophis brachychir*	+	+	–	+	–	+
5	*Boophis jaegeri*	+	+	+	–	+	+
6	*Boophis tephraeomystax*	+	+	–	+	–	+
7	*Mantella betsileo*	+	+	+	+	+	+
8	*Mantidactylus granulatus*	+	+	+	+	+	+
9	*Mantidactylus horridus*	+	–	–	–	–	–
10	*Mantidactylus pseudoasper*	+	+	+	+	+	–
11	*Mantidactylus ulcerosus*	+	+	+	+	+	+
12	*Mantidactylus wittei*	+	+	+	–	–	+
	MICROHYLIDAE						
13	*Cophyla phyllodactyla*	+	+	+	+	–	+
14	*Platypelis milloti*	+	+	+	+	–	–
15	*Platypelis occultans*	+	+	+	–	–	+
16	*Rhombophryne testudo*	+	+	+	+	+	+
17	*Stumpffia psologlossa*	+	+	+	+	+	+
18	*Stumpffia pygmaea*	+	+	+	+	+	+
	TOTAL NUMBER OF AMPHIBIANS	18	17	12	12	8	15
	CROCODYLIDAE						
1	*Crocodylus niloticus*	+	+	–	–	–	+
	PELOMEDUSIDAE						
2	*Pelusios castanoides*	+	–	–	–	–	+
	CHAMAELEONIDAE						
3	*Brookesia ebenaui*	+	+	+	+	–	+
4	*Brookesia minima*	+	+	+	+	–	–
5	*Brookesia stumpffi*	+	+	+	+	+	+
6	*Calumma boettgeri*	+	+	–	+	+	+
7	*Calumma nasuta*	+	+	–	+	+	–
8	*Furcifer pardalis*	+	+	+	+	+	+
	GEKKONIDAE						
9	*Ebenavia inunguis*	+	+	+	+	–	–
10	*Geckolepis maculata*	+	+	–	+	+	+
11	*Gehyra mutilata*	–	+	–	–	–	+
12	*Hemidactylus* cf. *frenatus*	+	+	–	–	+	–
13	*Hemidactylus* cf. *mabouia*	+	+	–	+	–	+
14	*Lygodactylus heterurus*	+	+	+	+	+	–
15	*Lygodactylus madagascariensis*	+	+	–	+	+	–
16	*Paroedura oviceps*	+	+	–	+	+	–
17	*Paroedura stumpffi*	+	+	–	+	+	+
18	*Phelsuma abbotti*	+	+	–	+	+	+
19	*Phelsuma dubia*	+	+	–	–	–	+

Table 1. (*Continued*).

		Literature/ Museum	Survey	RNI de Lokobe 1992	RNI de Lokobe 1993	RNI de Lokobe 1999	Unprotected areas
20	*Phelsuma laticauda*	+	+	–	+	–	+
21	*Phelsuma madagascariensis*	+	+	+	+	+	+
22	*Phelsuma* cf. *quadriocellata*	+	+	–	+	–	–
23	*Phelsuma seippi*	+	+	–	+	–	–
24	*Uroplatus ebenaui*	+	+	+	+	+	–
25	*Uroplatus henkeli*	+	+	+	+	+	–
	GERRHOSAURIDAE						
26	*Zonosaurus boettgeri*	+	+	–	+	–	–
27	*Zonosaurus madagascariensis*	+	+	+	+	+	+
28	*Zonosaurus rufipes*	+	+	+	+	+	–
29	*Zonosaurus subunicolor*	+	+	+	+	+	+
	SCINCIDAE						
30	*Amphiglossus stumpffi*	+	+	–	+	–	–
31	*Amphiglossus* n. sp.	–	+	–	+	–	–
32	*Androngo elongatus*	+	–	–	–	–	–
33	*Cryptoblepharus cognatus*	+	+	–	+	+	–
34	*Mabuya gravenhorsti*	+	+	–	+	+	+
35	*Mabuya lavarambo*	+	+	–	+	–	–
36	*Paracontias hildebrandti*	+	+	–	+	–	+
	BOIDAE						
37	*Sanzinia madagascariensis*[c]	+	+	–	+	–	+
38	*Acrantophi madagascariensis*	+	+	–	–	–	+
	TYPHLOPIDAE						
39	*Ramphotyphlops braminus*	+	–	–	–	–	–
40	*Typhlops* n. sp.	–	+	–	+	–	–
41	*Typhlops madagascariensis*	+	–	–	–	–	–
42	*Typhlops mucronatus*	+	+	–	+	–	–
43	*Typhlops reuteri*	+	–	–	–	–	–
	COLUBRIDAE						
44	*Alluaudina bellyi*	+	+	–	+	–	–
45	*Dromicodryas bernieri*	+	+	+	–	–	+
46	*Dromicodryas quadrilineatus*	+	+	+	+	+	+
47	*Ithycyphus miniatus*	+	+	–	+	–	–
48	*Langaha madagascariensis*	+	+	+	+	–	–
49	*Leioheterodon madagascariensis*	+	+	+	+	+	+
50	*Liophidium torquatum*	+	+	+	+	–	–
51	*Liopholidophis stumpffi*	+	+	+	+	–	+
52	*Madagascarophis citrinus*[d]	+	+	+	+	+	–
53	*Madagascarophis colubrinus*	+	+	+	+	–	+
54	*Micropisthodon ochraceus*	+	–	–	–	–	–
55	*Pararhadinaea melanogaster*	+	–	–	–	–	–
56	*Pseudoxyrhopus microps*	+	+	–	+	–	–
57	*Lycodryas granuliceps*[f]	+	+	–	+	+	–
	TOTAL NUMBER OF REPTILES	54	50	20	44	23	25
	TOTAL NUMBER OF AMPHIBIANS AND REPTILES	72	67	32	56	31	40

Table 1. (*Footnotes*).

Literature/Museum = occurrence after bibliography and museum specimens; Survey = occurrence after recent inventories; RNI de Lokobe (1992, 1993, 1999) = taxa found during three surveys carried out at Lokobe; Unprotected areas = occurrence in non-protected sites.

[a]*Hoplobatrachus tigerinus* is a species introduced to Madagascar from SE Asia.

[b]For the classification of Malagasy 'ranids' we here follow the recent proposal of Vences and Glaw (2001), including the genera *Aglyptodactylus*, *Boophis*, *Laliostoma*, *Mantidactylus* and *Mantella* within the family Mantellidae.

[c]The Malagasy tree-boa *Sanzinia madagascariensis* has been considered as belonging to the genus *Boa* (*B. manditra*) by Kluge (1991).

[d]We here maintain as separate taxa *Madagascarophis colubrinus insularis* and *M. citrinus*, although their status is doubtful.

[e]The Malagasy species of the genus *Lycodryas* have been attributed to the genus *Stenophis* by Domergue (1994) and Glaw and Vences (1994).

taken into account that on Nosy Be, the amphibians are represented by rather generalist species, which are widely distributed along the western sites of Madagascar (e.g. Sahamalaza, Andreone *et al.*, 2001). Only two species (*Mantidactylus pseudoasper* and *Platypelis milloti*) have been so far found at Lokobe only. All the other Lokobe amphibian species were also found at other places on Nosy Be. On the other hand, the much more diverse reptile fauna may be explained by the fact that it is composed of a mixture of species rather closely tied to the dense Lokobe forest (e.g. *Calumma nasuta*, *Uroplatus ebenaui*, *Zonosaurus boettgeri*, *Ithycyphus miniatus*, *Lycodryas granuliceps*), and by species which become much more abundant in, or even exclusive to altered areas (e.g. *Phelsuma laticauda*, *Hemidactylus* cf. *mabouia*, *Mabuya gravenhorsti* and *Leioheterodon madagascariensis*). In this sense, the reptile fauna seems to have experienced a diversity increase due to an ecotonal situation, but this is not so evident in amphibians, which are represented by rather generalist species.

During the last study week of the 1993 survey, there was no increase in the number of reptile species. Therefore, only a few supplementary species, especially snakes, which are usually rarely encountered and in general are scarce in the forests (Andreone and Luiselli, 2000) could be found with a longer survey or, as already stressed, redirecting the active search in other habitats.

The much shorter survey carried out in 1999 does not differ in terms of discovered species per day, either for amphibians, or for reptiles (figure 2). It is evident that a short duration survey, especially when carried out in habitats subject to seasonal fluctuations, allows the discovery of only a limited portion of the herpetofauna present.

The herpetofauna of the satellite islands

Data on the seven analysed islands and Nosy Mitsio archipelago are scattered in the literature and among museum specimens. Only for Nosy Tanikely and Nosy Mitsio specific and organic contributions are available (Köhler *et al.*, 1997; Krüger, 1999). A total of 11 species of amphibians and 26 reptiles for the islands considered together was reported in literature, present in museum collections or found during our visits (table 3). One amphibian species reported for Nosy Mamoko, *Heterixalus betsileo* (Blommers-Schlösser and Blanc, 1991) is not taken into consideration because reliable data are lacking (see *Appendix I*). It is noteworthy that only the reptile species were able to colonize more than two islands, while the amphibian

Table 2. Characteristics and captures (Amphibia, Reptilia) for all pitfall lines at RNI de Lokobe (Nosy Be).

Year	1993				1999	
Locality	Ampasindava				Antsaharavy	
Pitfall line	1	2	3	4	5	6
Altitude	60–90	45–70	110–150	195–210	20–35	10–30
Month	October	October	October	October	February	February
Duration of trapping	5–27	6–27	6–27	7–27	8–15	8–15
Number of pitfalls	11	11	11	11	11	11
Trapnights Trapdays	22	21	21	20	7	7
Forest type	ridge	slope/ ridge	slope/ valley	valley	slope/ valley	slope
Total bucket trap days	253	242	242	231	77	77
AMPHIBIANS						
Rhombophryne testudo	–	–	–	–	2	2
Stumpffia pygmaea	1	1	–	5	–	–
Stumpffia psologlossa	1	1	–	9	2	–
Stumpffia sp.[f]	2	1	8	17	–	–
TOTAL AMPHIBIANS	4	3	8	31	4	2
AMPHIBIAN CAPTURE RATE	1.58%	1.24%	3.31%	13.42%	5.19%	2.59%
REPTILES						
Lygodactylus madagascariensis	–	–	2	–	–	–
Paroedura oviceps	–	–	–	–	–	1
Brookesia ebenaui	1	–	–	–	–	–
Brookesia stumpffi	–	1	–	–	–	–
Amphiglossus stumpffi	–	1	–	–	–	–
Amphiglossus n. sp.	–	1	–	–	–	–
Zonosaurus boettgeri	1	–	–	–	–	–
Zonosaurus madagascariensis	1	1	3	1	–	–
Zonosaurus rufipes	3	10	9	6	1	1
Typhlops mucronatus	1	–	–	–	–	–
Alluaudina bellyi	–	1	–	–	–	–
Liophidium torquatum	–	–	–	1	–	–
Liopholidophis stumpffi	–	–	–	1	–	–
TOTAL REPTILES	7	15	14	9	1	2
REPTILE CAPTURE RATE	2.77%	6.20%	5.79%	3.90%	1.30%	2.59%
OVERALL TOTAL (AMPHIBIANS+REPTILES)	11	18	22	40	5	4
TOTAL CAPTURE RATE	4.35%	7.44%	9.10%	17.30%	6.49%	5.18%
OVERALL CAPTURE RATE	38.19%				11.67%	

[f]Undetermined *Stumpffia* specimens.

species were usually found on a single island, except for *Mantella betsileo* and *Boophis tephraeomystax*, which were found on two small islands (Nosy Komba and Nosy Faly). The reptiles found on more than one island are: *Brookesia stumpffi* (two islands), *Geckolepis maculata* and *Phelsuma madagascariensis* (three islands), *Furcifer pardalis*, *Hemidactylus* cf. *mabouia*, *Phelsuma abboti*, *Mabuya gravenhorsti* and *Zonosaurus madagascariensis* (four islands). One species, *Cryptoblepharus cognatus*, appears to be the best at island colonization, being found on five islands. This is indeed in accord with observations on the species' ecology, which indicates that this skink (as well as other species belonging to this genus) is extremely prone to

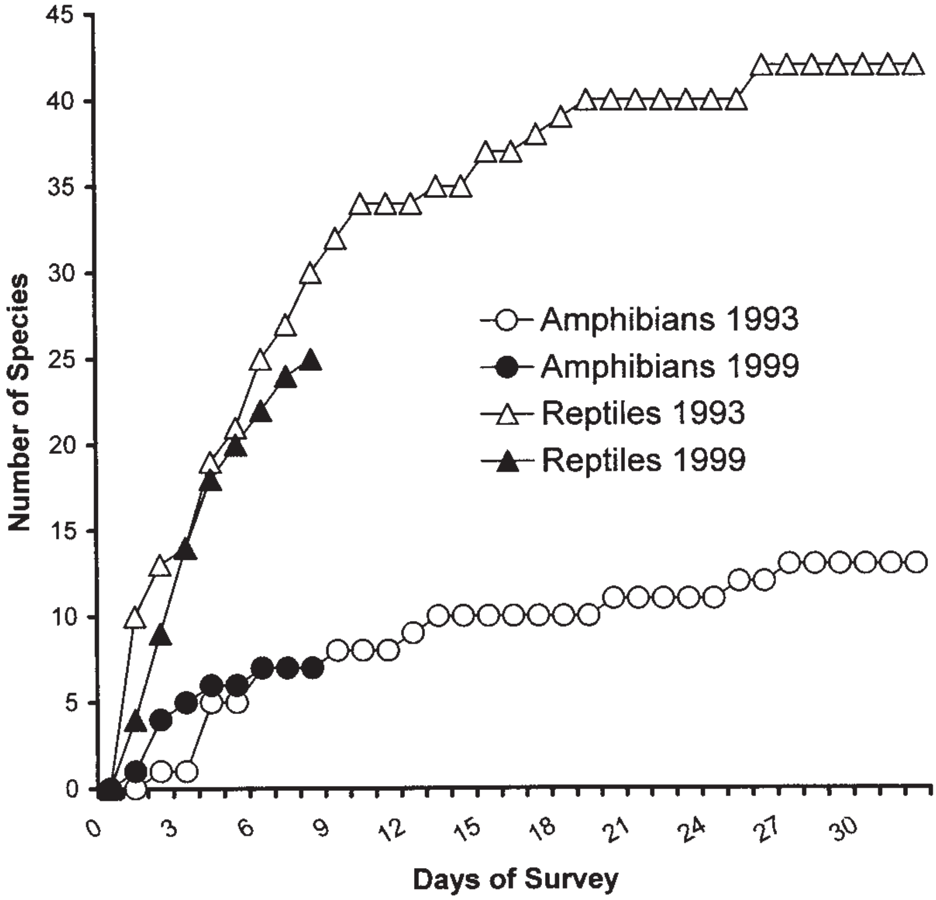

FIG. 2. Species accumulation curves for all techniques combined amphibian and reptile species at RNI de Lokobe (Nosy Be) during 1993 and 1999 surveys.

colonizing tropical islands and coasts (Fricke, 1970; Glaw and Vences 1994; Andreone and Greer, in press).

In general, all of these reptiles are species adaptable to harsh and edge habitats, and have characteristics that make them especially able to survive rafting (e.g. upon coconuts, dead roots, debris) from one island to another. Some of these species also are likely to be dispersed by human activities. In contrast, it is well known that amphibians have reduced capacity to disperse to and survive on small islands (Duellman and Trueb, 1986; Stebbins and Cohen, 1995). Amphibians often need free standing water and relatively high humidity to survive and reproduce, and these conditions are often not met on small, low islands. It is also well known that amphibians, with their permeable skin, are far less tolerant of salt water than are reptiles. These might be among the reasons for the considerably lower number of amphibians found on the small islands surveyed.

Among the reptiles, two species, the turtle *Kinixys belliana* and the skink *Mabuya comorensis* [considered as a *M. maculilabris* subspecies by Ramanamanjato *et al.* (1999)], respectively from Nosy Faly and Nosy Tanikely, are considered as being introduced (Glaw and Vences, 1994; Köhler *et al.*, 1997, Pedrono *et al.*, 2000). The

Table 3. Amphibians and reptiles occurring on the considered islands next to Nosy Be.

			Satellite islands								Number of colonized satellite islands
		Nosy Be	Nosy Ambariobe	Nosy Faly	Nosy Fanihy	Nosy Komba	Nosy Mamoko	Nosy Mitsio	Nosy Sakatia	Nosy Tanikely	
	HYPEROLIIDAE										
1	*Heterixalus tricolor*	+	–	–	–	+	–	–	–	–	1
2	*Heterixalus* '*variabilis*'[g]	–	–	+	–	–	–	–	–	–	1
	MANTELLIDAE										
3	*Aglyptodactylus madagascariensis*	–	–	–	–	–	+	–	–	–	1
4	*Boophis tephraeomystax*	+	–	+	–	+	–	–	–	–	2
5	*Mantella betsileo*	+	–	+	–	+	–	–	–	–	2
6	*Mantidactylus pseudoasper*	+	–	–	–	+	–	–	–	–	1
7	*Mantidactylus wittei*	+	–	Call		–			–	–	1
	MICROHYLIDAE										
8	*Cophyla phyllodactyla*	+	–	–	–	+	–	–	–	–	1
9	*Rhombophryne testudo*	+	–	–	–	+	–	–	–	–	1
10	*Stumpffia psologlossa*	+	–	–	–	–	–	–	+	–	1
11	*Stumpffia pygmaea*	+	–	–	–	+	–	–	–	–	1
	TOTAL NUMBER OF AMPHIBIANS		0	4	0	7	1	0	1	0	
	CROCODYLIDAE										
1	*Crocodylus niloticus*	+	–	+	–	–	–	–	–	–	1
	TESTUDINIDAE										
2	*Kinixys belliana*[h]	–	–	+	–	–	–	–	–	–	1
	CHAMAELEONIDAE										
3	*Brookesia stumpffi*	+	–	–	–	+	–	–	+	–	2
4	*Calumma nasuta*	+	–	–	–	+	–	–	–	–	1
5	*Furcifer oustaleti*	+	–	+	–	–	–	–	–	–	1
6	*Furcifer pardalis*	+	–	+	–	–	–	+	+	+	4
	GEKKONIDAE										
7	*Geckolepis maculata*	+	–	–	+	–	–	+	+	–	3
8	*Hemidactylus* cf. *frenatus*	+	–	–	–	–	–	+	–	–	1
9	*Hemidactylus* cf. *mabouia*	+	–	–	+	–	–	+	+	+	4

Table 3. (*Continued*).

		Nosy Be	Satellite islands								Number of colonized satellite islands
			Nosy Ambariobe	Nosy Faly	Nosy Fanihy	Nosy Komba	Nosy Mamoko	Nosy Mitsio	Nosy Sakatia	Nosy Tanikely	
10	*Paroedura oviceps*	+	–	–	–	–	–	–	+	–	1
11	*Paroedura stumpffi*	+	–	–	–	–	–	+		–	1
12	*Phelsuma abbotti*	+	–	–	–	–	+	+	+	+	4
13	*Phelsuma laticauda*	+	–	–	–	–	–	+	–	–	1
14	*Phelsuma madagascariensis*	+	–	–	–	+	–	–	+	+	3
	GERRHOSAURIDAE										
15	*Zonosaurus madagascariensis*	+	+	–	–	+	–	–	+	+	4
16	*Zonosaurus subunicolor*	+	–	–	–	+	–	–	–	–	1
	SCINCIDAE										
17	*Cryptoblepharus cognatus*	+	+	–	+	–	–	+	+	+	5
18	*Mabuya comorensis*[i]		–	–	–	–	–	–	–	+	1
19	*Mabuya elegans*	–	–	+	–	–	–	–	–	–	1
20	*Mabuya gravenhorsti*	+	–	+	+	–	–	+	+	–	4
21	*Paracontias hildebrandti*	+	–	–	–	–	–	–	–	+	1
22	*Paracontias milloti*	–	–	–	–	–	+	+	–	–	1
	COLUBRIDAE										
23	*Leioheterodon madagascariensis*	+	–	–	–	–	–	–	+[j]	–	1
24	*Liophidium torquatum*	+	–	–	–	–	–	–	–	+	1
25	*Madagascarophis citrinus*	+	–	–	–	–	–	–	–	+	1
26	*Madagascarophis colubrinus*	+	–	–	–	+	–	–	–	–	1
	TOTAL NUMBER OF REPTILES		2	6	4	6	2	9	11	10	
	TOTAL NUMBER OF AMPHIBIANS AND REPTILES		2	10	4	13	3	9	12	10	

[g]*Heterixalus* '*variabilis*' is of uncertain taxonomic validity.
[h]Species introduced to Madagascar.
[i]Species introduced to Madagascar.
[j]Mounted skeleton housed at University of Antananarivo.

period of their introduction is not known, although *Mabuya comorensis* was collected on Nosy Tanikely much earlier than reported by Köhler *et al.* (1997), respectively on 23 April 1984 by L. G. Hoevers, as witnessed by the specimens CAS 156795–156801. *Kinixys belliana* has an introduction history much older, and this explains the reason for applying to it a distinct suspecific rank (*K. b. domerguei*) (Bour, 1985).

Among the islands assessed, Nosy Komba, with 13 species, is the richest in terms of herpetofaunal species, followed respectively by Nosy Sakatia (12 species), Nosy Tanikely and Nosy Faly (both with ten species) and Nosy Mitsio (nine species). The other islands are characterized by considerably fewer species. Nosy Komba, Nosy Sakatia, and Nosy Faly are quite large, and this might partly explain their species richness. Furthermore, Nosy Komba and Nosy Sakatia are very close to Nosy Be, with which they share their geological history (Battistini, 1960). Nosy Faly, on the other hand, has probably been connected more recently with mainland Madagascar, from which it is separated by a narrow sea channel. For this reason, some of the species present on Nosy Faly are typical of northern Madagascar, but were not found on Nosy Be (e.g. *Heterixalus variabilis*, *Furcifer oustaleti*, *Mabuya elegans*). Finally, the comparatively high reptile species diversity of Nosy Tanikely, an island of quite limited surface area (30 ha), is remarkable. This might be explained by the easy access from Nosy Be, either in historical or recent times, which possibly facilitated the observations and captures, or the transport of animals and plants from Nosy Be and other localities, as is the case for *Mabuya comorensis*.

Biogeography and endemicity patterns

An important biogeographic question is whether Nosy Be and its satellite islands harbour endemic forms not present on the Malagasy mainland. For islands separated from the mainland by a sufficiently long duration, endemism should not be as rare.

Of the total 19 amphibian and 41 reptile taxa described from Nosy Be and nearby islands (table 4), 14 amphibians and 29 reptiles are currently recognized as valid (*Zonosaurus brygooi* being considered as not present on Nosy Be, see *Appendix II*). Some taxa, retained as Nosy Be endemics until recently, were found in other parts of Madagascar. This is the case for *Boophis jaegeri*, a frog described by Glaw and Vences (1992b), whose presence on the mainland was recently confirmed by a survey at Sahamalaza Peninsula (Andreone *et al.*, 2001). A similar case concerns *Zonosaurus subunicolor* and *Z. rufipes*, recently found either at other islands (such as Nosy Komba for *Z. subunicolor*) or mainland territories, such as Benavony and Marojejy (Glaw and Vences, 1994; Raselimanana *et al.*, 2000).

The taxa apparently exclusive (and thus possibly endemic) to Nosy Be are two amphibians (*Stumpffia pygmaea* and *Heterixalus tricolor*) and four reptiles (*Lygodactylus h. heterurus*, *Mabuya lavarambo*, *Lycodryas granuliceps*, *Typhlops reuteri*). A fifth reptile taxon, *Paracontias milloti*, is known exclusively from Nosy Mamoko, a small island next to the mainland. Another two species found during our surveys and belonging to the genera *Amphiglossus* and *Typhlops* were not assigned to any known taxon, and are currently in the phase of description (by R. A. Nussbaum, C. J. Raxworthy and collaborators): they are therefore regarded as possible Nosy Be endemics.

It is likely that some of these 'Nosy Be taxa' were overlooked during other field surveys and are present on the mainland. Identification of the small *Stumpffia* frogs and *Lygodactylus* geckos is often difficult in the field. As an example, a form close to *Lygodactylus heterurus* has been found recently in NE Madagascar and described

Table 4. Amphibian and reptile taxa described from specimens from Nosy Be and/or nearby islands.

	Original name	Author(s)	Current name	Distribution and notes
	AMPHIBIA			
	HYPEROLIIDAE			
1	*Megalixalus tricolor*	Boettger, 1881b	*Heterixalus tricolor**	NW (NB). Its presence on the mainland is dubious (likely referable to other taxa)
2	*Hyperolius nossibeensis*	Ahl, 1930	*Hyperolius viridiflavus* complex	non Malagasy taxon (mainland Africa)
3	*Megalixalus variabilis*	Ahl, 1930	*Heterixalus* '*variabilis*'	NW (M, Nosy Faly)
	MANTELLIDAE			
4	*Rhacophorus brachychir*	Boettger, 1882	*Boophis brachychir*	NW (NB, M), N, NE, E, C
5	*Boophis jaegeri*	Glaw and Vences, 1992b	*Boophis jaegeri*	NW (NB, M)
6	*Polypedates dispar*	Boettger, 1879	*Boophis tephraeomystax*	N, NW, W, NE, E, C
7	*Polypedates dispar* var. *leucopleura*	Boettger, 1881a	*Boophis tephraeomystax*	N, NW, W, NE, E, C
8	*Polypedates tephraemystax*	Duméril, 1853	*Boophis tephraeomystax*	N, NW, W, NE, E, C
9	*Dendrobates ebenaui*	Boettger, 1880a	*Mantella betsileo*	N, NW (NB, M), W, NE
10	*Mantella attemsi*	Werner, 1901	*Mantella betsileo*	N, NW (NB, M), W, NE
11	*Limnodytes granulatus*	Boettger, 1881c	*Mantidactylus granulatus*	N, NW (NB, M), NE
12	*Hemimantis horrida*	Boettger, 1880a	*Mantidactylus horridus*	NW (NB, M)
13	*Limnodytes ulcerosus*	Boettger, 1880a	*Mantidactylus ulcerosus*	N, NW (NB, M), W, NE?, E?, C?
	MICROHYLIDAE			
14	*Cophyla phyllodactyla*	Boettger, 1880a	*Cophyla phyllodactyla*	N, NW (NB, M), NE?
15	*Platypelis milloti*	Guibé, 1950	*Platypelis milloti*	NW (NB, M)
16	*Platypelis occultans*	Glaw and Vences, 1992a	*Platypelis occultans*	NW (NB), NE, E
17	*Rhombophryne testudo*	Boettger, 1880b	*Rhombophryne testudo*	NW (NB), NE
18	*Stumpffia psologlossa*	Boettger, 1881c	*Stumpffia psologlossa*	NW (NB, M)
19	*Stumpffia pygmaea*	Vences and Glaw, 1991	*Stumpffia pygmaea**	NW (NB, Nosy Komba)
	REPTILIA			
	CROCODYLIDAE			
1	*Crocodilus vulgaris* var. *madagascariensis*	Boettger, 1877	*Crocodylus niloticus*	All Madagascar (extinct in many regions)
	CHAMAELEONIDAE			
2	*Brookesia legendrei*	Ramanantsoa, 1979	*Brookesia ebenaui*	NW (NB, M)
3	*Brookesia minima*	Boettger, 1893	*Brookesia minima*	NW (NB, M)
4	*Brookesia stumpffi*	Boettger, 1894	*Brookesia stumpffi*	NW (NB, M)
5	*Chamaeleo ebenaui*	Boettger, 1880a	*Brookesia ebenaui*	NW (NB, M)
6	*Chamaeleon boettgeri*	Boulenger, 1888	*Calumma boettgeri*	N, NW (NB, M), NE
7	*Chamaeleon guentheri*	Boulenger, 1888	*Furcifer pardalis*	N, NW (NM, M), NE
	GEKKONIDAE			
8	*Ebenavia inunguis*	Boettger, 1878	*Ebenavia inunguis*	N, NW (NB), NE, E
9	*Lygodactylus heterurus*	Boettger, 1913	*Lygodactylus heterurus heturурus**	NW (NB)—A second subspecies was recently described for the Sambava region (NE)
10	*Scalabotes madagascariensis*	Boettger, 1881c	*Lygodactylus madagascariensis*	N, NW (NB, Nosy Mamoko)
11	*Pachydactylus dubius*	Boettger, 1881a	*Phelsuma dubia*	N, W, NW (NB, M)
12	*Pachydactylus laticauda*	Boettger, 1880a	*Phelsuma laticauda*	NW (NB, M), NE
13	*Phelsuma madagascariensis notissima*	Mertens, 1970	*Phelsuma madagascariensis grandis*	N, NW (NB, M), NE
14	*Phyllodactylus oviceps*	Boettger, 1881c	*Paroedura oviceps*	N, NW (NB, M)
15	*Phyllodactylus stumpffi*	Boettger, 1879	*Paroedura stumpffi*	N, NW (NB, M), NE
16	*Uroplatus boettgeri*	Fischer, 1883	*Uroplatus ebenaui*	N, NW (NB, M), NE?
17	*Uroplatus ebenaui*	Boettger, 1878	*Uroplatus ebenaui*	N, NW (NB, M), NE?
18	*Uroplatus henkeli*	Böhme and Ibisch, 1990	*Uroplatus henkeli*	NW (NB, M), W?
	GERRHOSAURIDAE			
19	*Gerrhosaurus rufipes*	Boettger, 1881c	*Zonosaurus rufipes*	N, NW (NB, M), NE
20	*Gerrhosaurus rufipes* var. *subunicolor*	Boettger, 1881c	*Zonosaurus subunicolor*	NW (NB, Nosy Komba), NE
21	*Zonosaurus boettgeri*	Steindachner, 1891	*Zonosaurus boettgeri*	NW (NB), NE

Table 4. (*Continued*).

	Original name	Author(s)	Current name	Distribution and notes
22	*Zonosaurus brygooi*	Lang and Böhme, 1990	*Zonosaurus brygooi*	NE, E—probably not present at Nosy Be
	SCINCIDAE			
23	*Gongylus stumpffi*	Boettger, 1882	*Amphiglossus stumpffi*	N, NW (NB, M)
24	*Scelotes astrolabi boettgeri*	Angel, 1942	*Amphiglossus stumpffi*	N, NW (NB, M)
25	*Ablepharus boutoniii* var. *cognatus*	Boettger, 1881c	*Cryptoblepharus cognatus*	NW (NB, M)
26	*Mabuya lavarambo*	Nussbaum and Raxworthy, 1998	*Mabuya lavarambo**	NW (NB)
27	*Paracontias milloti*	Angel, 1949	*Paracontias milloti**	NW (Nosy Mamoko)
	COLUBRIDAE			
28	*Langaha intermedia*	Boulenger, 1888	*Langaha madagascariensis*	W, NW (NB), NE, E
29	*Dromicus stumpffi*	Boettger, 1881c	*Liopholidophis stumpffi*	N, NW (NB, M)
30	*Liophidium gracile*	Mocquard, 1909	*Liopholidophis stumpffi*	N, NW (NB, M)
31	*Eteiroipsas colubrina* var. *citrina*	Boettger, 1877	*Madagascarophis citrinus*	NW (NB, Nosy Tanikely, M)
32	*Herpetodryas bernieri* var. *trilineata*	Boettger, 1877	*Domicodryas bernieri*	W, NW (NB, M), E, S, SW, SE
33	*Madagascarophis colubrinus insularis*	Domergue, 1987	*Madagascarophis colubrinus insularis*	NW (NB, Nosy Komba, M?)
34	*Micropisthodon ochraceus*	Mocquard, 1894	*Micropisthodon ochraceus*	NW (NB), NE, E
35	*Dipsas* (*Heterurus*) *gaimardi* var. *granuliceps*	Boettger, 1877	*Lycodryas granuliceps**	NW (NB)
36	*Pararhadinaea melanogaster*	Boettger, 1898	*Pararhadinaea melanogaster*	NW (NB), NE
	TYPHLOPIDAE			
37	*Typhlops* (*Typhlops*) *euproctus*	Boettger, 1882	*Ramphotyplops braminus*	W, NW (NB, M), E—cosmopolitan
38	*Typhlops madagascariensis*	Boettger, 1877	*Typhlops madagascariensis**	NW (NB)
39	*Typhlops* (*Ophthalmidion*) *mucronatus*	Boettger, 1880a	*Typhlops mucronatus*	N, NW (NB)
40	*Typhlops* (*Typhlops*) *lenzi*	Boettger, 1882	*Typhlops reuteri**	NW (NB)
41	*Typhlops* (*Typhlops*) *reuteri*	Boettger, 1881a	*Typhlops reuteri**	NW (NB)

The provenance of NW specimens is reported in round brackets: NB = Nosy Be; M = mainland Sambirano and nearby territories; C = central plateau. Question marks (?) indicate doutbts about the referred provenance (based upon the synthesis provided by Glaw and Vences (1994) and personal observations). All the taxa here reported were described from specimens from Nosy Be, excepting for *Heterixalus* '*variabilis*' (described from Nosy Faly and not found at Nosy Be), and *Paracontias milloti* (described from Nosy Mamoko, and not found at Nosy Be). Taxa marked with an asterisk are here considered as endemics of Nosy Be and nearby islands.

by Rösler (1998) as *L. h. trilineigularis*. Therefore, we believe that *L. heterurus* might be found at other Sambirano sites. This also applies to the species of *Typhlops*, which are only sporadically collected even by systematic pitfall trapping. Further conclusions regarding typhlopids are to be postponed until a revision is available (V. Wallach, in preparation). The real differences between *Heterixalus tricolor* and *H.* '*variabilis*' are still a matter of controversy, and we cannot exclude that the former is only an insular form of the latter. Another species stated to be exclusive to Nosy Be is the arboreal colubrid *Lycodryas granuliceps*. Distinction between *L. granuliceps* and *L. pseudogranuliceps* (present in the Sabirano region) is often difficult, and the specific status of the latter is not corroborated by robust data so far.

In general, it appears that the Malagasy island herpetofauna of this region represents a subset of the richer herpetofauna present on the mainland, with only a few (possible) endemics which may have been differentiated from closely related mainland taxa in relatively recent times. For this purpose we analysed the known amphibian fauna of two further islands, which are Nosy Mangabe and Sainte Marie (or Nosy Boraha). In this analysis we considered amphibians only, due to the fact that the status of knowledge is far better than for reptiles. Both these islands are located off the north-eastern and eastern coasts: Nosy Mangabe near the town of Maroantsetra in Antongil's Bay (15°30′S, 49°46′E; 520 ha), and Sainte Marie, at about 7 km from the nearest mainland (16°42′–17°07′S, 49°48′–50°02′E; 20,000 ha).

We compared the batrachofauna of these islands with that of the respective mainland forests, which are Masoala Peninsula [based upon data in Glaw and Vences (1994), and 1998/1999 unpublished observations at Ambatoledama and Ilampy areas by F. Andreone and J. E. Randrianirina], and Tampolo Forest (Raselimanana *et al.*, 1998), plus data from central-eastern rainforests (Glaw and Vences, 1994). The Nosy Be batrachofauna was then compared to that from Sambirano (1992–2001 surveys at Benavony and Ambanja by F. Andreone, F. Glaw, J. E. Randrianirina and M. Vences; and literature/museum data) and Sahamalaza Peninsula (Andreone *et al.*, 2001).

All amphibian species found on Nosy Mangabe and Sainte Marie were also known from the mainland. The island batrachofauna represented the following indicative percentage of the respective mainland areas: 40% at Nosy Mangabe, 53% at Sainte Marie, and 69% at Nosy Be. Although the situation in terms of ecological conditions and anthropogenic processes are different for the three islands, these values do not differ significantly ($\chi^2 = 1.92$; $P > 0.05$) and indicate a common history of colonizing processes for the amphibians This should also be taken into account together with an analysis of the geological history of Nosy Be and the other satellite islands of Madagascar. According to Battistini (1960, pers. comm.) all the islands of the NW region of Madagascar are placed on the continental plateau. They are separated from the mainland by sea depths which do not exceed 30 metres. Nosy Be, like the other islands, has been isolated from the mainland for about 8000 years. During the last glacial period of Würm 3, the world sea level was about 110 m lower than at present (Colonna *et al.*, 1996). About 15,000 years ago all the islands were merged. Nosy Be has been attached to the continent several times during the Quaternary according to data for Mayotte Reef (Colonna *et al.*, 1996). This recent connection explains the similarity in terms of faunal compositions between mainland Madagascar and offshore islands.

Conservation conclusions

Regarding the herpetofauna of Nosy Be, we should take into account ecological and human-induced factors. Most notable is the protected status of RNI de Lokobe: although the surface area of the reserve is relatively small (740 ha), the herpetological diversity is quite large. With 60 species currently recorded within its boundaries, Lokobe hosts 80% of the total Nosy Be herpetofauna. As an obvious consequence, this forest should be carefully managed in the future for two reasons. First, because of its great species diversity, and second because it is one of the last relatively undisturbed, low altitude Sambirano forests.

According to local people (R. Tombosoa, pers. comm.), there is still occasional illegal collecting activity at Lokobe of some reptile species (such as *Uroplatus ebenaui* and *U. henkeli*) for the pet trade, although no data exist on the quantity of these captures. Considering that many of the tourists visiting Madagascar are especially attracted by its unique flora and fauna, there is great interest in gaining access to the Lokobe primary forest. Changing its protection status would allow controlled visits of tourists at least to parts of this reserve. Such a measure could help to create further awareness of the importance of this area and contribute to the sustainable management of Nosy Be's natural resources.

Apart from RNI de Lokobe, it is evident that the environmental situation is rather heterogeneous on Nosy Be. The diversity, in terms of amphibian and reptile species, on other parts of Nosy Be is significant, as witnessed by our surveys at some unprotected and degraded areas. The number of species in and along ricefields is very low, while the herpetofauna is almost non-existent in the sugar cane fields. However, it is remarkable that ylang-ylang and coffee plantations still host a considerable number of species. In fact, herpetofaunal diversity is in general rather high in cultivated areas that are maintained using certain agricultural methods. (e.g. at Nosy Be, Ambanja and other localities). Among the species found in these anthropogenic habitats (at Nosy Be) are *Boophis brachychir*, *B. tephraeomystax*, *Heterixalus* spp., *Ptychadena mascareniensis*, *Rhombophryne testudo*, *Stumpffia* spp., *Cophyla phyllodactyla*, *Calumma boettgeri*, *Furcifer pardalis*, *Brookesia stumpffi*, *Hemidactylus* cf. *mabouia Phelsuma laticauda*, *P. abbotti*, *P. madagascariensis*, *Geckolepis maculata*, *Zonosaurus madagascariensis*, *Mabuya gravenhorsti*, *Dromicodryas* spp., *Madagascarophis colubrinus*. This rather long list stresses the importance of agriculture in safeguarding biodiversity, as already pointed out for the traditional coffee systems in other parts of the world (e.g. Thiollay, 1995; Moguel and Toledo, 1999).

With respect to conservation, it is worth noting the importance of the 'pseudo-forest' band which runs along the major roads of Nosy Be. This band is 5–10 m wide and is composed of ornamental and fruit trees of a certain size and height, which evidently constitute a sort of 'surrogate' for the original forest coverage. As we observed on several occasions, a large portion of the Nosy Be populations of *Furcifer pardalis* occur mainly in this habitat (F. Andreone and J. E. Randrianirina, unpublished). It is noteworthy that one of the main activities of potentially high impact on the herpetofauna of Nosy Be concerns the capture of huge numbers of *F. pardalis* for the pet trade (Jenkins and Rakotomanampison, 1994; Jenkins, 2000). Indeed, individuals of *F. pardalis* from Nosy Be have perhaps the most attractive coloration among the Malagasy populations of this species. These are the well known 'blue panther chameleons', known only from Nosy Be and the nearby mainland. This species, which is currently included in CITES Appendix II, is one of the four Malagasy chameleon species (together with *Furcifer oustaleti*, *F. lateralis* and *F. verrucosus*) for which commercial capture and exportation are allowed (Brady and Griffiths, 1999). The collection for the pet trade of *F. pardalis* is currently subject to control by the Malagasy authorities, and the yearly numbers exported dropped from 20,000 in 1999 to 2000 in the year 2000, half of which originated from Nosy Be (Brady and Griffiths 1999; O. Behra, pers. comm.). This chameleon constitutes an important resource, and it should therefore be carefully managed in terms of harvesting and sustainable use (Jenkins, 2000).

According to our observations it is worth noting that the most abundant populations of *Furcifer pardalis* occur in the forested bands along roads, which, like the traditional agricultural areas mentioned above, act as biotic refuges for several animal species (not only amphibians and reptiles, but also birds and small lemurs). In these roadside arboretums, the environmental conditions are probably more favourable in terms of food availability and microclimate than in typical agricultural habitats. Furthermore, a large part of this anthropogenic habitat forms a sort of 'network' of a considerable and remarkable total surface, yet to be estimated. It is therefore our opinion that the conservation of Nosy Be's peculiar inland fauna should therefore include, together with upgrading Lokobe to a national park, a more careful management of these 'pseudo-forest' bands, as well as the traditional ylang-ylang and coffee cultivations. Future management plans for Nosy Be should consider the importance of these landforms for biodiversity conservation.

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Appendix I

Specimens examined

Abbreviated codes for the collecting localities: APS = Ampasindava (RNI de Lokobe, Nosy Be); ADM = Andranomainty (RNI de Lokobe, Nosy be); ATH = Antsaharavy (RNI de Lokobe, Nosy Be); NA = Nosy Ambariobe; NF = Nosy Faly; NFH = Nosy Fanihy; NT = Nosy Tanikely; NS = Nosy Sakatia. Acronyms of institutions: CAS = California Academy of Sciences, San Francisco (USA); MRSN, MRSN-FAZC, MRSN-FN, MRSN-RJS = Museo Regionale di Scienze Naturali, Torino (Italy); PBZT-FAZC, PBZT-RJS = Parc Botanique et Zoologique de Tsimbazaza, Antananarivo (Madagascar); UADBA = Université d'Antananarivo, Departément de Biologie Animale (Madagascar); UMMZ University of Michigan, Museum of Zoology (USA); ZFMK = Zoologisches Forschungsinstitut und Museum 'A. Koenig', Bonn (Germany); ZSM = Zoologische Staatssammlung München (Germany).

HYPEROLIIDAE—*Heterixalus tricolor*, ZFMK 52580–52584; ZSM 463/2000–468/2000; *Heterixalus variabilis*, ZSM 428/2000–433/2000 (NF); **MICROHYLIDAE**—*Cophyla phyllodactyla*, UMMZ 211164 (APS); 211165 (APS); 211168 (APS); 211169 (APS); 211170 (ADM); 211171 (APS); 221050 (APS); ZFMK 53728–53733; ZSM 460/2000; *Platypelis milloti*, UMMZ 211201 (APS); 211202 (APS); ZFMK 53721–53722; *Platypelis occultans*, ZFMK 53734–53736 (holotype and paratypes); *Rhombophryne testudo*, MRSN-FAZC 8029 (ATH); 8057 (ATH); 8161 (ATH); 8243 (ATH); UMMZ 211421 (APS); 211422 (APS); 211423 (APS); 211424 (ADM); 211425 (ADM); 211426 (APS); ZFMK 53718–53719, 56156–56160; ZSM 474/2000–475/2000; *Stumpffia psologlossa*, MRSN-FAZC 8147 (ATH); UMMZ 211633 (APS); PBZT-FAZC 8147 (ATH); UMMZ 211634 (APS); 211637 (APS); 211639 (APS); 211641 (APS); 211643 (APS); 211645 (APS); 211647 (APS); 211648 (APS); 211651 (APS); 211652 (APS); 211653 (APS); 211655 (APS); 211656 (APS); 211657 (APS); 211659 (APS); 211660 (APS); 211661 (APS); 211662 (APS); 211663 (ADM); 211664 (ADM); 211666 (ADM); 211667 (ADM); 211669 (ADM); 211670 (ADM); ZFMK 52530–52535, 53750–53761, 53774; ZSM 479/2000, 480/2000–485/2000 (NS); *Stumpffia pygmaea*, MRSN-FAZC 8124 (ATH), 8242 (ATH), 8028 (ATH); PBZT-FAZC 8242 (ATH); PBZT-RJS 0136; UMMZ 211635 (APS); 211640 (APS); 211642 (APS); 211644 (APS); 211646 (APS); 211649 (APS); 211650 (APS); 211654 (APS); 211658 (APS); 211665 (ADM); 211668 (ADM); ZFMK 52541–52544 (holotype and paratypes), 53762–53773; *Stumpffia* sp., UMMZ 211630 (APS); **MANTELLIDAE**—*Boophis brachychir*, UMMZ 213676 (APS), CAS 156770 (Beomby), 156812 (Andranobe); *Boophis jaegeri*, ZFMK 52569 (holotype), 53616; ZSM 587/2001–588/2001; *Boophis tephraeomystax*, UMMZ 213938 (APS); 213939 (APS); 213940 (APS); 213941 (APS); 213942 (ADM); 213943 (ADM); 213944 (ADM); 213945 (ADM); 213946 (ADM); ZFMK 53651; ZSM 458/2000–459/2000; *Mantella betsileo*, MRSN-FAZC 8012 (ATH); 8047 (ATH); 8138 (ATH); 8154 (ATH); 8156 (ATH); 8158 (ATH); MRSN-RJS 0130, 0134, 0131; PBZT-FAZC 8046 (ATH); 8048 (ATH); 8123 (ATH); 8152 (ATH); 8153 (ATH); 8155 (ATH); 8157 (ATH); UMMZ 211891, Lokobe Reserve; 211909 (APS); 211910 (APS); 211911 (APS); 211912 (APS); 211913 (APS); 211914 (APS); 211915 (APS); 211916 (APS); 211917 (APS); 211918 (APS); 211919 (APS); 211920 (APS); 211921 (APS); 211922 (APS); 211923 (APS); 211924 (APS); 211925 (APS); 211926 (APS); 211927 (APS); 211928 (APS); 211929 (APS); 211930 (APS); ZFMK 52745, 53708–53710; ZSM 409/2000 (NF), 461/2000–462/2000, 594/2001–595/2001; *Mantidactylus ulcerosus*, MRSN-FAZC 8006 (ATH); 8007 (ATH); 8010 (ATH); 8042 (ATH); 8139 (ATH); 8159 (ATH); 10741; PBZT-FAZC 8005 (ATH); 8008 (ATH); 8043 (ATH); 8044 (ATH); 8045 (ATH); 8160 (ATH); UMMZ 212563 (ADM); 212774 (APS); 212775 (APS); 212776 (APS); 212777 (APS); 212778 (APS); 212779 (APS); 212780 (APS); 212781 (APS); 212782 (APS); 212783 (APS); 212784 (APS); 212785 (APS); 212786 (APS); 212787 (APS); 212788 (APS); 212789 (APS); 212790 (APS); 212791 (APS); 212792; (APS); 212793 (APS); 212794 (ADM); 212795 (ADM); 212796 (ADM); 212797 (APS); 213030 (APS); 213031 (ADM); 213032 (ADM); 213141 (APS); 60296 (1924–3) (syntype of *Lymnodynastes ulcerosus*); ZFMK 52659, 52666–52668; ZSM 590/2001; ZFMK 53668–53670; *Mantidactylus granulatus*, MRSN-FAZC 8011 (ATH); 8030 (ATH); 8032 (ATH);

8125 (ATH); 8148 (ATH); 8149 (ATH); UMMZ 213002 (APS); 213003 (APS); 213004 (APS); 213005 (APS); 213006 (APS); 213007 (APS); 213008 (APS); 213009 (APS); 213010 (APS); 213011 (APS); 213013 (APS); 213014 (APS); 213012 (APS); 213015 (APS); ZFMK 53682–53687; *Mantidactylus pseudoasper*, MRSN-FAZC 8031 (ATH); 8038 (ATH); 8040 (ATH); PBZT-FAZC 8039 (ATH); 8041 (ATH); UMMZ 213303 (APS); 213304 (APS); 213305 (APS); 213306 (APS); 213307 (APS); ZFMK 53706–53707; *Mantidactylus wittei*, ZFMK 52596–52597; ZSM 591/2001; **RANIDAE**—*Ptychadena mascareniensis*, UMMZ 213516 (ADM). **PELOMEDUSIDAE**—*Pelusios castanoides*, CAS 156769; **CHAMAELEONIDAE**—*Brookesia ebenaui*, MRSN-FAZC 11189 (HV), 11190; UMMZ 206978 (APS); 206979 (APS); 206980 (APS); 206981 (APS); 206982 (APS); 206983 (APS); 206984 (APS); 210958 (APS); ZFMK 53970; ZSM 561/2001; *Brookesia minima*, UMMZ 204924 (APS); 204925 (APS); 204926 (APS); 204927 (APS); 204928 (APS); 204929 (APS); 204930 (APS); 204931 (APS); 204932 (APS); 209731 (APS); ZFMK 53965–53970; ZSM 443/2000; *Brookesia stumpffi*, MRSN-FAZC 8034 (ATH); 8036 (ATH); 8058 (ATH); 8059 (ATH); 8114 (ATH); 8116 (ATH); 11187 (HV); PBZT-FAZC 8035 (ATH); 8037 (ATH); 8115 (ATH); 8117 (ATH); UMMZ 65554 (1928-14) (MALE AND FEMALE); 207069 (APS); 207070 (APS); 207071 (APS); 207072 (APS); 207073 (APS); 207074 (APS); 207075 (APS); 207076 (APS); 207077 (APS); 207078 (APS); 207079 (ADM); 210957 (APS); ZFMK 53948–53964; ZSM 477/2000–478/2000, 562/2001; *Calumma boettgeri*, MRSN-FAZC 8055 (ATH); 8056 (ATH); 8230 (ATH); 11197 (HV); PBZT-FAZC 8019 (ATH); 8020 (ATH); 8025 (ATH); 8131 (ATH); 8132 (ATH); 8143 (ATH); 8144 (ATH); UMMZ 206588 (APS); 206589 (APS); 206590 (APS); 206591 (APS); 206592 (ADM); 206839 (APS); ZSM 440/2000–441/2000, 444/2000; *Calumma nasuta*, MRSN-FAZC 8141 (ATH); 8142 (ATH); UMMZ 206822 (APS); *Furcifer pardalis*, MRSN-FAZC 8118 (ATH); 10720, 10725, 10726, 10727, 10742, 10743, 11171, 11176; 11216; UMMZ 206904 (APS); 206911 (APS); 206912 (APS); 206913 (APS); 210956 (APS); **GEKKONIDAE**—*Ebenavia inunguis*, UMMZ 207486 (APS); ZSM 442/2000; *Geckolepis maculata*, MRSN-FAZC 8022 (ATH); 11191 (HV); PBZT-FAZC 8016 (ATH); 8136 (ATH); UMMZ 65488 (1928-14); 207368 (APS); 207369 (APS); 207370 (APS); 207371 (APS); 207372 (APS); 207373 (APS); 207374 (APS); 207375 (ADM); 220990 (APS) (two eggs); 220991 (APS) (three eggs and two hatchlings); 220992 (APS) (two hatchlings); ZSM 434/2000, 435/2000 (NS); *Gehyra mutilata*, ZSM 445/2000; *Hemidactylus* cf. *frenatus*, MRSN-FAZC 8232 (ATH); 8233 (ATH); 8229 (ATH); ZSM 454/2000, 456/2000; *Hemidactylus* cf. *mabouia*, MRSN-FAZC 7998 (HV); 7999 (HV); 8000 (HV); 8001 (HV); 8002 (HV); 8003 (HV); 11193 (HV), 11195 (HV); UMMZ 207589 (APS); 207590 (APS); 207591 (APS); 207592 (APS); 207593 (APS); 207594 (APS); 207595 (APS); ZSM 450/2000–451/2000, 452/2000 (NS), 453/2000 (NFH); *Lygodactylus heterurus*, MRSN-FAZC 8054 (ATH); UMMZ 207635 (APS); 207636 (APS); 207637 (APS); 207638 (APS); 207639 (ADM); *Lygodactylus madagascariensis*, MRSN-FAZC 8052 (ATH), 8053 (ATH); UMMZ 207664 (APS); 207665 (APS); 207666 (APS); 207667 (APS); 207668 (APS); 207669 (APS); 207670 (APS); 207671 (APS); 207672 (APS); 207673 (APS); 207674 (APS); 207675 (APS); 207676 (APS); 207677 (APS); 207678 (APS); 207679 (APS); 207680 (APS); 207681 (APS); 207682 (APS); 207683 (APS); 207684 (APS); 207685 (APS); 207686 (APS); 207687 (APS); 207688 (APS); 207689 (APS); 207690 (APS); 207691 (APS); 207692 (ADM); *Paroedura oviceps*, MRSN-FAZC 8013 (ATH); 8150 (ATH); UMMZ 207897; 207898 (APS); 207899 (APS); 207900

(APS); 207901 (ADM); *Paroedura stumpffi*, MRSN-FAZC 8017 (ATH); 8121 (ATH); 8122 (ATH); 8128 (ATH); 11188 (HV); PBZT-FAZC 8127 (ATH); 8129 (ATH); 8145 (ATH); UMMZ 207948 (APS); 207949 (APS); 207950 (APS); 207951 (APS); 207952 (APS); 207953 (APS); 207954 (APS); *Phelsuma abbotti*, MRSN-FAZC 8014 (ATH); UMMZ 207960 (APS); 207961 (APS); 207962 (APS); 207963 (APS); 207964 (APS); 207965 (APS); 207966 (APS); 207967 (APS); 207968 (APS); 207969 (APS); ZSM 455/2000 (NS); *Phelsuma laticauda*, MRSN-FAZC 8004 (HV); 8023 (ATH); 8235 (ATH); PBZT-FAZC 8021 (ATH); 8130 (ATH); 8234 (ATH); UMMZ 127727, without precise locality (cleared and stained skeleton); 173743 (1967–68 No 6) (without precise locality; cleared and stained skeleton), 208103 (APS); 208104 (APS); 208105 (APS); 208106 (APS); 208107 (APS); 221007 (APS) (two hatchlings); 208121 (APS); 208122 (APS); *Phelsuma madagascariensis*, MRSN-FAZC 11196 (HV); PBZT-FAZC 8226 (ATH); 8237 (ATH); 8244 (ATH); 8245 (ATH); UMMZ 208196 (APS); 208197 (APS); 208198 (APS); 208205 (APS); 221008 (APS) (hatchling); ZSM 457/2000; *Phelsuma seippi*, MRSN-FAZC 8135 (ATH); UMMZ 208351 (APS); 208352 (APS); 208353 (APS); 208354 (APS); 208355 (APS); 208356 (APS); 208357 (APS); 208358 (APS); 208359 (APS); *Uroplatus ebenaui*, MRSN-FAZC 8050 (ATH); 8033 (ATH); 8049 (ATH); 8146 (ATH); UMMZ 208442 (APS); 208443 (APS); 208444 (APS); 208445 (APS); 208446 (APS); 208447 (APS); 208448 (APS); 208449 (APS); ZFMK 53946–53947; *Uroplatus henkeli*, MRSN-FAZC 8051 (ATH); 8241 (ATH); UMMZ 208480 (APS); 208481 (APS); 208482 (APS); 208483 (APS); 208484 (APS); 208485 (APS); 208486 (APS); 208487 (APS); 208488 (APS); 208489 (APS); 208490 (ADM); 208491 (ADM); **GERRHOSAURIDAE**—*Zonosaurus boettgeri*, UMMZ 207188 (APS); 207189 (APS); 207190 (APS); *Zonosaurus madagascariensis*, MRSN-FAZC 8027 (ATH); 8227 (ATH); 8238 (ATH); PBZT-FAZC 8133 (ATH); 8137 (ATH); UMMZ 207257 (APS); 207258 (APS); 207259 (APS); 207260 (APS); 207261 (APS); 207262 (APS); 207263 (APS); 207264 (APS); 209741 (APS); 209742 (APS); ZFMK 53989–53991; ZSM 449/2000, 465/2001 (NT); *Zonosaurus rufipes*, MRSN-FAZC 8018 (ATH); 8228 (ATH); PBZT-FAZC 8120 (ATH); 8240 (ATH); UMMZ 207300 (APS); 207301 (APS); 207302 (APS); 207303 (APS); 207304 (APS); 207305 (APS); 207306 (APS); 207307 (APS); 207308 (APS); 207309 (APS); 207310 (APS); 207311 (APS); 207312 (APS); 207313 (APS); 207314 (APS); 207315 (APS); 207316 (APS); 207317 (APS); 207318 (APS); 207319 (APS); 207320 (APS); 207321 (APS); ZFMK 53978–53982; ZSM 446/2000–448/2000; *Zonosaurus subunicolor*, MRSN-FAZC 8009 (ATH); 8134 (ATH); UMMZ 207200 (APS); 207201 (APS); 207202 (APS); 207203 (APS); 207204 (APS); 207205 (APS); 207206 (APS); 207207 (APS); 207485 (APS); ZFMK 53984–53988; **SCINCIDAE**—*Amphiglossus* n. sp., UMMZ 208810 (APS); *Amphiglossus stumpffi*, UMMZ 208794 (APS); 208795 (APS); 208796 (APS); 208797 (APS); *Cryptoblepharus cognatus*, MRSN R1788 (NA); R1789 (NA); R1790 (NA; R1791 (NA); PBZT-FAZC 8164 (NA); 8166 (NA); 8222 (NA); 8224 (NA); UMMZ 208885 (APS); 208886 (APS); 208887 (APS); 208888 (APS); 208889 (APS); 208890 (APS); 208891 (APS); 208892 (APS); 208893 (ADM); 208894 (ADM); ZSM 469/2000–470/2000, 471/2000 (NFH), 472/2000 (NS), 473/2000 (NFH); *Mabuya comorensis*, MRSN R1731 (NT); R1793 (NT); R1794 (NT); R1795 (NT); R1796 (NT); ZSM 515/2001 (NT); *Mabuya gravenhorsti*, MRSN R1877–1881 (ATH), PBZT-FAZC 8024 (ATH); 8236 (ATH); UMMZ 209076 (APS); ZSM 436/2000–438/2000, 439/2000 (NFH) 509/2001; *Mabuya lavarambo*, UMMZ 209150 (APS) (paratopotype); 209151 (APS), (paratopotype); 209152 (APS) (holotype);

Paracontias hildebrandti, UMMZ 209167 (APS); 209168 (APS); 209169 (APS); 209170 (APS); 209171 (APS); 209172 (APS); CAS 156787–156793 (NT), 156818–156821, 156869, 156939–156940; **TYPHLOPIDAE**—*Typhlops* n. sp., UMMZ 209728 (APS); 209729 (APS); 209730 (APS); *Typhlops mucronatus*, UMMZ 209718 (APS); 209719 (APS); 209720 (APS); 209721 (APS); 209722 (APS); 209723 (APS); 209724 (APS); 209725 (APS); 209726 (APS); 209727 (ADM); **BOIDAE**—*Sanzinia madagascariensis*, PBZT (still living specimen), (HV); **COLUBRIDAE**—*Alluaudina bellyi*, UMMZ 209249 (APS); 209250 (APS); 209251 (APS); *Dromycodryas bernieri*, MRSN-FAZC 8239 (ATH); *Dromycodryas quadrilineatus*, UMMZ 209292 (APS); 209293 (APS); 209294 (APS); *Ithycyphus miniatus*, UMMZ 209345 (APS); 209346 (APS); 209347 (APS); *Langaha madagascariensis*, UMMZ 208460 (APS); 209371 (APS); 209372 (APS); 209373 (APS); 209374 (APS); 209375 (ADM); 209376 (APS); *Leioheterodon madagascariensis*, MRSN-FAZC 8026 (ATH); UMMZ 209751 (APS); 209752 (ADM); 209753 (ADM); 209447 (APS); *Liophidium torquatum*, MRSN-FAZC 8231 (ATH); UMMZ 209448 (APS); 209449 (APS); 209450 (APS); 209451 (APS); 209452 (APS); 209453 (APS); 209454 (APS); 209455 (APS); 209456 (APS); 209457 (APS); 209458 (APS); *Liopholidophis stumpffi*, UMMZ 209519 (APS); 209520 (APS); 209521 (APS); 209522 (APS); 209523 (APS); 209524 (APS); 209525 (APS); 209526 (APS); 209527 (APS); 209528 (APS); 209541 (APS); ZSM 579/2001; *Lycodryas granuliceps*, MRSN-FAZC 8140 (ATH); UMMZ 209565 (APS); 209566 (APS); 209567 (APS); *Madagascarophis citrinus*, MRSN-FAZC 8151 (ATH); *Madagascarophis colubrinus*, MRSN-FAZC 8126 (ATH); UMMZ 209583 (APS); 209584 (APS); 209585, (APS); 209586 (APS); 209612 (APS); 209613 (APS); 209614 (APS); 209615 (APS); 209616 (APS); 209617 (ADM); 209618 (APS); 209619 (APS); ZSM 476/2000; *Pseudoxyrhopus microps*, UMMZ 209684 (APS); 209685 (APS); 209686 (APS); 209687 (APS).

Appendix II

Comments on species reported from Nosy Be and nearby islands and here considered as likely erroneous

A number of species which have been recorded from Nosy Be or even described from material presumably originating from this island were not found during our fieldwork. We propose to consider these species as absent from Nosy Be, in some cases only tentatively, based on the following arguments.

(1) ***Hyperolius nossibeensis***. Glaw and Vences (1993) concluded that the locality was wrong and likely based on a mistake with the locality of a *Mantidactylus granulatus* which was originally preserved in the same jar. The types of *nossibeensis* most likely correspond to the African species *Hyperolius viridiflavus* and should thus be considered as synonym of this species (or of another species of the *H. viridiflavus* complex).

(2) ***Heterixalus betsileo***. Blommers-Schlösser and Blanc (1991) report the presence of this species on Nosy Mamoko. As far as known *H. betsileo* does not occur in N. Madagascar, where it is replaced by other species (e.g. *H. luteostriatus*, *H. tricolor*, *H.* '*variabilis*'). At Nosy Be only *H. tricolor* has been reliably signalled. On the other hand, the finding of *H.* '*variabilis*' at Nosy Faly would possibly support the presence of this taxon at another island next to mainland Madagascar, as for Nosy Mamoko.

(3) ***Mantella baroni***. The occurrence of this species is based on Busse (1981), who gave the generic locality '*Nosy Cumba–Nosy Be*' (under the name *M. madagascariensis*), subsequently reported by Blommers-Schlösser and Blanc (1991). This record was almost certainly based on the types of *Phrynomantis maculatus*, today considered as a junior synonym of *M. baroni* (Vences *et al.*, 1999). The type locality '*La Réunion*' of this taxon was due to the supplier—which was '*Com. scientifique de Bourbon*' (Bourbon being a former name for La Réunion). This locality was changed into '*Nossi-Be et Nossi-Cumba*' in a later Paris catalogue, and to '*Madagascar*' in another catalogue. As stressed by Vences *et al.* (1999) the species was never found at either Nosy Be or Nosy Komba, and these localities must currently be considered as erroneous.

(4) ***Mantidactylus betsileanus***. The presence of *M. betsileanus* on Nosy Be as quoted by Blommers-Schlösser and Blanc (1991) is apparently corroborated by two voucher specimens housed in Paris (both adult females). Colour pattern of MNHN 1975.584 (SVL 38.8 mm) is largely faded, but the main characters are still recognizable. There is only a poorly marked light spot on the snout tip, and no distinct dark and light crossbands on the upper lip. The tibiotarsal articulation reaches the anterior eye corner when the hindlimb is adpressed along the body. Webbing on toes 4 and 5 is 4i/e (2), 5 (0.5). In MNHN 1962.877 (SVL 39.5 mm), a broad light vertebral band spans to the snout tip; however, the snout tip does not show a distinct white spot, only a slight light continuation of the vertebral band. Tibiotarsal articulation reaches anterior eye corner. Webbing, as far as recognizable, is similar to that of MNHN 1975.584. By general aspect and the described characters, both specimens clearly fit into the variation of typical *M. ulcerosus*, while *M. betsileanus* specimens are mostly smaller and have longer hindlimbs. *M. ulcerosus* generally has a more extended webbing (Blommers-Schlösser and Blanc, 1991), but in several ZFMK specimens of *M. ulcerosus* the webbing approaches the state of the MNHN specimens (e.g. ZFMK 52667, an adult female). The records of *M. betsileanus* on Nosy Be are thus due to confusion with *M. ulcerosus*; we consider *M. betsileanus* as absent from Nosy Be, as well as probably from north-western and northern Madagascar.

(5) ***Mantidactylus femoralis***. Quoted by Blommers-Schlösser and Blanc (1991, 1993). According to present information the northernmost locality for *M. femoralis* is Montagne d'Ambre, where it occurs in syntopy with *M. ambreensis* (Raxworthy and Nussbaum, 1994), while at Sambirano only *M. ambreensis* is known (Glaw and Vences, 1994). No specimen of either *M. femoralis* or *M. ambreensis* is held at Amsterdam or Paris. At Nosy Be the occurrence of *M. femoralis* is therefore doubtful, and in absence of voucher specimens we exclude it from its fauna.

(6) ***Calumma brevicornis***. Reported for Nosy Be by Ramanantsoa (1974) as follows: '*Il a été récolté dans la Montagne d'Ambre et Nosy Be, à la lisière de la forêt.*' This record was mentioned by Brygoo (1978) without providing more details. However, the species was not found by any other survey on Nosy Be although it is comparatively easy to survey. In addition, apparently no voucher specimens are known to support this record. We therefore consider this record as dubious.

(7) ***Calumma gallus***. Specimens of this species apparently from Nosy Be are conserved in Hamburg Museum (catalogue number ZMH 13352) according to Mertens (1933). A further specimen is housed at Munich under the number ZSM 868/1920 ('*Nossi Be 1884*', collected by '*Schneider*'). Another specimen with label indicating '*Nossi Be*' is present at Genoa (MCSNG 27992). Due to these vague original data, and waiting for more complete information, we exclude *C. gallus* from the Nosy Be fauna.

(8) (9) ***Calumma parsoni*** and ***Brookesia superciliaris***. Both these species are reported for Nosy Be by IUCN/UNEP/WWF (1987). Concerning *C. parsoni* this indication is not corroborated by any direct or museological observation. However, a male and a female *Brookesia superciliaris* (respectively with a total length of 68.1 and 73.9 mm), with a label indicating as provenance locality '*Nossi Bé*', are present in the Michigan Museum [UMMZ 65555 (1928-14]. Since this taxon is apparently limited (similarly to *C. parsoni*) to the eastern Malagasy escarpment, and since it was not found in the NW, we are inclined to consider the two above specimens (moreover rather old) as mislabelled.

(10) ***Zonosaurus brygooi***. Species described by Lang and Böhme (1990) just from Lokobe at Nosy Be, on the basis of the holotype ZFMK 46795, collected by R. Seipp. All confirmed localities for this species are known from north-eastern and eastern Madagascar only (e.g. Vences *et al.*, 1998; Raselimanana *et al.*, 2000).

(11) ***Zonosaurus aeneus*** which has been recorded from Nosy Be by one voucher specimen (ZFMK 14365) collected by H. Meier with no additional collection information. The only taxa of the *Zonosaurus aeneus* group known from Nosy Be are *Z. subunicolor* and *Z. rufipes.* All confirmed localities for this species are known from the east and central regions (Raselimanana *et al.*, 2000).

(12) ***Zonosaurus laticaudatus***. Glaw and Vences (1994) consider as dubious the records of this species for Nosy Be, which is based upon a specimen housed at Hamburg Museum (ZMH R 02555–57, see Brygoo, 1985).

(13) ***Ithycyphus perineti***. The locality '*Nosy Be*' for *I. perineti* was already considered as dubious by Domergue (1987). Altogether, four *Ithycyphus* specimens from Nosy Be are housed at Paris; under the names either *I. miniatus* or *I. perineti*. MNHN 7631 (collected by L. Rousseau) is most probably the specimen on which Domergue's *I. perineti* reference was based on. It has a faded coloration, 200 ventral scales and 145 subcaudals (last piece of tail probably amputated), and a slightly keeled state in some vertebral scales. Other specimens are MNHN 1884.588 (vertebral scales not keeled, 204 ventrals, 159 subcaudals); MNHN 1966.961 (vertebral scales not keeled, 205 ventrals, 157 subcaudals); and MNHN 1986.1367, a juvenile with a brown-greyish anterior and reddish-brown posterior part of the body, 201 ventral and 166 subcaudal scales with unkeeled vertebral scales despite a superficially keeled appearance. According to Domergue (1987), the main differences between *Ithycyphus miniatus* and *I. perineti* are the keeled vertebral and paravertebral scales in the latter. His scale counts yielded a range of 186–198 ventrals and 140–162 subcaudals in *I. perineti*, and 199–215 ventrals and 157–174 subcaudals in *I. miniatus* (see also Glaw and Vences, 1994). All the *I. perineti* specimens from central eastern Madagascar (from the type locality Andasibe to Masoala Peninsula) show a typical yellowish colour on the anterior part of the body, while *I. miniatus* typically has a greyish-brown forebody. Available specimens from Nosy Be largely agree with *I. miniatus* in scale counts and coloration, and there is no convincing argument not to consider them as belonging to that species.

(14) (15) ***Lycodryas gaimardi*** and ***Lycodryas arctifasciatus***. IUCN/UNEP/WWF (1987) quoted *L. gaimardi* and *L. arctifasciatus* from Nosy Be. Domergue (1994) classified the *Lycodryas* specimens from Nosy Be as *L. granuliceps*, a taxon which in the past has been considered a subspecies of *Lycodryas gaimardi* (*L. g. granuliceps*). Two specimens are still catalogued under this name in Paris (MNHN 1887.260: 17 dorsals, 237 ventrals, 110 subcaudals; 100 dark crossbands on body and tail; MNHN 1966.960: 17 dorsals, 243 ventrals, tail mutilated). The scale counts for both these

specimens clearly correspond to *L. granuliceps*, and also show the colour pattern typical for this species, namely dark brown crossbands bordered by white, and with white colour inserted, resulting in a 'dirty' appearance. This coloration is not found in any other MNHN specimen catalogued as *gaimardi*. We conclude that the record of *L. gaimardi* from Nosy Be is due to confusion with *L. granuliceps*, easily explained by the fact that it was previously considered as subspecies of *gaimardi*. A single Paris specimen is catalogued as *L. arctifasciatus* and apparently comes from Nosy Be. The specimen (MNHN 1950.371) is largely faded and its skull removed. Its scale counts (23 dorsals, 246 ventrals, 153 subcaudals) do not correspond to *L. arctifasciatus* (21 dorsals, 222–240 ventrals, 152–165 subcaudals; Glaw and Vences, 1994). However, the high number of dorsal scales also make an attribution to *L. granuliceps* impossible. Species attribution of this specimen remains uncertain; although its locality remains to be confirmed, at present it can not be excluded that a second species of *Lycodryas* (beside *L. granuliceps*) may occur on Nosy Be.

(16) ***Liophidium rhodogaster***. Mentioned for Nosy Be by Guibé (1958) without giving any further details. Domergue (1983: 1121) provides only little information on the distribution of *L. rhodogaster* stating that *L. rhodogaster* and *L. torquatum* are species of the humid eastern coast and the Sambirano region. At Paris Museum there is one Nosy Be specimen (MNHN 1974.1049), labelled as *Liophidium rhodogaster.* At a careful analysis this specimen turned out to be in reality a juvenile of *L. torquatum.*

(17) ***Mimophis mahfalensis***. A specimen from Nosy Be is conserved in Paris (MNHN 1884-593, don. E. Deyrolle). This species is present on the mainland, and in face of Nosy Be it is known from Benavony. Another specimen from the same locality is housed under the number MNHN 1886-33, without any further information. This snake may indeed be present on Nosy Be, although it is strange that its occurrence was not confirmed, taking into mind the high abundance in which it usually occurs.