Chapter 3. Mammalian biodiversity at Bezà Mahafaly: An update

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Abstract

Documenting and monitoring biodiversity are essential for the study and understanding of processes of species diversification, the assessment of conservation priorities, and conservation management decisions. This paper updates previous reports on the biodiversity of mammals in and around the Bezà Mahafaly Special Reserve in southwest Madagascar, which protects 4,200 ha of forest contiguous with broad stretches of surrounding forest. Findings come from the Bezà Mahafaly Monitoring Team and many students and researchers who have worked at the reserve. Methods used to inventory mammals include direct field observation, recording scat and tracks, camera- and live-trapping, mist-netting, and searching in dead wood. The diversity of mammals recorded has not decreased since the last published inventory in 2001, despite long-term reduction of forest cover in the area and pressures resulting from human activity. Four species are reported for the first time (*Macrotarsomys bastardi*, *Triaenops menamena*, *Myotis goudoti*, and *Suncus murinus*). One species has been eliminated as a likely case of mistaken identification (*Hemicentetes semispinosus*), and *S. madagascariensis* has been synonymized with *S. etruscus*. The balance of evidence indicates that *Microcebus murinus* is not present and that a *murinus*-like form occurs as a pelage color variant of *M. griseorufus.* Further research is needed to explain the phenotypic diversity of this population. Questions also remain about the species status of *Lepilemur* and *Propithecus.* Resolving these points, pursuing a range of key questions in ecological and evolutionary biology, and continued monitoring of the status of the mammal populations of the Bezà Mahafaly landscape are all important and urgent issues to be addressed.

Key words: Bezà Mahafaly, monitoring, biodiversity, small mammals, lemurs, bats, carnivorans

Résumé détaillé

L'étude et le suivi de la biodiversité sont essentiels pour l'étude et la compréhension des processus de diversification des espèces, l'évaluation des priorités de conservation, et les décisions de gestion pour la conservation. Cette étude consiste en une mise à jour des connaissances sur la biodiversité des mammifères dans et autour de la Réserve Spéciale de Bezà Mahafaly, dans le Sud-ouest de Madagascar, qui protège 4 200 ha de forêts et d'autres écosystèmes naturels. Les résultats reflètent des observations et analyses de diverses activités de recherche et de suivi effectuées menées par l'équipe de suivi local, les chercheurs et les étudiants nationaux et internationaux dans la Réserve et les paysages environnants. Les méthodes d'identification et de suivi des mammifères à Bezà Mahafaly sont très diverses, comprenant l'observation directe sur le terrain, l'analyse d'excréments, des enregistrements sonores et vidéos, des observations avec des pièges-cameras, le piégeage d'animaux vivants et des fouilles systématiques. Les approches moléculaires ont également apporté de nouveaux éléments sur la diversité des mammifères de Bezà Mahafaly, et soulèvent des questionnements importants, souvent sujets à débat, sur la taxonomie de plusieurs espèces.

La diversité des mammifères enregistrée à Bezà Mahafaly reste stable malgré les différentes pressions résultant des activités humaines. Des questions subsistent quant à la taxonomie de *Lepilemur* trouvée à Bezà Mahafaly ne pouvant encore être divisée entre *L. leucopus* et *L. petteri*. *Propithecus*, autrefois décrite comme une sous espèce *P. v. verreauxi*, a été

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récemment promu au rang d'espèce *P*. *verreauxi* sur les bases morphologiques et biogéographiques alors que les analyses génétiques ne peuvent distinguer de *P*. *deckenii* et de *P*. *coronatus*. Une nouvelle analyse des preuves démontre que *Microcebus murinus* n'est pas présente à Bezà Mahafaly et qu'une forme similaire à *M*. *murinus* se révèle être une variante de la couleur du pelage de *M*. *griseorufus*. Des recherches complémentaires sont nécessaires pour expliquer la diversité phénotypique de cette population. En ce qui concerne les autres espèces de mammifères, quatre espèces sont signalées pour la première fois à Bezà Mahafaly dont *Macrotarsomys bastardi*, *Triaenops menamena*, *Myotis goudoti* et *Suncus murinus*. L'espèce *S*. *madagascariensis* a été identifiée comme synonyme avec *S*. *etruscus*. Des évidences ont pu être collectées sur la présence des carnivores *Cryptoprocta ferox*, *Felis silvestris* et *Viverricula indica.* Ces questionnements, ainsi que diverses questions clés sur la biologie écologique et évolutive, ainsi qu'un suivi continu de l'état des populations de mammifères du paysage de Bezà Mahafaly constituent des problématiques importantes qu'il convient de traiter et de résoudre.

Mots clés : Bezà Mahafaly, suivi, biodiversité, petits mammifères, lémuriens, chauve-souris, carnivores

Introduction

Documenting and monitoring biodiversity are essential for the study and understanding of processes of species diversification, the assessment of conservation priorities, and conservation management decisions (Zimmerman & Radespiel, 2014). Nowhere are these tasks more significant than Madagascar, which has been called a model region of species diversification (Vences *et al*., 2009), yet whose unique fauna and flora are increasingly threatened by habitat destruction and fragmentation.

The primary purpose of this chapter is to update Ratsirarson *et al*.'s (2001) description of mammalian species in the Bezà Mahafaly Special Reserve and surrounding forests. The Bezà Mahafaly Special Reserve, inaugurated in 1986, is located south of the Onilahy River, about 35 km northeast of Betioky Atsimo. Today, the reserve protects 4,200 ha of forest contiguous with broad stretches of surrounding forest. A steep soil moisture gradient supports striking transitions in the vegetation of the area, with closed canopy gallery forest along the river giving way to dry forest, bush, thickets and spiny forest.

The Bezà Mahafaly Monitoring Team has played a key role in inventorying and monitoring biodiversity in and around the reserve since 1995. Recruited from surrounding villages, most team members have had little formal schooling but know the forest well and care deeply about its future. Under the leadership of the Département des Eaux et Forêts, Ecole Supérieure des Sciences Agronomiques, Université d'Antananarivo, the team has gathered systematic data on climate, biodiversity, and the demography, socio-economy and perceptions of the local community. This work continues today. Many students and researchers have also made significant contributions to the findings presented here (see also publications to be found at www.bezamahafaly.yale.edu).

Methods used to inventory mammals at Bezà Mahafaly include direct field observation, recording scat and tracks, camera-and live-trapping, mist-netting, and searching in dead wood (see below). Ratsirarson *et al*. (2001) reported 22 mammal species in and around the reserve. Field research has added four new records to the list since then, and one species has been dropped as a case of misidentification. In addition, field and laboratory studies have generated new questions and uncertainties about the taxonomic status of some populations. We review this work, with a particular focus on primates, and summarize conclusions in Table 1, which lists 24 mammal species now known to occur in the Bezà Mahafaly forests.

Primates

The last 30 years have seen an increase in the number of lemur species recognized, from 22 (Tattersall, 1982) to over 100 today (Mittermeier *et al*., 2014). Yoder *et al*. (2005) attributed this explosion to the recent intensity of research on lemurs and a new ability to recognize cryptic species, particularly among nocturnal forms distinguishable by their molecular profiles while showing little contrast in pelage or morphology. Tattersall (2007), on the other hand, argued that the increase in species number has arisen partly through "taxonomic inflation", with subspecies almost completely eliminated by being elevated to species. He contended that only about 50 lemur species are fully justified by current evidence. Underpinning these different perspectives is a continuing discussion among evolutionary biologists about the criteria by which diverging lineages should be recognized as separate species (Groeneveld *et*

Table 1. Mammal species at Bezà Mahafaly, 2016. * = endemic species; + = species about which there is taxonomic uncertainty, discussed in text.

Scientific name	Family	Common name
Primates		
**Lemur catta*	Lemuridae	*Maki, hira*
**Lepilemur leucopus* (=*petteri*?)+	Lepilemuridae	*Hataka*
**Microcebus griseorufus*+	Cheirogaleidae	*Songiky*
**Propithecus verreauxi*+	Indriidae	*Sifaka*
Rodentia		
**Eliurus myoxinus*	Nesomyidae	*Voalavonala*
**Macrotarsomys bastardi*	Nesomyidae	*Kelibotra, kelobotra*
Mus musculus	Muridae	*Totozy*
Rattus rattus	Muridae	*Voalavo*
Afrosoricida		
**Echinops telfairi*	Tenrecidae	*Soky*
**Geogale aurita*	Tenrecidae	*Batiko*
**Setifer setosus*	Tenrecidae	*Sokina*
**Tenrec ecaudatus*	Tenrecidae	*Trandraka*
Soricomorpha		
Suncus etruscus	Soricidae	-
Suncus murinus	Soricidae	-
Carnivora		
**Cryptoprocta ferox*	Eupleridae	*Fosa*
Felis silvestris	Felidae	*Kary, ampaha*
Viverricula indica	Viverridae	*Jaboady, moloky, vontira*
Chiroptera		
**Hipposideros commersoni*	Hipposideridae	-
**Triaenops menamena*	Rhinonycteridae	-
**Pteropus rufus*	Pteropodidae	-
**Mormopterus jugularis*	Molossidae	-
**Myotis goudoti*	Vespertilionidae	-
Taphozous mauritianus	Emballonuridae	-
Artiodactyla		
Potamochoerus larvatus	Suidae	*Lambo*

al., 2009; Weisrock *et al*., 2010; Markolf *et al*., 2011; Tattersall, 2013).

All this has made the construction of a list of the Bezà Mahafaly primates more interesting and uncertain than it was in 2001. We present the findings below in the hope that they will lead to further research and, eventually, consensus.

Lepilemur

Tattersall (1982) described the geographical range of *Lepilemur leucopus* as the "dry south of Madagascar, from Fort Dauphin westward at least to Ejeda, and possibly to the Onilahy River". The Bezà Mahafaly population of *Lepilemur* is broadly distributed across the forest landscape. Ratsirarson *et al*. (2001) listed it as *L*. *leucopus*, and this designation was used in the only detailed field study of the population to date (Nash, 1998).

Louis *et al*. (2006) proposed separate species status for the *Lepilemur* population at Bezà Mahafaly, based on observations of pelage, morphometric data, and analyses of mitochondrial DNA (D-loop, PAST, and 12s RNA fragments) from five individuals. They named this species *L*. *petteri*. This nomenclature has been adopted in the most recent guide to the lemurs of Madagascar (Mittermeier *et al*., 2014).

Grounds for questioning this assignment include the following (and see Tattersall, 2007): 1) the authors analyzed only mitochondrial DNA, whereas analyses of both nuclear and mitochondrial DNA are widely accepted to yield more reliable results (Heckman *et al*., 2007; Markolf *et al*., 2011); 2) the mitochondrial sites analyzed are highly variable, so that intra-specific variation is to be expected; 3) fragment lengths were very short, and concatenated for analysis; 4) the sample of individuals was very

small; 5) the greatest molecular distance found in 21 informative sites was negligible -- only 3.4% ± 0.8%; and 6) the range of intra-specific variation in pelage color and morphology in *L*. *leucopus* is unknown, making it difficult to assess the significance of variation in the small sample of individuals described. Based on the above considerations, Table 1 retains the designation of the Bezà Mahafaly population as *L*. *leucopus*, with possible assignment to *L*. *petteri*.

Microcebus

From the outset in 1995, Monitoring Team members consistently reported two forms of *Microcebus* in the reserve differing markedly in size and pelage. Several researchers also inferred the presence of two species, with *M*. *murinus* and *Cheirogaleus medius* listed as present by Nicoll & Langrand (1989) and Mittermeier *et al*. (1994). Systematic studies had not been undertaken at the time, however, and no sightings of *C*. *medius* have been reported since.

In an extensive taxonomic revision of populations from 12 localities in western and southern Madagascar, Rasoloarison *et al*. (2000) recognized seven species of *Microcebus*, including *M. murinus* and *M. griseorufus*. Species were distinguished by morphometrics, and by differences in coat color and dental and other morphological characteristics. *Microcebus murinus* and *M*. *griseorufus* are sister taxa (Yoder *et al*., 2000). Yoder *et al*. (2002) subsequently found a clear genetic distinction between populations of these two species in southern Madagascar.

Ihazoara forest, part of the Bezà Mahafaly forest landscape and just a few kilometers from the reserve, was among the localities studied by Rasoloarison *et al*. (2000). They trapped six *Microcebus* there, which they assigned to *M*. *griseorufus*, and they designated Ihazoara as the neotype locality for the species. They also examined bones recovered from pellets regurgitated by two species of owls, *Tyto alba* and *Asio madagascariensis*, that had been collected in Ihazoara forest in 1990-91 by Goodman *et al*. (1993a, 1993b). Additional bones came from pellets collected in forest along the path to the village of Ambinda, about 2 km north of Ihazoara. The pellets contained a large number of *Microcebus* mandibles. When two measurements taken on the recovered mandibles were compared with samples from north of the Onilahy River that had been clearly identified as *M*. *murinus*, all but one of the Ihazoara/ Ambinda mandibles could readily be assigned to *M*. *griseorufus.* The exception fitted with *M. murinus* in metric and non-metric features (Rasoloarison *et al*., 2000). The authors concluded: “Thus it appears that *Microcebus griseorufus* and *M. murinus* occur sympatrically in the Ihazoara Valley area, and the former is a more common prey item of owls” (p. 1012).

Further support for the presence of at least two *Microcebus* species in the Bezà Mahafaly forests came from a preliminary study by Rasoazanabary (2004), based on 2,990 trappings (i.e. traps set). She reported the presence of *M*. *griseorufus* in gallery forest in the reserve, and in the dry forest at Ihazoara. Although *M*. *griseorufus* (n = 62) dominated the reserve spiny forest, a few individuals were identified as *M*. *murinus* based on coat color (n = 6). Rasoazanabary noted that a few individuals had distinctive coat colors not readily assignable to either species. She concluded that there might be as many as three species and that, although present, *M*. *murinus* was extremely rare.

Between 2003 and 2007, Rasoazanabary (2011) captured, marked, and in some cases recaptured several hundred individuals from the three habitats (reserve gallery, reserve spiny, Ihazoara), in a detailed study of morphology, development, reproductive biology, and population dynamics. She also studied the nesting and feeding behavior of 57 radio-collared individuals over a 12-month period.

Of 196 individuals captured in 2003, 2004, and 2005, 13 had gray *murinus*-like coloration, 165 a typically gray-brown *griseorufus* appearance, and 18 a distinctive, all-red pelage (cited in Heckman *et al*., 2006; see also Figure 1). Individuals in the three forests differed consistently and significantly in the relative proportions of the digits of the hands and feet: those in the gallery forest were more hook-like (with relatively longer digits 3-5 and shorter thumbs and big toes), while those in the spiny forest were more clamp-like (relatively larger thumbs and big toes). Rasoazanabary (2011) and Rasoazanabary & Godfrey (in press) attributed this morphological variation to differences in the two habitats and how animals used them. The mean body mass of adults was significantly (about 10%) higher in gallery than in spiny forest, but neither population differed significantly from the population of intermediately sized individuals at Ihazoara.

Subsequent molecular studies have found evidence of only one species, *M*. *griseorufus*. Heckman *et al*. (2006) amplified and sequenced the full cytochrome *b* gene region of mitochondrial DNA from 70 individuals sampled from those captured and released by Rasoazanabary in 2003, in addition

Figure 1. Pelage variation in *Microcebus* at Bezà Mahafaly. (Photographs by Emilienne Rasoazanabary.)

to six samples of *M*. *griseorufus* previously obtained from Ihazoara, and 11 *M*. *griseorufus* from Berenty. All individuals from Bezà Mahafaly (and Berenty) were "clearly nested within a *M*. *griseorufus* clade" and diverged from reference samples of *M*. *murinus* from other locations. Chi-square tests of differences in distributions of coat color type across the three habitats revealed no significant differences; the distributions were also uncorrelated with genetic distance, as evidenced by the distribution of haplotypes.

Heckman *et al*. (2006) concluded from their genetic findings that coat coloration was not diagnostic of species differentiation, and that all 70 individuals sampled should be classified as *M*. *griseorufus*. Analyses of mtDNA need to be interpreted cautiously, because it mutates at a high rate and may overestimate species diversity. It is particularly notable, thus, that mtDNA indicated the presence of only one species in the case of the Bezà Mahafaly *Microcebus*. Heckman *et al*.'s (2006) analysis also indicated reciprocal gene flow among the three habitats, despite the separation of Ihazoara from other sites by the Sakamena River. Noting that their analysis was limited to a single mtDNA gene and that intriguing questions remained, Heckman *et al.* (2006) called for further work to confirm their results and, in particular, for the inclusion of nuclear genetic markers, which can shed light on divergences at the population level.

Cuozzo *et al*. (2013) used these genetically derived conclusions as the basis for a study of the range and types of phenotypic variation that can occur within a single mouse lemur population, and to help interpret a single-locality museum sample of *Microcebus* collected at Amboasary-Sud in 1931. They analyzed 126 cranial and/or dental specimens of the Amboasary-Sud *Microcebus*, and compared them to 32 specimens from Bezà Mahafaly, 23 of which were found in owl pellets collected in the gallery forest. In addition, they compared pelage data from 196 live-caught individuals at Bezà Mahafaly with 72 dried skins housed in museums around the world. Altogether, the samples came from 19 sites including Amboasary-Sud, and from individuals attributed to eight species.

The authors found quite limited variation in cranial and dental measures in the Amboasary-Sud and Bezà Mahafaly samples, and the overall range of dental measures at Bezà Mahafaly fell within the range of variation at Amboasary-Sud. In contrast, nonmetric dental traits exhibited wide variation in both samples. The pattern of pelage variation in the Amboasary-Sud and Bezà Mahafaly specimens was distinct from that of other *Microcebus* species, and pelage variation in the Amboasary-Sud specimens fell within the range of variation at Bezà Mahafaly. Cuozzo *et al*. (2013) concluded that the Amboasary-Sud specimens could all be assigned to *M*. *griseorufus* and, of particular relevance to this discussion, emphasized the discordance between different aspects of species biology uncovered by their study.

The case of the Bezà Mahafaly *Microcebus* is rare in the context of taxonomic studies of lemur populations: most commonly, genetic evidence identifies populations as separate species that are indistinguishable by pelage or morphology, whereas the opposite is the case at Bezà Mahafaly. More generally, the profile of the Bezà Mahafaly *Microcebus* is as perplexing as it is intriguing, for it includes: 1) a preponderance of mandibles collected from regurgitated owl pellet in 1990 designated as *M*. *griseorufus*, with just one recognized as *M*. *murinus*; 2) polymorphism in coat coloration uncorrelated with habitat or genetic distance; 3) significant variation between habitats in body mass and the morphology of hands and feet; and 4) analysis of a long sequence of mtDNA from a large sample of individuals showing no evidence of more than a single species, *M*. *griseorufus*.

At least three interpretations of these incongruent findings are possible: 1) intra-specific variation is high in the *M*. *griseorufus* phenotype at Bezà Mahafaly; 2) recent research has sampled populations of *M*. *griseorufus* and *M*. *murinus* late in a process of species replacement, involving some level of hybridization; and 3) the population was sampled at an early stage in a speciation event (A. Yoder, personal communication).

Under (1), the single mandible from an owl pellet identified as *M*. *murinus* was actually an outlier belonging to *M*. *griseorufus*, or else was caught in another forest and then carried to Ihazoara. Analyses of intra-specific phenotypic variation in large samples captured at a single location are rare, and the well-documented variability of the Bezà Mahafaly sample could simply reflect its large size.

Under (2), polymorphism in coat coloration and variation between habitats in body mass and morphology are indicative of a late stage in a local process of species replacement of *M*. *murinus* by *M*. *griseorufus*. The absence of distinct *M*. *murinus* haplotypes in the Bezà Mahafaly sample indicates that the process is largely complete. Hybridization between these species has been reported in other forests (Heckman *et al*., 2007; Gligor *et al*., 2009; Hapke *et al*., 2011; Rakotondranary *et al*., 2011). Moreover, the disjunct geographical range of *M*. *murinus* (Mittermeier *et al*., 2014) suggests that this species was formerly present in forests south of the Onilahy River and would have been broadly sympatric with *M*. *griseorufus.*

Under (3), habitat-specific variation in body mass and in foot and hand measurements reflects divergent selection pressures, and is an indicator of incipient speciation.

Further research is needed to explore these interpretations and distinguish between them. We list only *M*. *griseorufus* in Table 1, in light of the extensive genetic evidence of a single species and the absence of genetic or geographical clustering of individuals with distinctive pelage.

Propithecus verreauxi

Historically, the *Propithecus* population at Bezà Mahafaly was assigned to the subspecies *P*. *v*. *verreauxi*, occurring in forested regions from just west of Tolagnaro to the Tsiribihina River (Tattersall, 1982). *Propithecus v*. *verreauxi* was recently raised to species level, *P*. *verreauxi*, on morphological and biogeographical grounds (Mittermeier *et al*., 2006; Groves & Helgen, 2007), although genetic analyses do not distinguish *P*. *deckenii*, *P*. *verreauxi*, and *P*. *coronatus* (Pastorini *et al*., 2001; Mayor *et al*., 2004). With diverse lines of evidence still not yielding a convergent outcome, we assign the Bezà Mahafaly population to the species *P*. *verreauxi*.

Other mammals

Rodentia

Youssouf (2010) set 118,560 box traps in the reserve gallery forest between October 2006 and September 2007, and confirmed the previously reported presence of the endemic rodent *Eliurus myoxinus*. The endemic *Macrotarsomys bastardi* was found for the first time, with the capture of three individuals in the reserve gallery forest (Youssouf & Rasoazanabary, 2008; Youssouf, 2010). *Macrotarsomys bastardi* is widely distributed in western and southern Madagascar. Nocturnal and terrestrial, it digs burrows in sandy, forest substrates, and feeds on grains and fruits (Soarimalala & Goodman, 2011). Remains of neither species have been found in owl pellets, whereas introduced rodents (and *Microcebus*) are abundant (S. M. Goodman, personal communication). The reasons for this are not known.

Two introduced species, *Mus musculus* and *Rattus rattus*, occur at Bezà Mahafaly. The earliest archaeological evidence for these species on Madagascar comes from the northwest site of Mahilaka in the 11th century (Rakotozafy, 1996). *Mus musculus* is absent or very rare in protected forests in the reserve, present at very low numbers in dry forest protected by traditional rules of usage, and abundant in three of four villages sampled. *Rattus rattus* is present in greater numbers in the forests sampled, and is particularly abundant in and around villages and agricultural fields (Youssouf, 2010, see also Richard *et al*., 2016).

Afrosoricida

The presence of *Echinops telfairi* in the reserve gallery forest was confirmed by trapping in 2006-2007 (Youssouf, 2010), and members of the Monitoring Team find *Setifer setosus*, *Tenrec ecaudatus*, and *Geogale aurita* from time to time. The absence of individuals of these species among those trapped by Youssouf is not surprising: insectivores rarely enter box traps and are usually found by searching preferred microhabitats (P. J. Stephenson, personal communication) or by capture in pitfall traps (Goodman *et al*., 1996). Goodman *et al*. (1993a,

1993b) also noted the presence of *G*. *aurita* in owl pellets found near the reserve.

Ratsirarson *et al*. (2001) included *Hemicentetes semispinosus* in their species list, but this almost certainly resulted from the mistaken identification of juvenile *T*. *ecaudatus* as *H*. *semispinosus*, which it resembles (Soarimalala & Goodman, 2011). *Hemicentetes semispinosus* was not found during the original survey of small mammals in 1985 (Nicoll & Langrand, 1989), and its known distribution is limited to eastern humid forests from north to south of the island (Goodman & Raherilalao, 2013). *Hemicentetes semispinosus* is therefore not included in Table 1.

Soricomorpha

Suncus etruscus is widespread in dry and spiny forest (Soarimalala & Goodman, 2011), and was found during a small-mammal survey in the reserve in 1985. Nicoll & Langrand (1989) listed it as *S*. *etruscus=madagascariensis*, whereas Ratsirarson *et al*. (2001) referred to it as *S*. *madagascariensis*. Once thought to be endemic to Madagascar, Omar *et al*. (2011) used mitochondrial cytochrome *b* gene sequences to demonstrate its close affinity to the widespread Old World species *S*. *etruscus,* and concluded that the species in Madagascar is an introduction, properly designated *S*. *etruscus*.

Youssouf (2010) did not capture *S*. *etruscus*, but noted that villagers reported seeing it. Like afrosoricids, *S*. *etruscus* is unlikely to enter box traps. Monitoring Team members have reported that they occasionally find *S*. *etruscus* in dead wood. It is included in Table 1 based on the team's observations and the testimony of villagers. Goodman *et al*. (1993a, 1993b) also noted the presence of *S*. *murinus* and *S*. *etruscus* remains in owl pellets found near the reserve. We include *S*. *murinus* in Table 1 based on these findings.

Carnivora

There are wild populations of three species of Carnivora at Bezà Mahafaly, among which *Cryptoprocta ferox* is the only endemic. Evidence for its presence is episodic, in marked contrast to the abundant population of *C*. *ferox* regularly seen in the western dry forest at Kirindy, north of Morondava (Dollar *et al*., 2007). The first sighting at Bezà Mahafaly was in March 1986 (Ratsirarson, 1987). Kubzdela (cited by Brockman *et al*., 2008) observed *C*. *ferox* in gallery forest in November 1993. The next documented sighting, by the Monitoring Team, was in March 2008. Since then, they have encountered occasional tracks and scat of *C*. *ferox* in transitional forest west of the gallery forest. An adult was photographed walking along a trail at night in the gallery forest during a 12-month camera-trapping program in 2008, and the remains of two *Lemur catta* and two *Propithecus verreauxi* characteristic of *C*. *ferox* kills were found in the forest over a two-week period during that time (Sauther *et al*., 2011; Bolt *et al*., 2015). In 2011, *C*. *ferox* was encountered in Parcel 1 moving on the ground, once at dusk and once at night (K. Fish, personal communication).

Felis was first reported in the reserve in 1986 (Ratsirarson, 1987), with many sightings in gallery and dry forest since then, and there is some indication that the population has increased in recent years and become a significant predator on lemurs (Sauther *et al*., 2011; Richard *et al*., 2016). Ratsirarson *et al*. (2001) listed it as *Felis* sp., reflecting uncertainty about the history and taxonomic status of Madagascar's widespread wildcat population. Preliminary genetic analyses of three individuals captured at Bezà Mahafaly indicate that they are clearly not feral domestics or known South African or European wildcats (M. Sauther, personal communication). Archival records suggest that *F*. *silvestris* was introduced from North Africa within the last few hundred years (Goodman, 2012 and personal communication). Table 1 lists the Bezà Mahafaly population as *F*. *silvestris*.

Viverricula indica is an introduced species now widespread in Madagascar (Goodman, 2012). The Monitoring Team reports seeing it at Bezà Mahafaly from time to time, usually around villages. K. Fish (personal communication, 2011) encountered an individual in degraded forest, under a tree in which a *L*. *leucopus* was sitting. Numerous camera trap pictures in 2008 attest to its presence in the reserve gallery forest as well (Sauther *et al*., 2011).

The domestic dog (*Canis lupus*) is not listed in Table 1 because it is a human commensal and does not occur as a feral population at Bezà Mahafaly. *Canis lupus* may be seen or heard in the reserve gallery forest during the day, moving alone or in small groups, and has been photographed by camera traps at night (Sauther *et al*., 2011; Bolt *et al*., 2015), but Monitoring Team members report that all individuals are village-based. Like wildcats, they may be increasingly important predators of diurnal lemurs (Brockman *et al*., 2008; Richard *et al*., 2016).

Chiroptera

Bats have not been a focus of study at Bezà Mahafaly. Ratsirarson *et al*. based their species list in 2001 on remains in owl pellets reported by Goodman *et al*. (1993b). In June and July 2011, Fish (2012) set multiple mist nets simultaneously in the reserve gallery forest and adjacent dry forest during 15 nights (256 hours). She captured two bats, *Triaenops menamena* (=*rufus*, see Goodman & Ranivo, 2009) and *Myotis goudoti* (S. M. Goodman, personal communication), increasing the previously reported bat diversity to six species. Bat echolocation calls were detected 16 times, and bats were observed 58 times with night vision scans.

Tadarida jugularis, listed in 2001, is now known as *Mormopterus jugularis* (Goodman, 2011) and is listed as such in Table 1.

Artiodactyla

The absence of *Potamochoerus larvatus* from camera-trap photographs in the reserve gallery forest in 2008 (M. Sauther, personal communication) suggests that this species is locally extinct, but tracks, scat and occasional sightings attest to its continued presence in the Bezà Mahafaly landscape. *Potamochoerus larvatus* probably reached Madagascar quite recently, even though widely distributed across the island today. It either arrived by swimming or rafting across the Mozambique Channel, or brought by people; the absence of any trace of its presence before historical times favors the latter pathway of introduction (Andrianjakarivelo, 2003; Goodman *et al*., 2003).

Discussion and conclusions

Knowledge of biodiversity is an essential foundation for biological research into paleobiogeography, speciation, micro-endemism, and hybridization. Recent molecular approaches to the study of diversity have identified new taxa, and raised important and unresolved questions about the taxonomic status of several genera. The *Microcebus* and *Lepilemur* populations at Bezà Mahafaly are good cases in point, and field and laboratory research are needed to resolve outstanding questions about their taxonomic status.

The high levels of regional micro-endemism characteristic of Madagascar's fauna have attracted much attention in recent years, with research and debate focused mostly on eastern and western forests and the causal roles of river barriers and shifts in species distribution associated with Quaternary changes in vegetation (Goodman & Ganzhorn, 2004; Wilmé *et al*., 2006; Vences *et al*., 2009). Biodiversity is generally lower in the west than the east, a difference attributed to the long dry season (Soarimalala & Goodman, 2011). Less attention has been given to the presence and determinants of variation in biodiversity along a north-south axis on the island's western flank.

Comparing three forests in the west with Bezà Mahafaly and Tsimanampetsotsa in the southwest, the diversity of endemic mammals appears quite similar with one exception (Table 2). The similarity is itself striking: even without taking into account north-south gradients in precipitation and temperature, it might be expected that differences in methodological protocols, duration of sampling period and, in particular, the area sampled would generate greater variation than seems to be the case. The much lower diversity of nocturnal primates in the southwest is a striking difference, however, and the lower diversity of Chiroptera, also nocturnal, is notable too. Extraneous factors are unlikely to account for the well-documented contrast between the primate communities. Differences in temperature or seasonal food availability, particularly plant exudates so

Table 2. Distribution of endemic mammals in western dry forests. Boldface figures in parentheses (Primates only) are the number of nocturnal species among those present. Italicized figures in parentheses (other orders) are the total species number including non-endemics (from [1]Dammhahn *et al*., 2013; [2]Soarimalala *et al*., 2013; [3]Randriandimbimahazo, 2013; [4]Mittermeier *et al*., 2014; [5]Soarimalala & Goodman, 2011; [6]Goodman, 2012; [7]Goodman, 2011; [8]Nicoll & Langrand, 1989).

	Beanka	**Bemaraha Nat. Park**	**Kirindy (CNFEREF)**	**BMSR**	**Tsimanampetsotsa Nat. Park**
Area (ha)	17,000	66,630	12,500	4,200	43,200
Primates[1,4,8]	11(**10**)	7(**5**)	8(**6**)	4(**2**)	5(**3**)
Rodentia[2]	2(*3*)	3(*5*)	3(*5*)	2(*4*)	2(*4*)
Afrosoricida[2,3,5]	4	5	7	4	4
Carnivora[6,8]	-	2(*4*)	2	1(*3*)	2(*3*)
Chiroptera[7]	-	11(*16*)	8(*13*)	4(*6*)	5(*6*)

important in the diets of many nocturnal primates in western dry forests, are more likely explanations but remain to be systematically explored.

In conclusion, the diversity of mammals occurring in and around the Bezà Mahafaly Special Reserve has not decreased since the first report by Ratsirarson *et al*. (2001), notwithstanding the long-term reduction of forest cover in the area and pressures resulting from human activities (Ranaivonasy *et al*., 2016; Richard *et al*., 2016). Four species are reported here for the first time (*Macrotarsomys bastardi*, *Suncus murinus*, *Triaenops menamena*, and *Myotis goudoti*); one has been eliminated as a case of mistaken identification (*Hemicentetes semispinosus*). *Suncus madagascariensis* has been synonymized with *S. etruscus*. The balance of evidence indicates that *Microcebus murinus* is not present but, rather, a color variant of *M. griseorufus*. Questions remain about the species status of *Lepilemur* and *Propithecus.* Resolving these questions, pursuing a range of key questions in ecological and evolutionary biology, and monitoring the status of the unique mammal populations of the Bezà Mahafaly landscape are all important and urgent issues to be addressed in future work.

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