LEMURS IN MANGROVES AND OTHER FLOODED HABITATS

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Mangroves on Madagascar

Recent estimates indicate that mangroves in Madagascar occupy an area of approximately 2.800 km^2, 98% of which lies along the western coast of the island, and representing about 2% of global mangroves (Giri *et al.* 2011; Giri & Muhlhausen 2008). This asymmetry is due mainly to tidal range differences, wider in the west than in the east of the island, and to the presence of large estuaries (Roger & Andrianasolo 2003). Being marginal habitats with extreme temperatures, solar radiations, winds, salinity, and flooding, mangrove forests are known to be relatively poor in species diversity (Vannucci 2001). Compared to other continents, mangroves in Madagascar are even poorer in plant species diversity than other areas, with only nine species compared to more than 45 species in Southeast Asia and about 17 in Africa (Ellison *et al*. 1999). This depauperate plant community matches a low diversity of animal groups, including lemurs which have radiated dramatically in other forest types of Madagascar. In fact, reports of lemur species in mangrove habitats are scarce (Roger & Andrianasolo 2003). This also contrasts with other continents where mangroves are key resources for some primate species, although mangrove specialists are very rare within the order (Matsuda *et al.* 2011; Nowak 2012).

The unpalatability of mangrove leaves, with some mangrove tree species being rich in tannins, has been suggested as one possible reason for the lack of lemurs in mangroves (Birkinshaw & Colquhoun 2003). Other hypotheses propose that the open mangrove canopy may be associated with higher predation pressure on lemurs from birds of prey and/or higher thermoregulatory stress (Birkinshaw & Colquhoun 2003). However, at present it is not clear whether the rare occurrence of lemurs in mangroves has ecological reasons or is simply the result of low survey effort and absence of systematic studies in this habitat.

In order to explore whether the occurrence of lemurs in mangroves is a rare event, we provide an updated review of observations of lemurs in this habitat as well as in other inundated habitats. The information has been compiled using the IUCN Red List and a questionnaire sent to the IUCN Lemur Specialist Group members and an additional list of researchers known to work or to have worked in areas where mangroves occur.

A case study is also used, focused on the littoral forest of the Mandena Conservation Zone in south-eastern Madagascar, to explore the hypothesis that mangroves represent low quality food resources for lemurs as compared to upland forest and freshwater swamp plants. This is achieved by comparing phytochemical contents of leaves available in forests, swamps, and mangroves.

Lemurs in mangroves

Although few studies of mangrove use by lemurs have been published and reports often lack contextual information, lemurs have been observed in at least several mangrove localities along the western coast of Madagascar (Fig. 1). Decary (1930) was the first to report the presence of a lemur, the aye-aye (*Daubentonia madagascariensis*), in an unspecified mangrove forest near Mahajanga. This was the only report of this species to be observed in this type of forest. Mouse lemurs, *Microcebus* spp., have been observed several times in this habitat. *Microcebus* cf *myoxinus* has been observed in Baie de Baly close to Antsakoamarovitiky (Hawkins *et al*. 1998), the Baie de Bombetoka, the largest area of mangroves in Madagascar (Schmid & Kappeler 1994), and in

Please, add here Fig. 1

the mangroves of Besalampy, south of Cap Sainte André (J.U. Ganzhorn, unpubl.). Hawkins and co-authors (1998) speculate that it is possible that this species occurs regularly in mangroves. Another species of mouse lemur, *M. griseorufus* has been observed in the mangrove area of Saint Augustin, in the south-west of the island (J. Youssouf, pers. comm.) Sifaka species have been observed several times as frequent inhabitants of mangroves. The presence of two species of sifakas, *Propithecus deckeni* and *P. coquereli*, has been reported in the areas of Katsepy and Anjohibe (near Mahajanga), respectively (M. Markoff, pers. comm.). More detailed reports come from the large mangrove patches of the Katsepy area, located between the estuaries of Betsiboka and the Mahavavy rivers, where *P. coronatus* has been observed regularly (Gauthier *et al*. 1999, 2000). Mangroves are used by this species as sleeping sites and for feeding. However, more systematic observations of two groups of *P. coronatus* revealed that they leave the mangrove sites for the upland, dry forest early in the morning and return late in the afternoon (Gauthier *et al*. 1999). *Propithecus coronatus* have also been reported in the area of Antrema (Roger & Andrianasolo 2003).

Facilitated by their known flexibility, several species of lemurids also appear to use the mangroves, at least as resting sites. In the Katsepy region *Eulemur rufus* and *E. mongoz* have been observed to rest in the same areas used by the sifakas (Gauthier *et al*. 1999, 2000). The latter species has also been observed in Antrema (E. Roger, pers. comm.). Further north, in the area of Afady, blue-eyed lemurs, *E. flavifrons*, have been observed in mangrove patches (J. Dumoulin, unpubl. report). At the extreme north of the island, north-west of Montagne d'Ambre, crowned lemurs (*E. coronatus*) and Sanford's lemurs (*E. sanfordi*) have been observed at the edge of mangrovesconnecting patches of forest (B. Freed, pers. comm.). The presence of identified groups of these species in areas only connected by mangroves implies their use of this habitat as a corridor (B. Freed, pers. comm.). Finally, in the south-western corner of the island, *Lemur catta* have been observed in the mangroves north and south of Toliara, such as in the mangroves of Ambanilia, Andalo, Andoharano, and Antsifotse, in the western portion of the new protected area of Tsinjoriake. Ring-tailed lemurs have been also inventoried in the mangroves of Andriambe, Antanifotsy, and Lovokampy located on the south shore of the Onilahy river, near Saint Augustin (J. Youssouf, unpubl.).

Lemurs in other flooded habitats

Despite the paucity of research conducted on lemurs in mangroves, a wealth of data has been collected on lemur species occupying other types of flooded habitats. The best known example is the Lac Alaotra gentle lemur (*Hapalemur alaotrensis*; see chapters xx and xy by Waeber *et al*., this volume). The area surrounding Lac Alaotra is devoid of bamboo (subfamily Bambusoideae) (Mutschler *et al*. 1998, Mutschler 1999), a resource that its congeners rely on heavily (Tan 1999, Tan 2006). Instead, the strict folivore *H. alaotrensis* inhabits the surrounding marshes, resting and feeding on cyperus (family Cyperaceae) and reeds (family Poaceae) (Mutschler *et al*. 1998; Mutschler 1999). Why this lemur species chose to exploit such a habitat is still a major question, especially since the overall dietary quality in such an environment is low (Mutschler 1999); but see Waeber et al. chapter xx (this volume) for possible explanations and ecological adaptations.

Another seasonally flooded habitat is that of the Mandena Conservation Zone, located in south-east Madagascar. The area contains two fragments of littoral forest comprising 148 hectares, with 82 hectares of interspersed swamps (Ganzhorn *et al*. 2007). Although some of this area remains wet year-round, much of it becomes seasonally inundated, with areas rising in water-depth up to 1.8 m (T.M. Eppley, unpubl.). Four lemur species (*Eulemur collaris*, *Hapalemur meridionalis*, *Avahi meridionalis*, and *Microcebus murinus*) have been observed within the swamp (Eppley, pers. obs.), and it is possible that *Cheirogaleus major* and *C. medius* utilize this area as well.

The collared brown lemur (*E. collaris*) is a cathemeral frugivore that in Mandena spends much of its feeding time in upland littoral forest where fruits are more available. However, they use the swamp extensively for travelling and resting (Donati *et al*. 2011), and have been observed to feed there, although this represents a marginal 12.1% (N = 7 items) of their total diet. By comparison, approximately 40% (N = 22) of the diet of the southern bamboo lemur (*H. meridionalis*) comprises plants in the swamp habitat (Eppley *et al*. 2011; J. Ralison, unpubl.). *H. meridionalis* in Mandena were observed to spend an average of 67.3% of their time feeding in swamp areas whereas the remaining 32.7% of feeding was spent in the littoral forest (Eppley *et al*. 2011), with similar figures for their overall activity budget (T.M. Eppley, unpubl.). Although this species tends to graze on the sedges and grasses (families Cyperaceae and Poaceae) that are available during the dry austral winter (Eppley *et al*. 2011), they also access this habitat during full inundation to forage for arboreal fruits, flowers, and leaves (J. Ralison, unpubl.). *Eulemur cinereiceps* also seems to spend a significant amount of time foraging in swamp areas in the eastern rainforest (Andriamaharoa *et al*. 2010).

Comparison of nutritional quality between upland forest plants, swamps and mangroves

To examine potential phytochemical differences between leaves available in different habitats, we contrasted leaves from randomly selected trees in the forest and in the swamp of Mandena. Overall, leaves analyzed from both the upland forest and swamp showed no significant differences (Table 1). Leaves from the forest, however, showed a strong tendency to contain higher nitrogen content ($z = -1.90$, $p = .057$). Mangrove biochemical characteristics (from leaves of *Avicennia marina* and *Bruguiera gymnorrhiza*) are shown in the table but the data were not included in the statistical analysis due to small sample size. Mangrove leaves appear to be lower in fibre and higher in sugar, tannin, and polyphenolic content.

Please, add here Table 1

Discussion

This brief review suggests that various lemur taxa use mangroves in one way or another. While no lemur species appear to specialize or display a preference for mangroves, subsets of the lemur community occurring in each area where mangroves are also present seem to utilize them. This first attempt to summarize available knowledge on lemur presence in mangroves indicates that the importance of this particular kind of forest as lemur habitat may have been under-estimated. This is in line with recent findings from other continents which suggest that in fact more than half of Old World monkey genera use mangroves at least seasonally or opportunistically (Nowak 2012; Rowe and Myers 2011).

Our review suggests that at least some of the observed lemur species use mangrove patches as part of a mosaic habitat where other forest types are also present. Mainly frugivorous lemurids, for example, seem to rely on mangroves opportunistically as refuges for their resting/sleeping or as corridors for travelling between preferred habitats, while feeding on mangroves is rarely observed. However, this interpretation may simply be the result of a lack of systematic follows in this habitat type, and therefore, further survey efforts are needed to verify this assumption. Other species are also known to use mangroves or inundated forests as part of an effective defence response to terrestrial predator risk (Galat-Luong & Galat, 2005; Matsuda 2009, 2011; Nowak 2012). The observation that frugivorous *E. collaris* in Mandena spend much of their resting time in the swamp while most of their feeding occurs in the forest fits well with an anti-predator strategy (G. Donati, pers. observ.).

Although observational data from mangrove areas are not available, a similar reasoning can be used to explain the opportunistic use of mangroves by other frugivorous lemurids which are unlikely to meet their dietary requirements in this habitat year-round. In fact, mangrove habitats have been shown to provide monotonous food supply as well as to have relatively low fruit availability (Matsuda *et al.* 2009; Nowak 2008).

Folivorous lemurs, such as *Propithecus* and *Hapalemur* species, seem to use mangroves or inundated forests, respectively, more extensively. Phytochemical analyses show similar nutritional values of leaves in forest and freshwater swamps in Mandena, although we found a trend for higher nitrogen content in leaves in upland forest. Keeping other factors constant, this finding would theoretically explain the large amount of time allocated by the resident folivore, *H. meridionalis*, to feeding in the swamp (Eppley *et al.* 2011), since clear nutritional benefits for feeding in the more exposed/risky upland forest seem to be lacking.

As for mangrove phytochemical characteristics, our sample of leaves was too small to allow for statistical comparisons to be made; however, the two species collected show nitrogen contents comparable to forest and freshwater swamp trees and lower fibre contents. This would make mangrove resources of potentially high value for folivores and would correspond to other studies reporting similar nitrogen content in upland forest and mangrove species (Agoramoorthy & Hsu 2005; De Lacerda *et al.* 1986; but see Ellison 2002). However, in our analysis, mangrove leaves also show substantially higher median values of tannins and polyphenolics, which are known to work as a deterrent to folivory (Ganzhorn 1988; Glander 1982). If our preliminary result is confirmed by future analyses of larger datasets, then this would support the hypothesis that mangroves do not represent a food source that lemurs may rely upon extensively or exclusively (Birkinshaw & Colquhoun 2003). High values of tannins and phenolics may induce thirst in mammals as animals need water to flush out salt and secondary plant metabolites (Glander 1982). For example, water consumption was found to be associated with mangrove leaf consumption and mangrove use in Zanzibar red colobus (*Procolobus kirkii*) (Nowak 2008). In Borneo, proboscis monkeys (*Nasalis larvatus*) occupy mangroves, but feed preferentially on non-mangrove leaves even though mangrove and non-mangrove leaves do not differ in protein concentration (Agoramoorthy & Hsu 2005; Yeager *et al.* 1998).We may hypothesize that some lemur species, such as *Propithecus* spp., may tolerate higher secondary component intakes and thus have more continuous access to mangrove habitats. However, this suggestion should be regarded as highly speculative until more data are collected.

Mangroves extent and diversity relative to other forest types in Madagascar are low, and world-wide comparative analyses indicate that species richness in any given mangrove habitat is correlated with its size (Ellison *et al*. 1999). Thus, the limited variety of plants in Malagasy mangrove swamps may be an additional factor which explains the presence of only subsets of lemur communities (or lack thereof) in these areas and lemurs' need to rely on other forest types. That said, mangrove deforestation rate in Madagascar is lower compared with other forested habitats and these swamps may thus represent a last refuge in areas where most other types of forest have disappeared (Giri & Muhlhausen 2008; but see also Jones 2013). Given that it is not known to what extent mangroves can be used for dietary complements, it seems crucial to conserve the matrix of mangroves and other forest types in an integrated way. The need to protect these neglected areas should be seriously considered in lieu of the growing threats to forests from expanding agriculture, aquaculture, and logging (Jones 2013).

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References

Agoramoorthy, G. & Hsu, M.J. 2005.Borneo's proboscis monkey-a study of its diet of mineral and phytochemical concentrations. *Scientific Correspondences* 89: 454–457.

Andriamaharoa, H., Birkinshaw, C. & Reza, L. 2010. Day-time feeding ecology of *Eulemur cinereiceps* in the Agnalazaha Forest, Mahabo-Mananivo, Madagascar. *Madagascar Conservation & Development* 5(1): 55-63.

Birkinshaw, C.R. & Colquhoun, I. 2003. Lemur food plants. In: Natural History of Madagascar. Goodman S. & Benstead J. (Eds.). Chicago: Chicago University Press. Pp. 1207-1220.

Decary, R. 1930. *La Faune Malgache*. Paris, Payot.

de Lacerda, L.D., José, D.V., de Rezenda, C.E., Francisco, M.C.F., Wasserman, J.C. & Martins, J.C. 1986. Leaf chemical characteristics affecting herbivory in a new world mangrove forest. *Biotropica* 18: 350-355.

Donati, G., Kesch, K., Ndremifidy, K., Schmidt, S.L., Ramanamanjato, J.-B., Borgognini-Tarli, S.M. & Ganzhorn, J.U. 2011. Better few than hungry: flexible feeding ecology of collared lemurs *Eulemur collaris* in littoral forest fragments. *PLoS ONE* 6(5): e19807. doi:10.1371/journal.pone.0019807.

Ellison, A.M. 2002. Macroecology of mangroves: large-scale patterns and processes in tropical coastal forests. *Trees* 16: 181-194.

Ellison, A.M., Farnsworth, E.J. & Merkt, R.E. 1999. Origins of mangrove ecosystems and the mangrove biodiversity anomaly. *Global Ecology and Biogeography* 8: 95-115.

Eppley, T.M., Verjans, E. & Donati, G. 2011. Coping with low-quality diets: a first account of the feeding ecology of the southern gentle lemur, *Hapalemur meridionalis*, in the Mandena littoral forest, southeast Madagascar. *Primates* 52: 7-13.

Galat-Luong, A., Galat, G. 2005. Conservation and survival adaptations of Temminck's red colobus *(Procolobus badius temmincki)* , in Senegal. *International Journal of Primatology* 26: 585–603.

Ganzhorn, J.U. 1988. Food partitioning among Malagasy primates. *Oecologia* 75: 436-450.

Ganzhorn, J.U., Andrianasolo, T., Andrianjazalahatra, T., Donati, G., Fietz, J., Lahann, P., Norscia, I., Rakotondranary, J., Rakotondratsima, B.M., Ralison, J., Ramarokoto, R.E.A.F., Randriamanga, S., Rasarimanana, S., Rakotosamimanana, B., Ramanamanjato, J.-B., Randria, G., Rasolofoharivelo, M.T., Razanahoera-Rakotomalala, M., Schmid, J. & Sommer, S. 2007. Lemurs in evergreen littoral forest fragments. In: Biodiversity, ecology, and conservation of the littoral ecosystems in southeastern Madagascar, Tolagnaro (Fort

Dauphin). Ganzhorn J.U., Goodman S.M. & Vincelette M. (Eds.). Washington, D.C.: Smithsonian Institution. Pp 223–225.

Gauthier, C.A., Deniaud, J.L., Leclerc-Cassan, M., Rakotomalala, M., Razafindramanana, S. & Renson, G. 2000. Observations of lemurs in the mangroves of North-West Madagascar. *Folia Primatologica* 71: 267.

Gauthier, C.A., Deniaud, J.L., Rakotomalala, M., Razafindramanana, S. & Renson, G. 1999. Note sur la découverte d'un nouvel habitat occupé par les propithéques couronnés (*Propithecus verreauxi coronatus*) au nord-ouest de Madagascar. *Primatologie* 2: 821-827.

Giri, C. & Muhlhausen, J. 2008. Mangrove forest distributions and dynamics in Madagascar (1975–2005). *Sensor* 8: 2004-2017.

Giri, C., Ochieng, E., Tieszen, L. L., Zhu, Z., Singh, A., Loveland, T., Masek, J. & Duke, N. 2011. Status and distribution of mangrove forests of the world using earth observation satellite data. *Global Ecology and Biography* 20: 154–159. (doi:10.1111/j.1466-8238.2010.00584.x)

Glander, K. E. 1982. The impact of plant secondary compounds on primate feeding behavior, *Yearbook of Physical Anthropology* 25: 1-18.

Hawkins, A.F.A., Durbin, J.C. & Reid, D.B. 1998. The primates of the Baly Bay area, North-Western Madagascar. *Folia Primatologica* 69: 337-345.

Jones, T.G. 2013. Shining a light on Madagascar's mangroves. *Madagascar Conservation and Development* 8: 4-6.

Matsuda, I., Tuuga, A., Higashi, S. 2009. Ranging behaviour of proboscis monkeys in a riverine forest with special reference to ranging in inland forest. *International Journal of Primatology* 30: 313-325.

Matsuda, I., Tuuga, A. & Bernard, H. 2011 Riverine refuging by proboscis monkeys (*Nasalis larvatus*) and sympatric primates: implications for adaptive benefits of the riverine habitats. *Mammalian Biology* 76: 165-171.

Mutschler, T. 1999. Folivory in a small-bodied lemur: the nutrition of the Alaotran gentle lemur (*Hapalemur griseus alaotrensis*). In: New directions in lemur studies. Rasamimanana H., Rakotosamimanana B., Ganzhorn J.U. & Goodman S.M. (Eds.). New York: Kluwer Academic/Plenum Publishing. Pp. 221–239.

Mutschler, T., Feistner, A.T.C. & Nievergelt, C.M. 1998. Preliminary field data on group size, diet and activity in the Alaotran gentle lemur *Hapalemur griseus alaotrensis*. *Folia Primatologica* 69: 325–330.

Nowak, K. 2008. Frequent water drinking by Zanzibar red colobus (*Procolobus kirkii*) in a mangrove forest refuge. *American Journal of Primatology* 70:1081–1092.

Nowak, K. 2012. Mangrove and peat swamp forests: refuge habitats for primates and felids. *Folia Primatologica* 83: 361–376.

Roger, E. & Andrianasolo, M. 2003. Mangroves and salt marshes. In: Natural History of Madagascar. Goodman S. & Benstead J. (Eds.). Chicago: Chicago University Press. Pp. 209-210.

Rowe, N. & Myers, M. 2011. *All the World's Primates*.URL:www.alltheworldsprimates.org.

Schmid, J. & Kappeler, P.M. 1994. Sympatric Mouse Lemurs (*Microcebus* spp.) in Western Madagascar. *Folia Primatologica* 63: 162-170.

Tan, C.L. 1999. Group composition, home range size, and diet of three sympatric bamboo lemur species (Genus *Hapalemur*) in Ranomafana National Park, Madagascar. *International Journal of Primatology* 20: 547–566.

Tan, C.L. 2006. Behavior and ecology of gentle lemurs (genus *Hapalemur*). In: Lemurs: ecology and adaptation. Gould L. & Sauther M. (Eds.).New York: Springer. Pp. 369–381.

Vannucci, M. 2001. What is so special about mangroves? *Brazilian Journal of Biology* 61: 599-603.

Yeager, C.P. 1989. Feeding ecology of the proboscis monkey (*Nasalis larvatus*). *International Journal of Primatology* 10: 497‐530.

Table 1. Phytochemical characteristics of mature leaves from upland littoral forest, inundated swamp, and mangroves in south-east Madagascar. N = nitrogen; SP = soluble protein; SC = soluble carbohydrates; NDF = neutral detergent fibre; ADF = acid detergent fibre. Values are medians and quartiles.

Habitat	N	SP	SC	NDF	ADF	Tannins	Phenol	Ash
Forest	**1.25**	**2.72**	**6.50**	**42.01**	**30.89**	**0.20**	**2.74**	**7.18**
(n=11)	1.15-1.49	2.08-4.13	4.68-9.77	38.59-51.48	26.20-34.01	0.00-0.65	1.58-3.99	5.19-9.89
Swamp	**1.01**	**2.97**	**5.13**	**40.73**	**33.43**	**0.00**	**1.72**	**6.82**
(n=10)	0.78-1.24	1.35-3.40	4.66-6.76	35.68-49.93	24.43-39.39	0.00-0.34	0.73-2.48	5.45-10.46
Mangroves	**1.36**	**3.87**	**12.01**	**30.79**	**19.20**	**1.45**	**4.63**	**9.24**
(n=2)	1.23-1.50	3.08-4.65	11.08-12.22	28.92-32.66	18.75-19.64	0.72-2.1	4.49-4.76	8.64-9.85

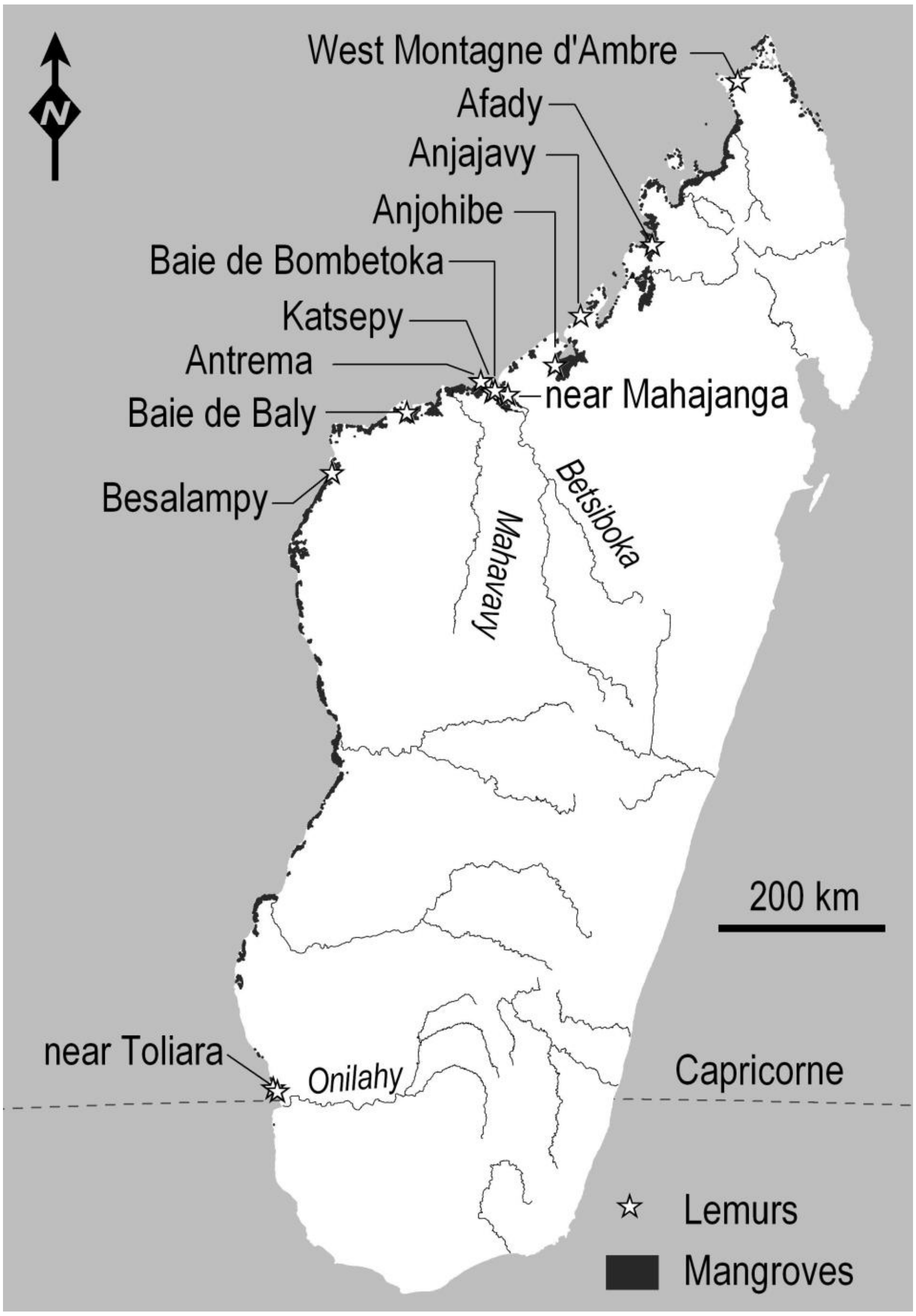

Fig. 1. Mangrove distribution in Madagascar and locations where lemurs have been observed. The observations labelled as "near Toliara" include the following sites: Ambanilia, Andalo, Andoharano, Andriambe, Antanifotsy, Antsifotse, Lovokampy, and Saint Augustin.