

ARTICLE

<http://dx.doi.org/10.4314/mcd.v10i2.3>

The value of the spineless monkey orange tree (*Strychnos madagascariensis*) for conservation of northern sportive lemurs (*Lepilemur milanoii* and *L. ankaranensis*)

Jordi Salmona^I, Matthew Banks^{II}, Tantely Nirina Ralantoharijaona^{III}, Emmanuel Rasolondraibe^{III}, Radavison Zaranaina^{III}, Ando Rakotonanahary^{III}, Sébastien Wohlhauser^{IV}, Brent J. Sewall^{III}, Lounès Chikhji^{V, VI}

Correspondence:

Jordi Salmona
Instituto Gulbenkian de Ciência, Oeiras, Portugal
E-mail: jordi.salmona@gmail.com

ABSTRACT

Tree hollows provide shelters for a large number of forest-dependent vertebrate species worldwide. In Madagascar, where high historical and ongoing rates of deforestation and forest degradation are responsible for a major environmental crisis, reduced availability of tree hollows may lead to declines in hollow-dwelling species such as sportive lemurs, one of the most species-rich groups of lemurs. The identification of native tree species used by hollow-dwelling lemurs may facilitate targeted management interventions to maintain or improve habitat quality for these lemurs. During an extensive survey of sportive lemurs in northern Madagascar, we identified one tree species, *Strychnos madagascariensis* (Loganiaceae), the spineless monkey orange tree, as a principal sleeping site of two species of northern sportive lemurs, *Lepilemur ankaranensis* and *L. milanoii* (Lepilemuridae). This tree species represented 32.5% (n=150) of the 458 sleeping sites recorded. This result suggests that *S. madagascariensis* may be valuable for the conservation of hollow-dwelling lemurs.

RÉSUMÉ

De nombreux vertébrés forestiers à travers le monde trouvent refuge dans des cavités et des trous d'arbres. À Madagascar, les taux de déforestation historiques et actuels sont responsables d'une crise environnementale majeure. Dans ce contexte, une disponibilité réduite d'arbres pourvus de cavités pourrait entraîner le déclin des espèces dépendant de ces abris comme par exemple les lépilemurs, un des groupes de lémuriens les plus riches en espèces. L'identification des espèces d'arbres indigènes creusés de trous et utilisés par les lémuriens pourrait faciliter la mise en place d'actions de conservation ayant pour but de maintenir ou améliorer l'habitat de ces lémuriens. Au cours d'une étude réalisée dans le Nord de Madagascar, nous avons observé

que *Strychnos madagascariensis* (Loganiaceae) était fréquemment utilisé comme site dodoir par les deux espèces de lépilemurs présentes, *Lepilemur ankaranensis* and *L. milanoii* (Lepilemuridae). Cette espèce d'arbre concernait 32,5% (n = 150) des 458 sites dodoirs enregistrés. Ce résultat suggère que *S. madagascariensis* pourrait être important pour la conservation des lémuriens dépendant de sites dodoirs.

INTRODUCTION

The identification of important interspecific interactions can be of significant value for conservation management (Caro 2007, Berger-Tal et al. 2011). For instance, knowing the major plant species on which an endangered species relies for feeding, resting or dwelling can be of particular importance when establishing conservation, reforestation and/or timber and forest use plans (Rose et al. 2001, Lindenmayer et al. 2006). Sleeping sites are crucial for the survival of terrestrial vertebrates (Anderson 1998), and in particular burrows, nests, tree hollows, and other structures provide protection from climatic extremes (e.g., *Cheirogaleus* sp., Dausmann et al. 2004) and predators (e.g., *Allocebus trichotis*, Biebow et al. 2009). Tree hollows are a critical structural attribute of native forests worldwide and a large number of vertebrate species (e.g., Cheirogaleidae family of primates, nocturnal birds of the Strigidae family, etc.) are closely associated with these hollows (Newton 1994, Gibbons and Lindenmayer 2002).

Primates spend about half of their life at sleeping sites, and their use has been suggested to be important for understanding the diversity of primates' adaptations to their environment (Anderson 1998). In Madagascar two families of lemurs (Cheirogaleidae and Lepilemuridae) are known to extensively use tree hollows (Mittermeier et al. 2010).

I Instituto Gulbenkian de Ciência, Rua da Quinta Grande 6, 2781-901 Oeiras, Portugal
II Department of Biology, Temple University, 1900 N. 12th St., Philadelphia, Pennsylvania 19122, United States
III Université de Mahajanga, Faculté des Sciences, BP 652, Mahajanga 401, Madagascar
IV -, Madagascar
V Laboratoire Evolution & Diversité Biologique, UMR 5174 CNRS – Université Paul Sabatier, Toulouse, France
VI Université de Toulouse, UMR 5174 EDB, Toulouse, France



Madagascar Conservation & Development is the journal of Indian Ocean e-Ink. It is produced under the responsibility of this institution. The views expressed in contributions to MCD are solely those of the authors and not those of the journal editors or the publisher.

All the Issues and articles are freely available at <http://www.journalmcd.com>



Contact Journal MCD
info@journalmcd.net for general inquiries regarding MCD
funding@journalmcd.net to support the journal

Madagascar Conservation & Development
 Institute and Museum of Anthropology
 University of Zurich
 Winterthurerstrasse 190
 CH-8057 Zurich
 Switzerland

io@i

Indian Ocean e-Ink
 Promoting African Publishing and Education
www.ioeink.com

 MISSOURI BOTANICAL GARDEN

Missouri Botanical Garden (MBG)
 Madagascar Research and Conservation Program
 BP 3391
 Antananarivo, 101, Madagascar

Lepilemur milanoii and *L. ankaranensis* are two sportive lemur species of the family Lepilemuridae with neighboring and partly overlapping distributions in northern Madagascar (Figure 1, Louis Jr. et al. 2006). They can be very abundant in some forests (e.g., in Ankarana and Solaniampilana, Hawkins et al. 1990, Salmona et al. 2014a), yet, little is known about the biology of these nocturnal species. Apart from several estimates of their population densities and population sizes (Meyers and Ratsirarson 1989, Hawkins et al. 1990, Meyler et al. 2012, Salmona et al. 2014a), their ecology and behavior remains understudied. In particular, while it is known that these species use tree sleeping sites during the day (Mittermeier et al. 2010), no specific study has yet been published that identifies the tree species used as sleeping sites in these regions. However a large body of literature covers the biology and behavioral ecology of several other sportive lemur species. Schmid and Ganzhorn (1996) studied for instance *L. ruficaudatus* and showed that they have the lowest basal metabolic rate of all folivorous mammals, which may allow them to subsist on leaves with a high toxic allelochemicals but low energy and protein content. This further suggests that sleeping sites may provide sportive lemurs shelters to limit energy expenses and maintain low diurnal basal metabolism in adverse climatic conditions. Indeed, the presence of Sahamalaza sportive lemurs (*L. sahamalazensis*) in tree hollows was negatively correlated to rainfall, and tree hollows were reported as not occupied at all in the rainy season (Seiler 2012). This stresses the function of potential tree hollows as a kind of 'dry season residence' in dry regions of Madagascar. Moreover it may also serve as shelter from aerial and terrestrial predators (Fichtel 2007, Seiler et al. 2013). Several studies reported the use of a diversity of sleeping sites per individual and the shared use of sleeping sites by partners or relatives (Rasoloharijaona et al. 2003, Zinner et al. 2003) in some species and solitary in use in others (Rasoloharijaona et al. 2008, Seiler et al. 2013). The spatial repartition of individuals has been repeatedly linked to sleeping site availability for several species (Rasoloharijaona et al. 2003, 2006, Zinner et al. 2003, Rasoloharijaona et al. 2008) and is considered to be an important factor of the low overlap in home ranges of non-mated, unrelated individuals. Rasoloharijaona et al. (2010) suggested that sleeping sites may be limited and defendable resources providing reproductive benefits, and among the main drivers of ritualized aggressive loud call displays and tree gouging behavior used for territory and resource defense.

Forest quality and maturity may affect tree hollow availability as old mature forests are more likely to harbor old and hollowed trees (Gibbons and Lindenmayer 2002). The presence and density of sportive lemur populations may thus depend on the existence of old forests providing suitable food, substrates for locomotion, and sleeping sites (Rasoloharijaona et al. 2008, Seiler et al. 2013).

During an extensive survey whose primary goal was to assess population densities and carry out genetic sampling of sportive lemurs in northern Madagascar, we also noticed the prevalence of the use of one tree species as a sleeping site. As a first step toward describing the roosting ecology of the northern sportive lemurs *L. milanoii* and *L. ankaranensis*, we report in this paper the prevalence of the use of this species, the spineless monkey orange tree *Strychnos madagascariensis* (Loganiaceae) for sleeping sites by these two lemur species. Our aim was not to provide a detailed analysis of sleeping sites or tree species but rather call attention to one particularly striking species.

MATERIAL AND METHODS

STUDY REGION. We visited all 17 major forests within the known distribution of the two *Lepilemur* species (Figure 1) during the dry seasons (April–November) of 2011, 2012, and 2013. Specifically, we visited the Loky-Manambato region (Daraina) and the Andrafiarena-Andavakoera massif, both Category V protected areas managed by the NGO Fanamby, as well as the Ankarana National Park and the Analamerana Special Reserve, both managed by Madagascar National Parks (Figure 1). These study sites have been previously described in detail by several authors (Hawkins et al. 1990, Goodman and Wilmé 2006a, Ranirison 2006, Burivalova 2011). Briefly, these are mainly fragmented dry forests, frequently surrounded and/or connected by riparian corridors or smaller fragments. Yet, some forests in the south of the Loky-Manambato region (Binara, Antsahabe, Bobankora) as well as some valleys of Andrafiarena, and some corridors of the Ankarana Plateau harbor sub-humid forests (Moat and Smith 2007). While most forests of the Loky-Manambato region lie on distinct granito-migmatic blocks separated by alluvium, Ankarana is a typical *tsingy* limestone plateau, bisected by basalt corridors, that extends in the east to the limestone blocks in the northern part of Analamerana and Andrafiarena. The southern part of Andrafiarena forest lies above sandstone soil and Andavakoera basement rocks (igneous and metamorphic, Goodman and Wilmé 2006b).

FIELD PROCEDURES. During diurnal surveys we actively and opportunistically (during other research activities) searched for sportive lemurs. From most of the 36 camp sites, surveys spread, when allowed by the topography, in a star-like manner, and included transects, existing trails, and areas off trail. Additional maps of all surveyed sites and recorded Global Positioning System (GPS) coordinates and other description of the field are available in Salmona (2014), and in Salmona et al. (2013, 2014a,b). When a sportive lemur was spotted we recorded the geographical position of its sleep site using a Garmin® Etrex-H GPS receiver (maximum error: ±5m) and the WGS84 referencing system. The vernacular names of tree species (and scientific names when known) were recorded for all sleeping site trees by trained botanical guides experienced in the regional inventory of native plants. In particular, *Strychnos madagascariensis* was identified on the basis of distinctive characteristics of its leaves and fruits (Schatz 2001). Vernacular names sometimes varied from site to site. For instance *S. madagascariensis* was called synonymously as *vakokoa*, *vakakoagna*, *vakakoana*, *vahipendela*; other vernacular names for single species may have varied similarly.

Our experience was that the two sportive lemur species (*Lepilemur milanoii* and *L. ankaranensis*) are not distinguishable morphometrically. Attribution of these lemurs and their sleeping sites to either sportive lemur species is therefore based on the schematic approximate distribution range (Figure 1) as defined by Louis Jr. et al.'s (2006) taxonomy. According to these authors, however, the two species occur in sympatry in the Andrafiarena forest (Figure 1). Our observations of *Lepilemur* in the Andrafiarena forest hence cannot in theory be attributed without error to either of the two species. To avoid confusion, therefore, we exclude Andrafiarena observations from species-level results, but included it in overall results. Further taxonomic work might help to clarify the exact distribution of these species. For each species and forest we calculated the percentages of sleeping sites in *S. madagascariensis* relative to the total number of sleeping sites. We

further compared the proportion of *S. madagascariensis* and other tree taxa used by each sportive lemur species using a Chi-squared test.

STRYCHNOS MADAGASCARIENSIS DISTRIBUTION IN MADAGASCAR. To foster potential interest from other researchers and forest conservation managers within a broader geographic context, we also clarified the distribution of *S. madagascariensis* in Madagascar on the basis of existing collections of this tree species. We used the Tropicos® specimen online data base <<http://www.tropicos.org/>>, which lists 179 specimens in Madagascar from several institutions. The map of the distribution (Figure 1) was produced using the online SimpleMappr mapping tool (Shorthouse 2010).

RESULTS

Out of 458 sleeping sites, four records (0.6%) were vegetative tangles; the rest were in tree hollows. *Strychnos madagascariensis* represented 150 observations (32.5% of the total, Table 1). There was no difference in the frequency of use of *S. madagascariensis* by the two species of sportive lemurs (*Lepilemur milanoii*: 37.4%, 104 out of 278 observations; *L. ankaranensis*: 35.5%, 43 out of 121 observations, Table 1, Chi-squared test p -value = 1). *S. madagascariensis* was by far the tree species most used by sportive lemurs, with about seven times more records than the second most frequently used category of trees. For *L. milanoii*, mampay trees

(corresponding to several genera from the Fabaceae family Schatz 2001; 13 observations) were the second-most used species of tree. For *L. ankaranensis*, hazoatambo trees (probably *Sarcolaena* spp.; 21 observations) were the second-most used species of tree.

Table 1 and Figure 1 show that the proportion of *Strychnos madagascariensis* is not evenly distributed within and between forests. If we discard sites with very few (≤ 3) observations, the proportion of *S. madagascariensis* sleeping sites ranges from 12.5% in the wet mountainous forest of Binara to 68.2% in the dry forest of Solaniampilana for *Lepilemur milanoii*, and from 5.1% in Andriamena to 45.9% in Analamerana Special Reserve for *L. ankaranensis*. The geographical distribution of observations (Figure 1) shows that the western lowland edge of the Ankarana plateau, covered with very dry forest, the Solaniampilana and Ambohitsitondroina dry forest and the forest of the Analamerana Special Reserve, harbor high proportions of observations of *S. madagascariensis* sleeping sites.

There are a few local exceptions to this regional pattern. The Andriamena forest had the lowest frequency of *Strychnos madagascariensis* sleeping sites for *Lepilemur ankaranensis* or *L. milanoii*; rather, most sleeping sites were in hazoatambo trees (*Sarcolaena* sp.; 20 out of 21 observations). Since in this area, *Sarcolaena* sp. seems to dominate parts of the landscape, it is possible that *Strychnos madagascariensis* is present at low density. In the core of Antsahabe and Binara forests, where the use of *S. madagascariensis* sleeping sites was low for *L. milanoii*, tree hollows

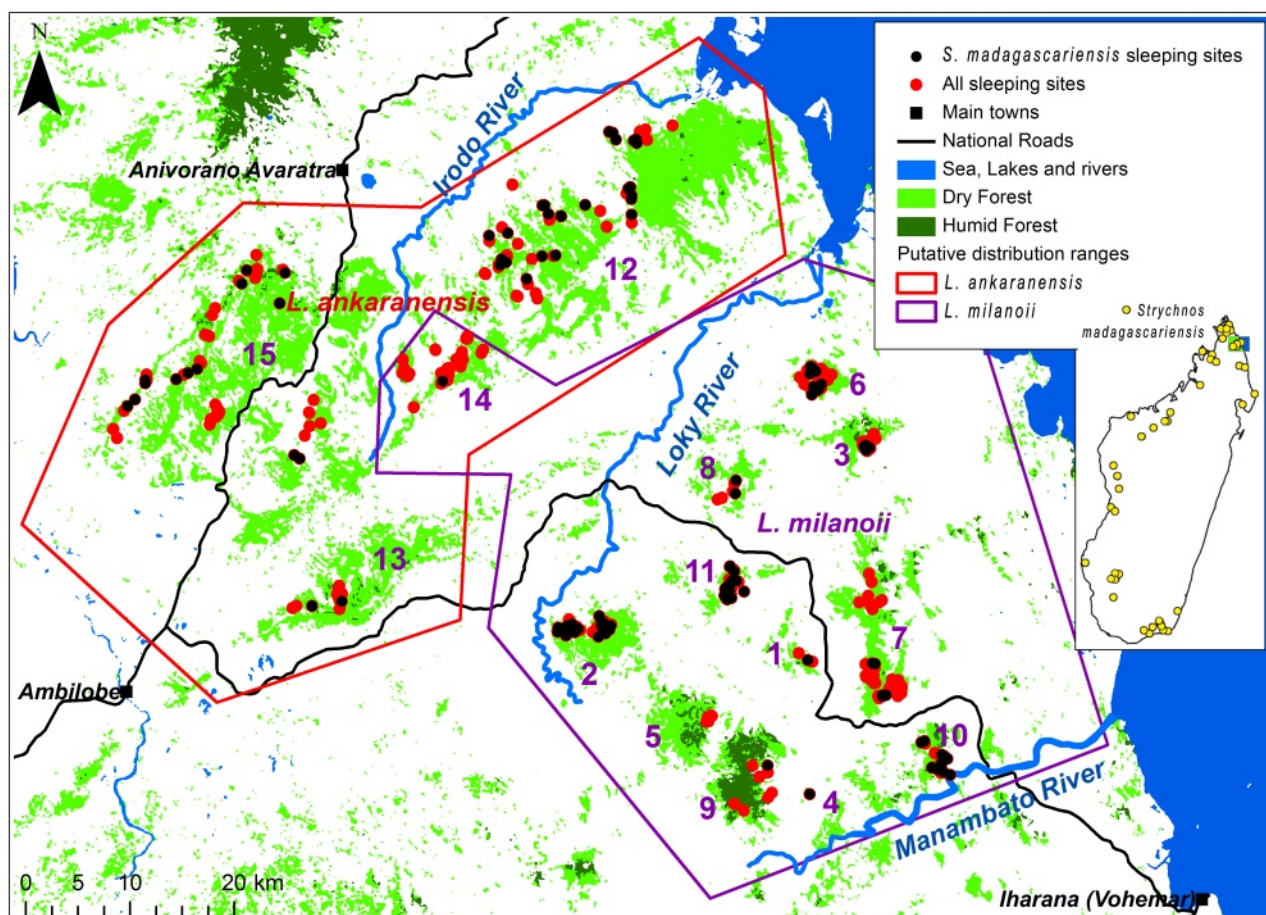


Figure 1. Studied sportive lemur sleeping sites. (Purple numbers correspond to locality numbers (ID) mentioned in Table 1. The schematic approximate distribution ranges are based on Louis Jr. et al. 2006 taxonomy. Tattersall (2007) suggested that the *Lepilemur* species reported by Louis Jr. et al. (2006), all diagnosed exclusively on genetic distance, should be treated with caution. Inset map showing the distribution of *Strychnos madagascariensis* specimens' origin within Madagascar (western areas tend to be the drier areas of Madagascar, eastern areas tend to be wetter; the northern tip of Madagascar tends to be dry or transitional. Modified from: Catalogue of the Vascular Plants of Madagascar. Tropicos.org. Missouri Botanical Garden. 14 May 2015).

Table 1. Number and proportion of *Strychnos madagascariensis* sleeping sites per surveyed forest fragment. (Id = forest identification numbers as purple numbers in Figure 1; *S. mad* = *Strychnos madagascariensis* occurrences; % = percentage of *S. madagascariensis* occurrences out of all sleeping site records; Forest type: D = Dry, T = Transitional, H = Humid, D/T or T/H = site that includes both forest types; Protected Area: L-M = Loky Manambato managed by Fanamby in the SAVA Region, ASR = Analamerana Special Reserve, and ANP = Ankarana National Park, both managed by Madagascar National Park in the DIANA Region, A-A = Andrafiomena-Andavakoera managed by Fanamby in the DIANA Region. Attribution to either sportive lemur species (*L. milanoii* and *L. ankaranensis*) is based on the schematic approximate distribution range (Figure 1) as defined by taxonomy by Louis et al. (2006), with Andrafiomena records assigned to *L. ankaranensis* or *L. milanoii*)

Species	Forest	Id	S. mad	all trees	%	Forest type	Protected area
<i>L. milanoii</i>	Ambilondambo	1	1	3	33.3	D	L-M
<i>L. milanoii</i>	Ambohitsitondroina	2	23	39	59.0	D	L-M
<i>L. milanoii</i>	Ampondrabe	3	12	45	26.7	D/T	L-M
<i>L. milanoii</i>	Ankaramy	4	1	1	100.0	D/T	L-M
<i>L. milanoii</i>	Antsahabe	5	0	3	0.0	T/H	L-M
<i>L. milanoii</i>	Antsaharaingy	6	14	45	31.1	D	L-M
<i>L. milanoii</i>	Bekaraoka	7	2	25	8.0	D/T	L-M
<i>L. milanoii</i>	Benanofy	8	2	8	25.0	D	L-M
<i>L. milanoii</i>	Binara	9	1	8	12.5	T/H	L-M
<i>L. milanoii</i>	Bobankora	10	18	57	31.6	T/H	L-M
<i>L. milanoii</i>	Solaniampilana	11	30	44	68.2	D	L-M
Sub total <i>L. milanoii</i>			104	278	37.4		
<i>L. ankaranensis</i>	Analamerana	12	28	61	45.9	D/T	ASR
<i>L. ankaranensis</i>	Andavakoera	13	3	16	18.8	D/T	A-A
<i>L. ankaranensis</i>	Ankarana	15	12	44	27.3	D/T	ANP
Sub total <i>L. ankaranensis</i>			43	121	35.5		
<i>L. spp</i>	Andrafiomena	14	3	59	5.1	D/T	A-A
Total			150	458	32.8		

were rare overall (J. Salmona and T. Ralantoharijaona pers. obs.); we rarely observed sportive lemurs during diurnal surveys, and of the five sportive lemur individuals that were observed in Antsahabe, three were sleeping or resting in dense vegetation, not in tree hollows.

Records of collections of *Strychnos madagascariensis*, at an island-wide scale in Madagascar show that the species has been mostly collected in the western parts of the island, where forests are generally drier (Figure 1). However, a few collections of the species have been obtained from the eastern coastal areas, where forests are generally more humid.

DISCUSSION

Consistent with previous research suggesting that some sportive lemurs prefer tree hollow shelters over open sleeping sites in dense vegetation (Rasoloharijaona et al. 2008), we found that northern sportive lemurs chose tree hollow shelters almost exclusively. However, since sportive lemurs resting in dense vegetation may be more difficult to detect than in tree hollows, it would be important to confirm that the observed percentages are not dramatically affected by this possible differential detection.

Strychnos madagascariensis is often used as a sleeping site. However, to state that it is preferentially chosen by sportive lemurs we would need data on both tree species and hollowed tree frequency in all of the visited forests. Given that we did not collect such data, our study remains preliminary. However our findings show that northern sportive lemurs were found in *S. madagascariensis* hollows with much higher frequency than in any other tree species. This occurred for both *Lepilemur ankaranensis* and *L. milanoii*, and occurred in the large majority of forests across northern Madagascar, especially in dry and transitional forest types.

Further study might help determine the hollow characteristics that are associated with *S. madagascariensis* use as a sleep-

ing site. In particular, parameters such as the height of shelter, the width and depth of the hollow, as well as the density of the cover above the tree hollow has been shown to influence sleeping site choice in *Lepilemur sahamalazensis* (Seiler et al. 2013).

A DRY AND TRANSITIONAL FORESTS TREE? The geographic focus of this study was on northern Madagascar, within the ranges of two species of northern sportive lemurs. However, given that *Strychnos madagascariensis* is distributed across the northern, western and southern (e.g., dry and subarid) regions of the island suggests that this tree species is likely used by other *Lepilemur* species. From north to south it is reported and might particularly benefit hollow-dwelling fauna in the following localities: Analamerana (this study), Andrafiomena (Burivalova 2011, this study), Ankarana National Park (Wilson et al. 1989, this study), the Loky-Manambato region (this study), Sahamalaza peninsula (Schwitzer et al. 2007), Nosy Faly Peninsula (Simmen et al. 2007), Anjajavy (JS and LC unpub. data), Ankarafantsika (Rajolison et al. 2002, Rakotodratsimba 2008), Antrema (Ramanankirahina 2004), the northern banks of the Mahavavy river (Boeny region, JS and LC unpub. data), Kirindy (Ganzhorn 2002, Dausmann et al. 2008), and Berenty, Antserananomby, and Beza-Mahafaly (Simmen et al. 2006). Further, the geographic origins of herbaria specimens of *S. madagascariensis* confirm that it has a wide distribution. Its distribution covers mostly dry and transitional forests on the northern tip and mostly dry forests in the western parts of the island. This is consistent with the deciduous to semi-persistent characteristic of *S. madagascariensis*' leaves (Schatz 2001), which suggest that it is adapted to dry or transitional forests. However the few specimens from more humid localities (e.g., on the Masoala peninsula, Figure 1, Inset) suggest that its presence and role as a sleeping site for Malagasy fauna in humid forests also need further investigation.

A VALUABLE SLEEPING SITE FOR LEMURS? From the 150 *Strychnos madagascariensis* sleeping site observations, we noted that this tree shows a high propensity for hollow formation. It was not rare for trees to harbor several hollows of various sizes, hollows with several entries and sizes corresponding to most of, if not the entire trunk height. Altogether, *S. madagascariensis* could provide important shelter resources for tree-hollow-dwelling fauna in Madagascar. For instance, in what is to our knowledge the only two other studies to date systematically reporting tree species used by lemurs as resting or sleeping sites, *S. madagascariensis* was identified as the most preferentially chosen by *Lepilemur ruficaudatus* (D. Zinner pers. com.) in Kirindy and was among the tree species predominantly used by *Cheirogaleus medius* (Dausmann 2013) as a resting/hibernating site in Kirindy in southwestern Madagascar. We hope that our study will generate interest among other researchers in improving understanding of other species that may also benefit from *S. madagascariensis* tree hollows.

Apart from protection against predators (Anderson 1998, Biebow et al. 2009), tree hollow sleeping sites enable some species to tolerate climatic extremes (Dausmann et al. 2004). Hibernation and daily torpor of lemurs of the Cheirogaleidae family and the low resting metabolic rates of sportive lemurs (Lepilemuridae), may have evolved as strategies to counter the challenges of pronounced seasonality with food and water shortage (Drack et al. 1999, Wright 1999, Dausmann et al. 2004, Blanco et al. 2013, Kobbe and Dausmann 2009). Selection of suitable tree hollows as

sleeping sites may provide thermoregulatory benefits for these lemur species by shielding them from rain, wind and strong fluctuations in temperature (Dausmann 2013); but see also Seiler et al. (2013) who reported that *Lepilemur sahamalazensis* was not observed in hollows during the rainy season.

In addition, *Strychnos madagascariensis* leaves and fruits were reported to enter the diet of *Lepilemur ruficaudatus* in Kirindy (Ganzhorn 2002), and of *L. edwardsii* in Ankarafantsika (Thalman 2001). Its leaves are consumed by *Microcebus ravelobensis*, *Propithecus coronatus* (Ramanankirahina 2004), *P. verreauxi* (Simmen et al. 2003), *P. tattersalli* (Rasolondraibe 2011) and *Lemur catta* (LaFleur and Gould 2009). Its fruits are commonly eaten by *Eulemur sanfordi* and *E. coronatus* (Wilson et al. 1989), and are part of the diet of *E. macaco* (Simmen et al. 2007), *E. fulvus* (Sato 2012, Sato et al. 2014), *E. flavifrons* (Volampeno et al. 2011), *E. rufifrons* (Dausmann et al. 2008), *L. catta* (Simmen et al. 2003, 2006), *M. ravelobensis*, *M. murinus* (Thorén et al. 2011), *P. verreauxi* (Ralisomalala 1996 in Dausmann et al. 2008) and *P. perrieri* (Banks 2013). The fruits are also a resource for rodents (*Hypogeomys antimena*, *Eliurus* spp., *Macrotarsomys* spp. and *Rattus* spp.), bushpigs (*Potamochoerus larvatus*), invertebrates (e.g., *Aphaenogaster swammerdami* ants (Dausmann et al. 2008) and birds (as shown for Southern African brown-headed parrot, *Poicephalus cryptoxanthus* (Taylor and Perrin 2006)). This suggests that the species may be an important food resource for a diversity of Malagasy animals.

More speculatively, a potential hidden benefit to some vertebrate species of these trees could come from the anti-parasitic properties of toxic compounds in *Strychnos madagascariensis* leaves, bark and seeds; the *Strychnos* genus produces strychnine-related alkaloids (Philippe et al. 2004). In particular, *S. madagascariensis* leaves have strong toxic and repellent effects against ticks (Habeeb 2010). Leaf decoctions and/or dry pounded bark of *S. madagascariensis* are traditionally used in eastern Africa against skin sores and ringworm infections caused by bacteria and fungi (De Wet et al. 2013). Additionally, the stem and leaves of several *Strychnos* species exhibit antiplasmodial activity (Philippe et al. 2005). Further study is needed to determine the potential role of this tree species in fighting parasites in lemurs and other vertebrate species, but one could hypothesize that sleeping in a *S. madagascariensis* hollow or (for vertebrates able to detoxify its alkaloids) ingesting its leaves, stems, or seeds may present an anti-parasitic effect.

CONCLUSION

The extensive use of tree hollows by northern sportive lemurs suggests that they strongly depend on the availability of sleeping sites. The extensive historical habitat loss in Madagascar (Harper et al. 2007), coupled with the ongoing (0.4–2.5% per year) and predicted high rates of deforestation in Madagascar (up to +1.17% per year; Vieilledent et al. 2013) are challenging current lemur conservation (Schwitzer et al. 2014). Further, the often fragmented and isolated state of remaining habitat, and ominous threats from global warming throughout the island (Brown and Yoder 2015, Brown et al. 2015), call for further conservation attention to hollow-dwelling species. In particular, inclusion of tree species that offer good quality sleeping sites such as *S. madagascariensis* in reforestation and forest management projects could prove beneficial for these lemur species.

ACKNOWLEDGEMENTS

We thank CAFF/CORE, the Direction Générale de l'Environnement et des Forêts, Madagascar National Parks, the Fanamby NGO (including S. Rajaobelina and V. Rasoloarison and in particular P. Ranarison), the Direction Régionale de l'Environnement et des Forêts région DIANA and SAVA, and the Madagascar Institut pour la Conservation des Ecosystèmes Tropicaux. The field work was possible thanks to the continuous support of the Département de Biologie Animale et Ecologie, University of Mahajanga, the University of Antsirananana, and particularly N. V. Andriaholinirina. We also thank the many great local guides and cooks for their help in the field and for sharing their incomparable expertise of the forest, and C. Kun-Rodrigues, M. Carreira, A. Beck, M. T. Ibouroi, H. Andrianotahiana, D. S. Ousseni for their participation to the field work as well as K. Dausmann, L. Wilmé, D. Zinner and S. Goodman for early constructive discussion on the project, and two anonymous reviewers that helped improving the manuscript. Financial support for this study was provided by the 'Fundação para a Ciência e a Tecnologia' (ref. SFRH/BD/64875/2009 to JS and PTDC/BIA-BIC/4476/2012 PTDC/BIA-BEC/100176/2008 to LC), the GDRI Madagascar, the Laboratoire d'Excellence (LABEX) entitled TULIP (ANR-10-LABX-41), the Rufford Small Grant Foundation, grant 10941-1, the Instituto Gulbenkian de Ciência, the LIA BEEG-B (Laboratoire International Associé - Bioinformatics, Ecology, Evolution, Genomics and Behaviour) (CNRS), and the National Science Foundation (DEB-1257916). This study was conducted in agreement with the laws of the countries of Portugal, France, United States of America, and Madagascar.

REFERENCES

- Anderson, J. R. 1998. Sleep, sleeping sites, and sleep-related activities: awakening to their significance. *American Journal of Primatology* 46, 1: 63–75. (doi:10.1002/(SICI)1098-2345(1998)46:1<63::AID-AJP5>3.0.CO;2-T)
- Banks, M. A. 2013. Determinants of Abundance and the Distribution of Primates in Northern Madagascar (Physical Anthropology). Unpub. PhD thesis. Stony Brook University, Stony Brook, NY.
- Berger-Tal, O., Polak, T., Oron, A., Lubin, Y., Kotler, B. P. and Saltz, D. 2011. Integrating animal behavior and conservation biology: a conceptual framework. *Behavioral Ecology* 22, 2: 236–239. (doi:10.1093/beheco/arq224)
- Biebow, K., Beader, S. and Nekaris, A. 2009. Tree hole utilisation by the hairy-eared dwarf lemur (*Allocebus trichotis*) in Analamazaotra Special Reserve. *Folia Primatologica* 80, 2: 89–103. (doi:10.1159/000225905)
- Blanco, M. B., Dausmann, K. H., Ranaivoarisoa, J. F. and Yoder, A. D. 2013. Underground hibernation in a primate. *Scientific Reports* 3: #1768. (doi:10.1038/srep01768)
- Brown, J. L. and Yoder, A. D. 2015. Shifting ranges and conservation challenges for lemurs in the face of climate change. *Ecology and Evolution* 5, 6: 1131–1142. (doi:10.1002/ece3.1418)
- Brown, K. A., Parks, K. E., Bethell, C. A., Johnson, S. E. and Mulligan, M. 2015. Predicting plant diversity patterns in Madagascar: understanding the effects of climate and land cover change in a biodiversity hotspot. *PLoS ONE* 10, 4: e0122721. (doi:10.1371/journal.pone.0122721)
- Burivalova, Z. 2011. Remote Sensing of Vegetation in Conservation, A Case Study from the Dry and Transitional Forests of Andrafiarana, Northern Madagascar. Unpub. Master's dissertation. Université de Genève and Conservatoire et Jardin botaniques de la Ville de Genève, Genève.
- Caro, T. 2007. Behavior and conservation: a bridge too far? *Trends in Ecology & Evolution* 22, 8: 394–400. (doi:10.1016/j.tree.2007.06.003)
- Dausmann, K. H. 2013. Spoilt for choice: Selection of hibernacula by *Cheirogaleus medius*. In: *Leaping Ahead*, J. Masters, M. P. Gamba and F. Génin (eds.), pp 205–214. Springer. (doi:10.1007/978-1-4614-4511-1_23)

- Dausmann, K. H., Glos, J., Ganzhorn, J. U. and Heldmaier, G. 2004. Physiology: hibernation in a tropical primate. *Nature* 429, 6994: 825–826. (doi:10.1038/429825a)
- Dausmann, K. H., Glos, J., Linsenmair, K. E. and Ganzhorn, J. U. 2008. Improved recruitment of a lemur-dispersed tree in Malagasy dry forests after the demise of vertebrates in forest fragments. *Oecologia* 157, 2: 307–316. (doi:10.1007/s00442-008-1070-6)
- De Wet, H., Nciki, S. and van Vuuren, S. F. 2013. Medicinal plants used for the treatment of various skin disorders by a rural community in northern Mputaland, South Africa. *Journal of Ethnobiology and Ethnomedicine* 9, 1: #51. (doi:10.1186/1746-4269-9-51)
- Drack, S., Ortmann, S., Bührmann, N., Schmid, J., Heldmaier, R. D. et al. 1999. Field metabolic rate and the cost of ranging of the red-tailed sportive lemur (*Lepilemur ruficaudatus*). In: *New Directions in Lemur Studies*, B. Rakotosamimanana, H. Rasamimanana, J. U. Ganzhorn and S. M. Goodman (eds.), pp 83–91. Springer US.
- Fichtel, C. 2007. Avoiding predators at night: antipredator strategies in red-tailed sportive lemurs (*Lepilemur ruficaudatus*). *American Journal of Primatology*, 69, 6: 611.
- Ganzhorn, J. U. 2002. Distribution of a folivorous lemur in relation to seasonally varying food resources: integrating quantitative and qualitative aspects of food characteristics. *Oecologia* 131, 3: 427–435. (doi:10.1007/s00442-002-0891-y)
- Gibbons, P. and Lindenmayer, D. 2002. Tree hollows and wildlife conservation in Australia. CSIRO publishing, Clayton, Australia.
- Goodman, S. M. & Wilmé, L. (eds.) 2006a. Inventaires de la Faune et de la Flore du Nord de Madagascar dans la Région Loky-Manambato, Analamerana et Andavakoera. Recherches pour le Développement. Série Sciences Biologiques. Centre d'Information et de Documentation Scientifique et Technique, Antananarivo.
- Goodman, S. M. & Wilmé, L. 2006b. Introduction. In: Inventaires de la Faune et de la Flore du Nord de Madagascar dans la Région Loky-Manambato, Analamerana et Andavakoera, S. M. Goodman & L. Wilmé (eds.), pp 1–36. Recherches pour le Développement. Série Sciences Biologiques. Centre d'Information et de Documentation Scientifique et Technique, Antananarivo.
- Habeeb, S. M. 2010. Ethno-veterinary and medical knowledge of crude plant extracts and its methods of application (traditional and modern) for tick control. *World Applied Sciences Journal* 11, 9: 1047–1054. Available at <http://ow.ly/QLRud>
- Harper, G. J., Steininger, M. K., Tucker, C. J., Juhn, D. and Hawkins, F. 2007. Fifty years of deforestation and forest fragmentation in Madagascar. *Environmental Conservation* 34, 4: 325–333. (doi:10.1017/S0376892907004262)
- Hawkins, A. F. A., Chapman, P., Ganzhorn, J. U., Bloxam, Q. M. C., Barlow, S. C. and Tonge, S. J. 1990. Vertebrate conservation in Ankarana special reserve, northern Madagascar. *Biological Conservation* 54, 2: 83–110. (doi:10.1016/0006-3207(90)90136-D)
- Kobbe, S. and Dausmann, K. H. 2009. Hibernation in Malagasy mouse lemurs as a strategy to counter environmental challenge. *Naturwissenschaften* 96, 10: 1221–1227. (doi:10.1007/s00114-009-0580-3)
- LaFleur, M. and Gould, L. 2009. Feeding outside the forest: the importance of crop raiding and an invasive weed in the diet of gallery forest ring-tailed lemurs (*Lemur catta*) following a cyclone at the Beza Mahafaly Special Reserve, Madagascar. *Folia Primatologica* 80, 3: 233–246. (doi:10.1159/000240968)
- Lindenmayer, D. B., Franklin, J. F. and Fischer, J. 2006. General management principles and a checklist of strategies to guide forest biodiversity conservation. *Biological Conservation* 131, 3: 433–445. (doi:10.1016/j.biocon.2006.02.019)
- Louis Jr., E. E., Engberg, S. E., Lei, R., Geng, H., Sommer, J. A. et al. 2006. Molecular and morphological analyses of the sportive lemurs (Family Megaladapidae: Genus *Lepilemur*) reveals 11 previously unrecognized species. *Special Publications*, Museum of Texas Tech University 49: 1–47.
- Meyers, D. M. and Ratsirarson, J. 1989. Distribution and conservation of two endangered sifakas in northern Madagascar. *Primate Conservation* 10: 81–86.
- Meyler, S. V., Salmona, J., Ibouroi, M. T., Besolo, A., Rasolondraibe, E. et al. 2012. Density estimates of two endangered nocturnal lemur species from Northern Madagascar: new results and a comparison of commonly used methods. *American Journal of Primatology* 74, 5: 414–422. (doi:10.1002/ajp.21997)
- Mittermeier, R. A., Louis, E. E., Richardson, M., Schwitzer, C., Langrand, O. et al. 2010. *Lemurs of Madagascar: Third Edition*. Conservation International, Washington, DC.
- Moat, J. and Smith, P. 2007. *Atlas of the Vegetation of Madagascar*. The Royal Botanic Gardens, Kew. Kew Publishing.
- Newton, I. 1994. The role of nest sites in limiting the numbers of hole-nesting birds: a review. *Biological Conservation* 70, 3: 265–276. (doi:10.1016/0006-3207(94)90172-4)
- Philippe, G., Angenot, L., Tits, M. and Frédérick, M. 2004. About the toxicity of some *Strychnos* species and their alkaloids. *Toxicon* 44, 4: 405–416. (doi:10.1016/j.toxicon.2004.05.006)
- Philippe, G., Angenot, L., De Mol, P., Goffin, E., Hayette, M.-P. et al. 2005. In vitro screening of some *Strychnos* species for antiplasmodial activity. *Journal of Ethnopharmacology* 97, 3: 535–539. (doi:10.1016/j.jep.2004.12.011)
- Rajolison, G., Raharimalala, J., Rahajaso, G., Andriambelo, L. H., Rabevohitra, R. and Razafindrianilana, N. 2002. Evaluation de la diversité floristique dans la Réserve d'Ankarafantsika. Une évaluation biologique de la Réserve Naturelle Intégrale d'Ankarafantsika, Madagascar, 37–62. Available at <https://library.conservation.org/Published Documents/2009/RAP_23_Madagascar.pdf>
- Rakotodratsimba, H. M. 2008. Etudes Ethnobotaniques, Biologiques et Ecogéographiques des *Dioscorea* spp. Sauvages d'Ankarafantsika en Vue de leur Conservation. Unpub. Master's dissertation. Université d'Antananarivo, Antananarivo.
- Ramanankirahina, R. 2004. Rythme d'Activité et Régime Alimentaire de *Propithecus verreauxi coronatus* (Milne Edwards, 1871) et d'*Eulemur mongoz* (Linné, 1766) dans la Station Forestière à Usage Multiple d'Antrema Katsepy. Unpub. Master's dissertation. Université d'Antananarivo, Antananarivo.
- Ranirison, P. 2006. Les Massifs Forestiers de la Région de la Loky-Manambato (Dairaina), Ecorégion de Transition Nord: Caractéristiques Floristiques et Structurales. Essai de Modélisation des Groupements Végétaux. Unpub. PhD Thesis, Université d'Antananarivo, Antananarivo.
- Rasoloharijaona, S., Rakotosamimanana, B., Randrianambinina, B. and Zimmermann, E. 2003. Pair-specific usage of sleeping sites and their implications for social organization in a nocturnal Malagasy primate, the Milne Edwards' sportive lemur (*Lepilemur edwardsi*). *American Journal of Physical Anthropology* 122, 3: 251–258. (doi:10.1002/ajpa.10281)
- Rasoloharijaona, S., Randrianambinina, B., Braune, P. and Zimmermann, E. 2006. Loud calling, spacing, and cohesiveness in a nocturnal primate, the Milne Edwards' sportive lemur (*Lepilemur edwardsi*). *American Journal of Physical Anthropology* 129, 4: 591–600. (doi:10.1002/ajpa.20342)
- Rasoloharijaona, S., Randrianambinina, B. and Zimmermann, E. 2008. Sleeping site ecology in a rain-forest dwelling nocturnal lemur (*Lepilemur mustelinus*): implications for sociality and conservation. *American Journal of Primatology* 70, 3: 247–253. (doi:10.1002/ajp.20487)
- Rasoloharijaona, S., Randrianambinina, B. and Joly-Radko, M. 2010. Does nonnutritive tree gouging in a rainforest-dwelling lemur convey resource ownership as does loud calling in a dry forest-dwelling lemur? *American Journal of Primatology* 72, 12: 1062–72. (doi:10.1002/ajp.20865)
- Rasolondraibe, E. 2011. Distribution Spatiale des Ressources Alimentaires chez *Propithecus tattersalli* (Simons 1988), *P. coquereli* (Grandidier, 1867) et *P. coronatus* (Milne-Edwards 1871) ainsi que certains Aspects de sa distribution. Unpub. Master's thesis. Université de Mahajanga, Mahajanga.
- Rose, C. L., Marcot, B. G., Mellen, T. K., Ohmann, J. L., Waddell, K. L. et al. 2001. Decaying wood in Pacific Northwest forests: concepts and tools for habitat management. In: *Wildlife-Habitat Relationships in Oregon and Washington*. D. H. Johnson and T. A. O'Neil (eds.), pp 580–623. Oregon State University Press, Corvallis, USA.
- Salmona, J., Jan, F., Rasolondraibe, E., Zaranaina, R., Saïd Ousseni, D. et al. 2013. Survey of the critically endangered Perrier's sifaka (*Propithecus perrieri*) across most of its distribution range. *Lemur News*, 17: 9–12.

- Salmona, J. 2014. Conservation, distribution and population size update of endangered nocturnal lemur species from Northern Madagascar, Rufford Small Grant final report (Rufford Small Grant Final Report No. 1), p. 21. (doi:10.13140/RG.2.1.2531.8242) Available at <http://www.rufford.org/files/10941-1 Detailed Final Report.pdf>
- Salmona, J., Ralantoharijaona, T., Ibouroy, M. T., Rakotonanahary, A., Zaranaina, R. et al. 2014a. Daraina sportive lemur (*Lepilemur milanoii*) density and population size estimates in most of its distribution range: the Loky-Manambato region. *Lemur News* 18: 16–19.
- Salmona, J., Rakotonanahary, A., Thani, I.M., Zaranaina, R., Ralantoharijaona, T. et al. 2014b. Estimation des densités et tailles de population du Microcèbe Roux du Nord de (*Microcebus tavaratra*) dans la région Loky-Manambato (Daraina). *Lemur News* 18: 73–75.
- Sato, H. 2012. Frugivory and seed dispersal by brown lemurs in a Malagasy tropical dry forest. *Biotropica* 44, 4: 479–488. (doi:10.1111/j.1744-7429.2011.00838.x)
- Sato, H., Ichino, S. and Hanya, G. 2014. Dietary modification by common brown lemurs (*Eulemur fulvus*) during seasonal drought conditions in western Madagascar. *Primates*, 55, 2: 219–230. (doi:10.1007/s10329-013-0392-0)
- Schatz, G. E. 2001. Generic Tree Flora of Madagascar. Royal Botanic Gardens, Kew and Missouri Botanical Garden, St.-Louis.
- Schmid, J. and Ganzhorn, J. U. 1996. Resting metabolic rates of *Lepilemur ruficaudatus*. *American Journal of Primatology* 38, 2: 169–174. (doi:10.1002/(SICI)1098-2345(1996)38:2<169::AID-AJP5>3.0.CO;2-X)
- Schwitzer, N., Randriatahina, G. H., Kaumanns, W., Hoffmeister, D. and Schwitzer, C. 2007. Habitat utilization of blue-eyed black lemurs, *Eulemur macaco flavifrons* (Gray, 1867), in primary and altered forest fragments. *Primate Conservation* 22, 1: 79–87. (doi:10.1896/052.022.0106)
- Schwitzer, C., Mittermeier, R., Johnson, S., Donati, G., Irwin, M. et al. 2014. Averting lemur extinctions amid Madagascar's political crisis. *Science* 343, 6173: 842–843. (doi:10.1126/science.1245783)
- Seiler, M. 2012. The Impact of Habitat Degradation and Fragmentation on Ecology and Behaviour of the Sahamalaza Sportive Lemur, *Lepilemur sahamalazensis*, in Northwest-Madagascar. Ph.D. Thesis. Bristol: University of Bristol. Available at <https://www.researchgate.net/profile/Melanie_Seiler2/contributions>
- Seiler, M., Schwitzer, C. and Holderied, M. 2013. Anti-predator behaviour of Sahamalaza sportive lemurs, *Lepilemur sahamalazensis*, at diurnal sleeping sites. *Contributions to Zoology* 82, 3: 131–143. Available at <http://www.contributionstozoology.nl/vol82/nr03/a03>
- Shorthouse, D. P. 2010. SimpleMappr, an online tool to produce publication-quality point maps. Available at <http://www.simplemappr.net>
- Simmen, B., Hladik, A. and Ramasiarisoa, P. 2003. Food intake and dietary overlap in native *Lemur catta* and *Propithecus verreauxi* and introduced *Eulemur fulvus* at Berenty, Southern Madagascar. *International Journal of Primatology* 24, 5: 949–968. (doi:10.1023/A:1026366309980)
- Simmen, B., Sautther, M. L., Soma, T., Rasamimanana, H., Sussman, R. W. et al. 2006. Plant species fed on by *Lemur catta* in gallery forests of the southern domain of Madagascar. In: Ringtailed Lemur Biology, A. Jolly, R. W. Sussman, N. Koyama, H. Rasamimanana (eds.), pp 55–68. Springer. (doi:10.1007/978-0-387-34126-2_5)
- Simmen, B., Bayart, F., Marez, A. and Hladik, A. 2007. Diet, nutritional ecology, and birth season of *Eulemur macaco* in an anthropogenic forest in Madagascar. *International Journal of Primatology* 28, 6: 1253–1266. (doi:10.1007/s10764-007-9217-6)
- Tattersall, I. 2007. Madagascar's lemurs: cryptic diversity or taxonomic inflation? *Evolutionary Anthropology* 16, 1: 12–23. (doi:10.1002/evan.20126)
- Taylor, S. and Perrin, M. R. 2006. The diet of the Brown-headed Parrot (*Poicephalus cryptoxanthus*) in the wild in southern Africa. *Ostrich* 77, 3–4: 179–185. (doi:10.2989/00306520609485531)
- Thalmann, U. 2001. Food resource characteristics in two nocturnal lemurs with different social behavior: *Avahi occidentalis* and *Lepilemur edwardsi*. *International Journal of Primatology* 22, 2: 287–324. (doi:10.1023/A:1005627732561)
- Thorén, S., Quietzs, F., Schwochow, D., Sehen, L., Meusel, C. et al. 2011. Seasonal changes in feeding ecology and activity patterns of two sympatric mouse lemur species, the gray mouse lemur (*Microcebus murinus*) and the golden-brown mouse lemur (*M. ravelobensis*), in northwestern Madagascar. *International Journal of Primatology* 32, 3: 566–586. (doi:10.1007/s10764-010-9488-1)
- Vieilledent, G., Grinand, C. and Vaudry, R. 2013. Forecasting deforestation and carbon emissions in tropical developing countries facing demographic expansion: a case study in Madagascar. *Ecology and Evolution* 3, 6: 1702–1716. (doi:10.1002/ece3.550)
- Volampeno, M. S. N., Masters, J. C. and Downs, C. T. 2011. Life history traits, maternal behavior and infant development of blue-eyed black lemurs (*Eulemur flavifrons*). *American Journal of Primatology* 73, 5: 474–484. (doi:10.1002/ajp.20925)
- Wilson, J. M., Stewart, P. D., Ramangason, G., Denning, A. M. and Hutchings, M. S. 1989. Ecology and conservation of the crowned lemur, *Lemur coronatus*, at Ankarana, N. Madagascar. *Folia Primatologica* 52, 1–2: 1–26. (doi:10.1159/000156379)
- Wright, P. C. 1999. Lemur traits and Madagascar ecology: coping with an island environment. *American Journal of Physical Anthropology* 110, S29: 31–72. (doi:10.1002/(SICI)1096-8644(1999)110:29+<31::AID-AJPA3>3.0.CO;2-0)
- Zinner, D., Hilgartner, R. D., Kappeler, P. M., Pietsch, T., & Ganzhorn, J. U. 2003. Social organization of *Lepilemur ruficaudatus*. *International Journal of Primatology* 24, 4: 869–888. (doi:10.1023/A:1024684907250)

SUPPLEMENTARY MATERIAL.

Available online only.

Figure S1. Illustrations of *Strychnos madagascariensis* tree hollow hosting a Daraina sportive lemur.