# Population dynamics of *Lemur catta* at selected sleeping sites in the Tsimanampesotse National Park

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#### Abstract

Lemur catta is probably the lemur species known best by the public as it is found in many zoological gardens and has featured prominently in movies. Originally very wide-spread in the dry southwestern part of Madagascar, recent reports drew attention to the substantial decrease in suitable habitat due to forest clearing, possibly associated with intensive hunting. Despite this species being prominent at sites where it occurs, information on its population dynamics is only available from a handful of sites covering a very small portion of the species' range that may or may not be representative of its population dynamics in general. This species is known to have marked population changes due to droughts. Lemur catta are difficult to survey in the dry spiny thicket, as their distribution seems clumped within large tracts of seemingly unsuitable habitat. Since studies concentrate on sites where the animals occur in sufficient numbers to allow systematic studies, the question arises whether or not the results from these sites can be generalized over the species'range. In order to supplement the existing studies, we initiated a long-term population study of L. catta at sleeping sites in Tsimanampesotse National Park, the largest protected area within the range of this species. During the six years of inventories (2013-2018), the number of adults showed little change, but the number of juveniles declined consistently and significantly. The decline was most pronounced during two years with very low rainfall, matching the results of previous studies. If the local meteorological conditions shift towards lower rainfall, the species might be in serious trouble over a large portion of its assumed range that is without permanent watersources as there are basically no forests left where the animals could survive during periods of water and food shortage.

**Keywords:** *Lemur catta*, Tsimanampesotse National Park, Madagascar, population development

#### Résumé détaillé

Lemur catta est probablement l'espèce de lémuriens le mieux connue, comme il se trouve dans de nombreux jardins zoologiques et aussi le mieux filmé dans des reportages documentaires. Comme espèce de lémurien très répandue dans la partie Sud-ouest sèche de Madagascar, des rapports récents ont attiré l'attention sur la diminution importante de l'habitat approprié en raison de la destruction de la forêt, éventuellement associée à la chasse intensive. Les informations sur la dynamique de population de cette espèce ne sont disponibles qu'à partir d'une poignée de sites couvrant une très petite partie de sa zone de distribution qui peut être représentative ou non de sa dynamique démographique en général. Les populations ont montré un changement marqué dû à la sécheresse. L'espèce est difficile à inventorier dans l'écosystème forestier épineux, car sa distribution est concentrée dans des vastes étendues d'habitats apparemment inadaptés. Etant donné que études se concentrent sur les sites où les animaux sont en nombre suffisant pour permettre des études systématiques, la question se pose de savoir si les résultats de ces sites peuvent être généralisés ou non à l'aire de répartition de l'espèce. Afin de compléter les études existantes, nous avons mené une étude sur le suivi à long terme de la population de L. catta avec une approche de comptage des animaux par dortoir dans le Parc National de Tsimanampesotse, la plus grande zone protégée où cette espèce est largement distribuée. Au cours des cinq années d'inventaire, un faible changement du nombre d'individus adultes a été constaté. Par contre, la diminution du nombre de juvéniles est significatif et de facon constante.

Bien que les fluctuations quotidiennes des individus aient été très importantes, les moyennes mensuelles ont peu varié. Comme les animaux ne sont pas marqués, il est difficile de savoir si les individus se déplacent ou non entre les sites de repos. Le nombre d'adultes a fluctué de façon irrégulière entre les cinq sites de dortoirs. La diminution du nombre d'individus a été bien constatée au cours de deux ans pendant lesquelles la précipitation dans la région est très faible.

Le nombre de juvéniles a nettement diminué au cours des deux années avec peu de pluie (2016 et 2017). Surtout en 2016, les animaux semblaient être en très mauvaise condition physique. Si les conditions ambiantes s'aggravent, l'espèce pourrait avoir de graves problèmes sur une grande partie de sa zone de distribution supposée sans eau permanente, car il n'y a pratiquement pas de forêt galerie où les animaux pourraient survivre pendant les temps de pénurie d'eau et de nourriture.

Mots clés : Lemur catta, Parc National de Tsimanampesotse, dynamique de la population.

# Introduction

Recent reports have drawn attention to a substantial decline of Lemur catta over its range (Gould & Sauther, 2016; LaFleur et al., 2016). These reports have been debated due to methodological questions and the unreliability of surveys based on just a few days of inventory (Murphy et al., 2017). The debate seems futile as it is clear that the extent of suitable habitat for the species has declined substantially, thus justifying the assumption of a substantial reduction of the species' population size and its categorization as being "Endangered" (Goodman et al., 2006; Brinkmann et al., 2014; Schwitzer et al., 2014; Waeber et al., 2015). While the destruction of the dry spiny thicket can be measured precisely, population estimates of L. catta are difficult to compile within the vegetation formations of southern Madagascar as the vegetation can be very patchy, sometimes difficult to access, and the species can make extensive use of terrestrial travel and rocky habitats (Goodman & Langrand, 1996; Cameron & Gould, 2013; Gabriel, 2013; Gould & Gabriel, 2014). In addition, populations undergo substantial fluctuations due to droughts and

associated food and water shortage (Gould et al., 1999, 2003; Jolly et al., 2002, 2006).

For the present study we compiled information on a portion of the population of L. catta in Park. This Tsimanampesotse National park represents the largest protected area of southwestern Madagascar and thus a potential stronghold for biodiversity conservation. Yet, pressure of hunting and collection is high for all species that can be used or marketed (Walker & Rafeliarisoa, 2012; Sauther et al., 2013; Andriamparany et al., 2015; Ganzhorn et al., 2015; Randriamiharisoa et al., 2015; LaFleur et al., 2016; Manjoazy et al., 2017; Goodman et al., 2018). Here, we counted L. catta at five sleeping sites around the cave of Mitoho at the western edge of Tsimanampesotse National Park between 2013 and 2018 (Figure 1). Specific objectives of our study were: 1) to add baseline information for this species as part of the management plan for this protected area (Madagascar National Parks, 2013); 2) to provide baseline data for future estimates on the population development of L. catta at a selected site within Tsimanampesotse National Park; 3) to scrutinize whether or not counts at five sleeping sites can provide insight into conclusions about population dynamics as compared to spatially more extensive surveys.

# Methods Study site

Tsimanampesotse National Park covers about 230 km² and is located in southwestern Madagascar (24°03'-24°12'S, 43°46'-43°50'E), 85 km south of Toliara. The study was carried out at the western escarpment of the limestone Mahafaly Plateau between the Andranovao camp (24°01.578'S, 43°44.238'E) and the Grotte de Mitoho (24°02.973'S, 43°45.095'E), 40 to 115 m above sea level. The vegetation of the study region is xerophytic starting at the coastal plain with formations resting on sand and thin reddish clays, followed by an area at approximately 50 m above sea level near the foot of the Mahafaly Plateau, dominated by sparse vegetation in close vicinity to the soda lake (Tsimanampesotse Lake), and dry spiny thicket on the limestone Mahafaly Plateau. Trees on limestone are distinctly smaller and occur in much lower densities, resulting in reduced vegetation cover and biomass production compared to the littoral forest. More details of the study site are provided by Goodman et al. (2002, 2018), Andriatsimietry et al. (2009), Hammer & Ramilijaona (2009), Rakotondranary et

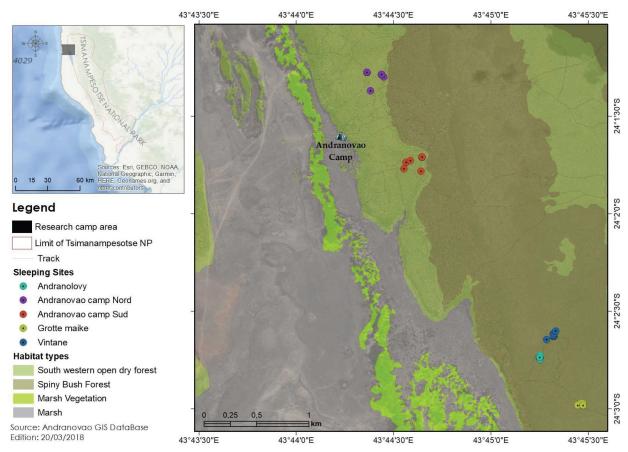


Figure 1. Location of the study site and sleeping sites of Lemur catta. The small black square in the left-hand figure, representing the northwest corner of the Tsimanampesotse National Park, is enlarged in the right-hand figure.

al. (2010), Rasoma et al. (2010), Bohr et al. (2011), Ratovonamana et al. (2011, 2013), Sauther et al. (2013), and LaFleur et al. (2014).

Rainfall in the southwestern region of Madagascar is highly seasonal and rarely exceeds 400 mm per year, most rains falling between December and February (Donque, 1975; Ratovonamana et al., 2011). Rainfall measured with conventional methods is supplemented by dew though the effect of dew is poorly understood (Hanisch et al., 2015). As a general classification, the year is divided in a wet season from December to April and a dry season from May to November, even though several years can pass without any measurable or significant rainfall or rainfall pattern can shift towards the season previously considered the dry season. The region experiences considerable variation in daily mean temperatures, ranging between 17 and 34°C (Ratovonamana et al., 2013). The exceptional spatial and temporal variation of weather conditions in the region makes conclusions on climate trends difficult when based on physical measurements. However, extrapolating climate models postulate the temperature to have increased over the last few decades. According to the models, precipitation also

is supposed to have increased, though the latter is not supported by the perception of people living in the region (Hannah et al., 2008; Stalenberg et al., 2018).

During the study period, rainfall was measured at the Andranovao camp with rain gauges. Temperature was measured with ibuttons (Hydrochron IButton, Dallas Semiconducter, USA) installed under the shade of the tree some 1.5 m above the ground. Each I-button was programmed to take temperature and relative hat the same site since 2006. In 2011, the collection of climate data was reinforced by the installation of a HOBO micro station, with 04 automatic sensors, to collect other climate variables.

Subterranean water surfaces occur at the western edge of the Mahafaly Plateau either at the foot of the plateau or accessed in caves. At these sites, some trees (such as Ficus spp. or Tamarindus indica) can reach substantial dimensions and are used as sleeping sites by Lemur catta (Rasoloariniaina et al., 2016).

# Population monitoring

Initially, we used several kilometers of transects originally installed to monitor tortoises (Astrochelys

radiata and Pyxis arachnoides) in Tsimanampesotse National Park (Hammer & Ramilijaona, 2009; Rasoma et al., 2010) and to survey Lemur catta as part of the conservation and monitoring objectives of Madagascar National Park (Madagascar National Parks, 2012, 2013). Sightings were infrequent and could not be used for population monitoring. Combining transects at sites known to be used by L. catta with transects at sites obviously not used by the animals seemed arbitrary as any result could have been obtained simply by different placements of transects. We therefore decided to count animals at known sleeping sites. Due to the rugged terrain, only sleeping sites in trees were considered though this species also spends nights on cliffs and in caves (Sauther et al., 2013). Five sleeping sites were identified within 4 km of the Andranovao research station (Figure 1). These were Andranovao Camp Nord, Andranovao Camp Sud, Vintane, Andranolovy, and Grotte maike. Geographic coordinates of the sites are listed in Appendix 1. Each sleeping site was visited early in the morning (arriving prior to sunrise) or just prior to sunset (leaving after sunset). Animals were counted when daylight allowed an overview over the group spread and numbers of individuals. Animals were counted at irregular intervals over the years (Appendix 1). We distinguished between adult males and females and juvenile males and females. The counting of animals took around 30 mn per sleeping site. Data were analyzed with IBM SPSS 25.

#### Results

# **Ambient conditions**

Rainfall patterns are shown for the years 2012 to 2018 (Figure 2). Even though lemur counts started

only in 2013, rainfall data for 2012 were included as lemur populations might respond to ambient conditions with a lag phase. The study region experienced a drought in 2012 with only 11 days of intermittent rain and an annual rainfall of less than 80 mm (Figure 2). Between 2013 and 2015 annual rainfall approached the long-term mean but dropped again to only 97.5 mm and 98 mm in 2016 and 2017, respectively.

#### **Population dynamics**

Between November 2013 and November 2018,107 counts were completed at the five sleeping sites (Appendix 1). Counts at sleeping sites yielded between 1 and 31 individuals during the 81 survey days. While day-to-day fluctuations were very high, monthly means varied little. Since animals were not marked, we do not know whether or not individuals moved between sleeping sites. The number of adults seemed to fluctuate inconsistently between the five sleeping sites. Except for the Andranolovy site, the number of juveniles dropped consistently between 2013 and 2017. When all data were pooled for the five sites, there was no consistent trend of the number of juveniles or adults over the six years of survey (Spearman correlation: juveniles:  $r_s = -0.77$ , P = 0.07, n = 6; adults:  $r_s = -0.27$ , P = 0.61, n = 6; Figure 3). On the temporal scale analyzed here, annual rainfall was related significantly to the number of juveniles  $(r_s = 0.83, P = 0.04, n = 6)$  but not to the numbers of adults ( $r_s = 0.387$ , P = 0.61, n = 6). The number of juveniles dropped markedly in the two years with little rain (2016 and 2017). Especially in 2016, the animals appeared to be in very poor body condition (Figure 4). The low amount of rain in 2012 did not seem to be reflected in the number of juveniles recorded in 2013.

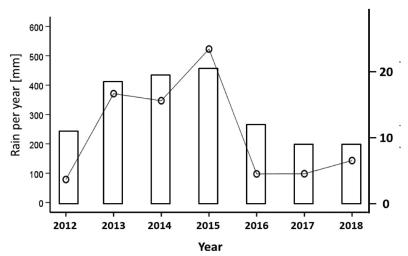


Figure 2. Rainfall measured at Andranovao camp between 2012 and 2018. Bars represent days with rain. The line indicates total annual rainfall.

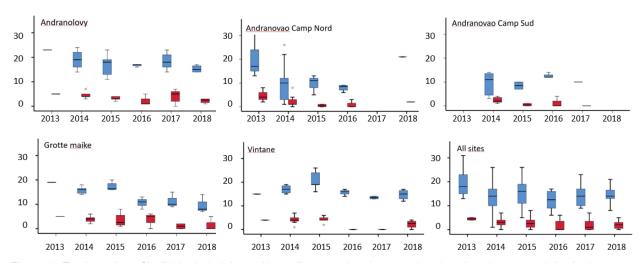


Figure 3. Total number of individuals (adults and juveniles; grey bars) counted at sleeping sites around the Andranovao camp and the Grotte de Mitoho in Tsimanampesotse between 2013 and 2018. Values for total counts are medians, quartiles, and ranges. Values for juveniles are shown separately (hatched bars). The circles mark outliers according to the data classification of SPSS. Note that no surveys were carried out at Andranovao Sud Camp in 2013 and in 2018, and at Andranovao Camp Nord in 2017.



Figure 4. Lemur catta in very poor condition probably due to the lack of food during the drought of 2016 (according to the scoring system by Berg et al. 2009; Millette et al. 2015). Photo taken in September 2016. (Photo by Yedidya Ratovonamana.)

# **Discussion**

With the data at hand, at least parts of Tsimanampesotse National Park, together with yet unpublished data by M. LaFleur from the same area, can provide an additional site to understand population trends of Lemur catta; the other sites being Berenty, Bezà Mahafaly, Anja, and Tsaranoro. For the

time being, the Tsimanampesotse data should only be considered a snapshot as "long-term" studies are considered to cover at least 10 years of data collection (Kappeler et al., 2017) and the southwestern part of Madagascar is characterized by recurrent droughts affecting humans and lemurs alike, making even 10 years of data collection look like a point in time

(Gould et al., 1999, 2003; Richard et al., 2000; Jolly et al., 2002, 2006; Ratovonamana et al., 2011). The challenge is to separate short-term effects of ambient conditions from long-term population trends. Long-term effects of the environmental conditions are poorly documented. The increase in ambient temperature by more than 1°C is likely to have negative effects (Hannah et al., 2008; Brown & Yoder, 2015). Though temperature changes will have major effects, increased unpredictability might even be of more concern and act more rapidly (Ganzhorn, 1995; Wright, 1999; Dewar & Richard, 2007). In addition, the unpredictable precipitation pattern seems to have shifted with rains falling later in the calendar year in southwestern Madagascar (Ratovonamana et al., 2013). Though L. catta exhibit substantial behavioral flexibility as illustrated by their responses to severe ambient conditions, weather unpredictability is certainly a problem, especially if reproduction would mainly be triggered by photoperiod (Pereira, 1993; Kelley, 2013; Gould et al., 2015).

For a semi-terrestrial species such as L. catta, that has no problem utilizing anthropogenic landscapes, human encroachment could be mitigated easily by strengthening conservation measures, thus countering fragmentation effects, such as establishing or maintaining hedges or groves with trees that could be used by animals and people (Gardner et al., 2009, 2013; Sauther & Cuozzo, 2009; Irwin et al., 2010; Cameron & Gould, 2013; Andriamparany et al., 2015; Antsonantenainarivony, 2015; Gérard et al., 2015; Gould & Andrianomena, 2015; Goetter et al., 2017; Nopper et al., 2017; Steffens et al., 2017). Yet, while these technical solutions are at hand, the actual problems on the ground (economic perspectives, conservation issues) are not addressed to the extent needed to make a difference. Any attempt to solve the problems is outrun by excessive human population growth, poor governance and aid, and conservation projects that pay too little attention to local peculiarities (Freudenberger, 2010; Richard & Ratsirarson, 2013; Waeber et al., 2016; Neudert et al., 2017).

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#### References

- Andriamparany, J. N., Brinkmann, K., Wiehle, M., Jeannoda, V. & Buerkert, A. 2015. Modelling the distribution of four *Dioscorea* species on the Mahafaly Plateau of south-western Madagascar using biotic and abiotic variables. *Agriculture Ecosystems & Environment*, 212: 38-48.
- Andriatsimietry, R., Goodman, S. M., Razafimahatratra, E., Jeglinski, J. W. E., Marquard, M. & Ganzhorn, J. U. 2009. Seasonal variation in the diet of *Galidictis grandidieri* Wozencraft, 1986 (Carnivora: Eupleridae) in a sub-arid zone of extreme southwestern Madagascar. *Journal of Zoology*, 279: 410-415.
- Antsonantenainarivony, O. G. 2015. Guide pratique pour la bouture de samata (*Euphorbia stenoclada* Baill.) dans la partie littorale de la région Sud-ouest de Madagascar. From http://www.sulama.de/index.php/en/literature/reports-english.html
- Berg, W., Jolly, A., Rambeloarivony, H., Andrianome, V. & Rasamimanana, H. 2009. A scoring system for coat and tail condition in ring-tailed lemurs, *Lemur catta*. *American Journal of Primatology*, 71: 183-190.
- Bohr, Y. E. M. B., Giertz, P., Ratovonamana, Y. R. & Ganzhorn, J. U. 2011. Gray-brown mouse lemurs (*Microcebus griseorufus*) as an example of distributional constraints through increasing desertification. *International Journal of Primatology*, 32: 901-913.
- Brinkmann, K., Noromiarilanto, F., Ratovonamana, R. Y. & Buerkert, A. 2014. Deforestation processes in southwestern Madagascar over the past 40 years: What can we learn from settlement characteristics? Agriculture, Ecosystems and Environment, 195: 231-243.
- **Brown, J. L. & Yoder, A. D. 2015.** Shifting ranges and conservation challenges for lemurs in the face of climate change. *Ecology and Evolution*, 5: 1131-1142.
- Cameron, A. & Gould, L. 2013. Fragment adaptive behavioral strategies and inter-site variation in the ringtailed lemur (*Lemur catta*) in south-central Madagascar. In *Primates in fragments*, eds. L. Marsh & C. Chapman, pp. 227-243. Springer, New York.
- Dewar, R. E. & Richard, A. F. 2007. Evolution in the hypervariable environment of Madagascar. *Proceedings* of the National Academy of Science USA, 104: 13723-13727.

- Donque, G. 1975. Contribution géographique à l'étude de climat de Madagascar. Nouvelles Imprimerie des Arts Graphiques, Tananarive.
- Freudenberger, K. 2010. Paradise lost? Lessons from 25 years of USAID environment programs in Madagascar. International Resources Group, Washington, D.C.
- Gabriel, D. N. 2013. Habitat use and activity patterns as an indication of fragment quality in a Strepsirrhine primate. International Journal of Primatology, 34: 388-406.
- Ganzhorn, J. U. 1995. Cyclones over Madagascar: Fate or fortune? Ambio, 24: 124-125.
- Ganzhorn, J. U., Manjoazy, T., Päplow, O., Randrianavelona, R., Razafimanahaka, J. H., Ronto, W. M., Vogt, E., Wätzold, F. & Walker, R. C. J. 2015. Rights to trade for species conservation: Exploring the issue of the radiated tortoise in Madagascar. Environmental Conservation, 42: 291-293.
- Gardner, C. J. 2009. A review of the impacts of anthropogenic habitat change on terrestrial biodiversity in Madagascar: Implications for the design and management of new protected areas. Malagasy Nature, 2: 2-29.
- Gardner, C. J., Nicoll, M. E., Mbohoahy, T., Oleson, K. L. L., Ratsifandrihamanana, A. N., Ratsirarson, J., Rene de Roland, L. A., Virah-Sawmy, M., Zafindrasilivonona, B. & Davies, Z. G. 2013. Protected areas for conservation and poverty alleviation: Experiences from Madagascar. Journal of Applied Ecology, 50: 1289-1294.
- Gérard, A., Ganzhorn, J. U., Kull, C. A. & Carrière, S. M. 2015. Possible roles of introduced plants for native vertebrate conservation: The case of Madagascar. Restoration Ecology, 23: 768-775.
- Goetter, J. F., Kobbe, S., Fricke, R. & Kübler, D. 2017. Sustainable propagation of the fodder tree Euphorbia stenoclada ("samata"). In Making sense of research for sustainable land management, eds. H. P. Liniger, R. Mekdaschi Studer, P. Moll & U. Zander, pp. 227-230. Berb: Centre for Development and Environment (CDE), University of Bern, Bern and Helmholtz-Centre for Environmental Research GmbH - UFZ, Leipzig.
- Goodman, S. M. & Langrand, O. 1996. A high mountain population of the ring-tailed lemur Lemur catta on the Andringitra Massif, Madagascar. Oryx, 30: 259-268.
- Goodman, S. M., Raherilalao, M. J., Rakotomalala, D., Rakotondravony, D., Raselimanana, A. P., Razakarivony, H. V. & Soarimalala, V. 2002. Inventaire des vertébrés du Parc National de Tsimanampetsotsa (Toliara). Akon'ny Ala, 28: 1-36.
- Goodman, S. M., Rakotoarisoa, S. V. & Wilmé, L. 2006. The distribution and biogeography of the Ring-tailed lemur (Lemur catta) in Madagascar. In Ring-tailed lemur biology, eds. A. Jolly, R. W. Sussman, N. Koyama, H. Rasamimanana & R. H. Tuttle, pp. 3-15. Springer, New
- Goodman, S. M., Raherilalao, M. J. & Wohlhauser, S. 2018. Les aires protégées terrestres de Madagascar: Leur histoire, description et biote / The terrestrial protected areas of Madagascar: Their

- history, description, and biota. Association Vahatra, Antananarivo.
- Gould, L. & Andrianomena, P. 2015. Ring-tailed Lemurs (Lemur catta), forest fragments, and community-level conservation in south-central Madagascar. Primate Conservation, 29: 67-73.
- Gould, L. & Gabriel, D. N. 2014. Wet and dry season diets of the endangered Lemur catta (Ring-tailed lemur) in two mountainous rocky outcrop forest fragments in south-central Madagascar. African Journal of Ecology, 53: 320-330.
- Gould, L. & Sauther, M. L. 2016. Going, going, gone. Is the iconic Ring-tailed lemur (Lemur catta) headed for imminent extirpation? Primate Conservation, 30: 89-101.
- Gould, L., Sussman, R. W. & Sauther, M. L. 1999. Natural disasters and primate populations: The effects of a 2-year drought on a naturally occurring population of Ring-tailed Lemurs (Lemur catta) in southwestern Madagascar. International Journal of Primatology, 20: 69-84.
- Gould, L., Sussman, R. W. & Sauther, M. L. 2003. Demographic and life-history patterns in a population of ring-tailed lemurs (Lemur catta) at Beza Mahafaly Reserve, Madagascar: A 15-year perspective. American Journal of Physical Anthropology, 120: 182-194.
- Gould, L., Kelley, E. A. & LaFleur, M. 2015. Reproductive female feeding strategies in spiny forest-dwelling Lemur catta in southern and southwestern Madagascar: How do females meet the challenges of reproduction in this harsh habitat? Folia Primatologica, 86: 16-24.
- Hammer, J. M. & Ramilijaona, O. 2009. Population study on Astrochelys radiata (Shaw, 1802) in the Tsimanampetsotsa National Park, southwest Madagascar. Salamandra, 45: 219-232.
- Hanisch, S., Lohrey, C. & Buerkert, A. 2015. Dewfall and its ecological significance in semi-arid coastal southwestern Madagascar. Journal of Arid Environments, 121: 24-31.
- Hannah, L., Dave, R., Lowry, P.P., Andelman, S., Andrianarisata, M., Andriamaro, L., Cameron, A., Hijmans, R., Kremen, C., MacKinnon, J., Randrianasolo, H.H., Andriambololonera, S., Razafimpahanana, Α., Randriamahazo, Randrianarisoa, J., Razafinjatovo, P., Raxworthy, C., Schatz, G. E., Tadross, M. & Wilmé, L. 2008. Climate change adaptation for conservation in Madagascar. Biology Letters, 4: 590-594.
- Irwin, M. T., Wright, P. C., Birkinshaw, C., Fisher, B., Gardner, C. J., Glos, J., Goodman, S. M., Loiselle, P., Rabeson, P., Raharison, J.-L., Raherilalao, J., Rakotondravony, D., Raselimanana, A., Ratsimbazafy, J., Sparks, J., Wilmé, L. & Ganzhorn, J. U. 2010. Patterns of species change in anthropogenically disturbed habitats of Madagascar. Biological Conservation, 143: 2351-2362.
- Jolly, A., Dobson, A., Rasamimanana, H. M., Walker, J., O'Connor, S., Solberg, M. & Perel, V. 2002. Demography of Lemur catta at Berenty Reserve,

- Madagascar: Effects of troop size, habitat and rainfall. International Journal of Primatology, 23: 327-353.
- Jolly, A., Sussman, R. W., Koyama, N. & Rasamimanana, H. 2006. Ring-tailed lemur biology. Springer, New York.
- Kappeler, P. M., Cuozzo, F. P., Fichtel, C., Ganzhorn, J. U., Gursky-Doyen, S., Irwin, M. T., Ichino, S., Lawler, R., Nekaris, K. A. I., Ramanamanjato, J.-B., Radespiel, U., Sauther, M. L., Wright, P. C. & Zimmermann, E. 2017. Long-term field studies of lemurs, lorises, and tarsiers. Journal of Mammalogy, 98: 661-669.
- Kelley, E. A. 2013. The ranging behavior of Lemur catta in the region of Cap Sainte-Marie, Madagascar. American Journal of Physical Anthropology, 150: 122-132.
- LaFleur, M., Sauther, M. L., Cuozzo, F., Yamashita, N., Youssouf Jacky, I. A. & Bender, R. 2014. Cathemerality in wild Ring-tailed lemurs (Lemur catta) in the spiny forest of Tsimanampetsotsa National Park: Camera trap data and preliminary behavioral observations. Primates, 55: 207-217.
- LaFleur, M., Clarke, T. A., Reuter, K. & Schaeffer, T. 2016. Rapid decrease in populations of wild Ring-tailed lemurs (Lemur catta) in Madagascar. Folia Primatologica, 87:
- Madagascar National Parks. 2012. Manuel suivi écologique. Rapport non publié. Madagascar National Parks, Antananarivo.
- Madagascar National Parks. 2013. Plan d'aménagement et de gestion. Parc National Tsimanampetsotse. Rapport non publié. Madagascar National Parks, Toliara.
- Manjoazy, T., Ronto, W., Randrianavelona, Razafimanahaka, J., Ganzhorn, J. U. & Jenkins, R. 2017. The supply of illegal tortoise meat in Toliara City, south-western Madagascar. Oryx, 51: 437-440.
- Millette, J. B., Sauther, M. L. & Cuozzo, F. 2015. Examining visual measures of coat and body condition in wild Ring-tailed lemurs at the Beza Mahafaly Special Reserve, Madagascar. Folia Primatologica, 86: 55-55.
- Murphy, A. L., Ferguson, B. & Gardner, C. J. 2017. Recent estimates of Ring-tailed Lemur (Lemur catta) population declines are methodologically flawed and misleading. International Journal of Primatology, 38: 623-628.
- Neudert, R., Ganzhorn, J. U. & Watzold, F. 2017. Global benefits and local costs - The dilemma of tropical forest conservation: A review of the situation in Madagascar. Environmental Conservation, 44: 82-96.
- Nopper, J., Laustroer, B., Rödel, M. O. & Ganzhorn, J. U. 2017. A structurally enriched agricultural landscape maintains high reptile diversity in sub-arid southwestern Madagascar. Journal of Applied Ecology, 54: 480-488.
- Pereira, M. E. 1993. Seasonal adjustment of growth rate and adult body weight in ring-tailed lemurs. In Lemur social systems and their ecological basis, eds. P. M. Kappeler & J. U. Ganzhorn, pp. 205-221. Plenum Press, New York.

- Rakotondranary, J. S., Ratovonamana, Y. R. J. U. 2010. Ganzhorn, Distributions caractéristiques des microhabitats de Microcebus griseorufus (Cheirogaleidae) dans le Parc National de Tsimanampetsotsa (Sud-ouest de Madagascar). Malagasy Nature, 4: 55-64.
- Randriamiharisoa, L. O., Rakotondravony, Ranirison, A., Raherilalao, M. J., Wilmé, L. & Ganzhorn, J. 2015. Effects of transhumance trail on the richness and composition of bird communities in Tsimanampetsotse National Park. Madagascar Conservation & Development, 10: 110-115.
- Rasoloariniaina, J. R., Ganzhorn, J. U., Riemann, J. C. & Raminosoa, N. 2016. Water quality and biotic interaction of two cavefish species: Typhleotris madagascariensis Petit, 1933 and Typhleotris mararybe Sparks & Chakrabarty, 2012, in the Mahafaly Plateau groundwater system, Madagascar. Subterranean Biology, 18: 1-16.
- Rasoma, R. V. J., Ranivoarivelo, S., Marquard, M., Ramilijaona, O. R., Raselimanana, A. P. & Ganzhorn, J. U. 2010. Estimation de la densité des populations d'une espèce menacée de tortue terrestre (Astrochelys radiata) dans le Parc National Tsimanampetsotsa au Sud de Madagascar. Malagasy Nature, 4: 33-48.
- Ratovonamana, Y. R., Rajeriarison, C., Edmond, R. & Ganzhorn, J. U. 2011. Phenology of different vegetation types in Tsimanampetsotsa National Park, south-western Madagascar. Malagasy Nature, 5: 14-38.
- Ratovonamana, Y. R., Rajeriarison, C., Edmond, R., Kiefer, I. & Ganzhorn, J. U. 2013. Impact of livestock grazing on forest structure, plant species composition and biomass in southwestern Madagascar. In African plant diversity, systematics and sustainable development, eds. N. Beau, S. Dessein & E. Robbrecht. Proceedings of the XIXth AETFAT Congress. Scripta Botanica Belgica, 50: 82-92.
- Richard, A. F. & Ratsirarson, J. 2013. Partnership in practice: Making conservation work at Bezà Mahafaly, southwest Madagascar. Madagascar Conservation & Development, 8: 12-20.
- Richard, A. F., Dewar, R. E., Schwartz, M. & Ratsirarson, J. 2000. Mass change, environmental variability and female fertility in wild Propithecus verreauxi. Journal of Human Evolution, 39: 381-391.
- Sauther, M. L. & Cuozzo, F. P. 2009. The impact of fallback foods on wild Ring-Tailed Lemur biology: A comparison of intact and anthropogenically disturbed habitats. American Journal of Physical Anthropology, 140: 671-686.
- Sauther, M. L., Cuozzo, F. P., Youssouf Jacky, I. A., Fish, K. D., LaFleur, M., Ravelohasindrazana, L. A. L., Ravoavy, J. F. & Garcia, S. M. 2013. Limestone cliff: Face and cave use by wild ring-tailed lemurs (Lemur catta) in southwestern Madagascar. Madagascar Conservation & Development, 8: 73-80.
- Schwitzer, C., Mittermeier, R. A., Johnson, S. E., Donati, G., Irwin, M., Peacock, H., Ratsimbazafy, J.Razafindramanana, J., Louis, E. E., Chikhi, L.,

- Colquhoun, I. C., Tinsman, J., Dolch, R., LaFleur, M., Nash, S., Patel, E., Randrianambinina, B., Rasolofoharivelo, T. & Wright, P. C. 2014. Averting lemur extinctions amid Madagascar's political crisis. Science, 343: 842-843.
- Stalenberg, E., Hutchinson, M. F. & Foley, W. J. 2018. Using historical normals to improve modern monthly climate normal surfaces for Madagascar. International Journal of Climatology, 38: 5746-5765.
- Steffens, K., Rakotondranary, S. M., Ratovonamana, Y. R. & Ganzhorn, J. U. 2017. Vegetation thresholds for the occurrence and dispersal of Microcebus griseorufus in southwestern Madagascar. International Journal of Primatology, 38: 1138-1153.
- Waeber, P. O., Wilmé, L., Ramamonjisoa, B., Garcia, G., Rakotomalala, D., Rabemananjara, Z. H.,

- Kull, C. A., Ganzhorn, J. U. & Sorg, J. P. 2015. Dry forests in Madagascar: Neglected and under pressure. International Forestry Review, 16: 127-148.
- Waeber, P. O., Wilmé, L., Mercier, J.-R., Camara, C. & Lowry II, P. P. 2016. How effective have thirty years of internationally driven conservation and development efforts been in Madagascar? PLoS ONE, 11 (8), e0161115.
- Walker, R. C. J. & Rafeliarisoa, T. H. 2012. Distribution of radiated tortoise (Astrochelys radiata) bushmeat poaching effort. Chelonian Conservation and Biology, 11: 223-226.
- Wright, P. C. 1999. Lemur traits and Madagascar ecology: Coping with an island environment. Yearbook of Physical Anthropology, 42: 31-72.

Appendix 1. Counts of *Lemur catta* at five sleeping sites in Tsimanampesotse National Park between 2013 and 2018.

Sleeping site	Date	Latitude	Longitude	Sleeping tree	Male	Female	Juvenile	Total
Andranolovy	25/11/2013	24.045650	43.754200	Tamarindus indica	6	12	5	23
Andranovao camp Nord	07/11/2013	24.021250	43.739433	Delonix floribunda	6	17	8	31
Andranovao camp Nord	08/11/2013	24.021250	43.739433	Delonix floribunda	4	11	2	17
Andranovao camp Nord	08/11/2013	24.021250	43.739433	Delonix floribunda	4	5	4	13
Vintane	24/11/2013	24.043833	43.755400	Ficus sp.	4	7	4	15
Grotte maike	26/11/2013	24.049583	43.757783	Tamarindus indica	5	9	5	19
Andranolovy	21/02/2014	24.045650	43.754200	Tamarindus indica	3	4	7	14
Andranovao camp Nord	25/02/2014	24.021650	43.740850	Delonix floribunda	1	1	1	3
Andranovao camp Nord	26/02/2014	24.021250	43.739433	Delonix floribunda	1	1	1	3
Andranovao camp Sud	28/02/2014	24.028483	43.744150	Commiphora marchandii	0	1	2	3
Grotte maike	23/02/2014	24.049583	43.757783	Tamarindus indica	6	7	3	16
Vintane	22/02/2014	24.043833	43.755400	Ficus sp.	6	5	4	15
Andranolovy	24/03/2014	24.045650	43.754200	Tamarindus indica	4	10	4	18
Andranovao camp Nord	07/03/2014	24.021433	43.740667	Boscia longifolia	1	0	0	1
Andranovao camp Nord	07/03/2014	24.021250	43.739433	Delonix floribunda	1	0	0	1
Andranovao camp Nord	08/03/2014	24.021250	43.739433	Delonix floribunda	3	4	3	10
Andranovao camp Sud	08/03/2014	24.028483	43.744150	Commiphora marchandii	3	4	3	10
Andranovao camp Sud	12/03/2014	24.029717	43.744050	Delonix floribunda	3	5	4	12
Grotte maike	25/03/2014	24.049583	43.757783	Tamarindus indica	4	7	4	15
Vintane	25/03/2014	24.043833	43.755400	Ficus sp.	3	9	4	16
Andranovao camp Nord	07/04/2014	24.021250	43.739433	Delonix floribunda	2	3	3	8
Andranovao camp Nord	09/04/2014	24.021433	43.740667	Boscia longifolia	3	12	2	17
Andranovao camp Nord	24/04/2014	24.021250	43.739433	Delonix floribunda	10	13	3	26
Andranovao camp Sud	08/04/2014	24.028483	43.744150	Commiphora marchandii	4	6	4	14
Grotte maike	26/04/2014	24.049583	43.757783	Tamarindus indica	4	7	3	14
Vintane	25/04/2014	24.043833	43.755400	Ficus sp.	8	8	3	19
Andranolovy	25/05/2014	24.045650	43.754200	Tamarindus indica	6	12	4	22
Grotte maike	24/05/2014	24.049583	43.757783	Tamarindus indica	5	10	2	17
Vintane	25/05/2014	24.043833	43.755400	Ficus sp.	6	8	4	18
Andranolovy	24/09/2014	24.045650	43.754200	Tamarindus indica	6	10	4	20
Andranovao camp Nord	04/09/2014	24.021250	43.739433	Delonix floribunda	4	5	1	10
Andranovao camp Nord	05/09/2014	24.021433		Boscia longifolia	3	4	1	8
Andranovao camp Sud	05/09/2014	24.028483	43.744150	Commiphora marchandii	1	1	1	3
Andranovao camp Sud	06/09/2014	24.028940	43.742780	Didierea	4	8	2	14
•				madagascariensis				
Grotte maike	25/09/2014	24.049583	43.757783	Tamarindus indica	5	7	4	16
Vintane	25/09/2014	24.043833	43.755400	Ficus sp.	4	10	1	15
Andranolovy	24/10/2014	24.045650	43.754200	Tamarindus indica	7	12	5	24
Andranovao camp Nord  Andranovao camp Sud	07/10/2014 08/10/2014	24.021250 24.028483	43.739433 43.744150	Delonix floribunda Commiphora	4 5	5 6	1 2	10 13
•				marchandii 				
Grotte maike	25/10/2014	24.049583	43.757783	Tamarindus indica	4	8	6	18
Vintane	24/10/2014	24.043833	43.755400	Ficus sp.	4	7	6	17
Andranolovy	24/11/2014	24.045650	43.754200	Tamarindus indica	5	8	3	16
Andranovao camp Nord	07/11/2014	24.021250	43.739433	Delonix floribunda	4	4	4	12
Andranovao camp Nord	08/11/2014	24.021433	43.740667	Boscia longifolia	6	8	8	22
Andranovao camp Sud	08/11/2014	24.028483	43.744150	Commiphora marchandii	2	3	1	6
Grotte maike	25/11/2014	24.049583	43.757783	Tamarindus indica	2	7	5	14
Vintane	25/11/2014	24.043833	43.755400	Ficus sp.	5	7	7	19
Andranolovy	25/03/2015	24.045650	43.754200	Tamarindus indica	10	10	3	23
Grotte maike	25/03/2015	24.049583	43.757783	Tamarindus indica	4	10	2	16
Vintane	24/03/2015	24.043833	43.755400	Ficus sp.	6	6	4	16

Sleeping site	Date	Latitude	Longitude	Sleeping tree	Male	Fomala	Juvenile	Total
Andranolovy	25/04/2015	24.045650	43.754200	Tamarindus indica	7	8	4	19
Andranovao camp Nord	07/04/2015	24.021250	43.739433	Delonix floribunda	5	6	0	11
Andranovao camp Nord	08/04/2015	24.021433	43.740667	Boscia longifolia	4	6	1	11
·				Commiphora	-			
Andranovao camp Sud	07/04/2015	24.028483	43.744150	marchandii	3	3	1	7
Vintane	24/04/2015	24.043833	43.755400	Ficus sp.	7	10	2	19
Andranolovy	24/05/2015	24.045650	43.754200	Tamarindus indica	6	5	2	13
Andranovao camp Nord	07/05/2015	24.021250	43.739433	Delonix floribunda	2	2	1	5
Andranovao camp Sud	07/05/2015	24.028483	43.744150	Commiphora marchandii	4	6	0	10
Grotte maike	25/05/2015	24.049583	43.757783	Tamarindus indica	7	9	1	17
Vintane	25/05/2015	24.043833	43.755400	Ficus sp.	7	8	4	19
Andranolovy	24/09/2015	24.045650	43.754200	Tamarindus indica	4	10	4	18
Andranovao camp Nord	07/09/2015	24.021250	43.739433	Delonix floribunda	4	9	0	13
Grotte maike	25/09/2015	24.049583	43.757783	Tamarindus indica	4	9	3	16
Vintane	25/09/2015	24.043833	43.755400	Ficus sp.	6	13	5	24
Andranolovy	25/10/2015	24.045650	43.754200	Tamarindus indica	4	4	3	11
Grotte maike	26/10/2015	24.049583	43.757783	Tamarindus indica	4	8	8	20
Vintane	26/10/2015	24.043833	43.755400	Ficus sp.	6	14	6	26
Andranovao camp Nord	07/04/2016	24.021250	43.739433	Delonix floribunda	3	6	0	9
Andranolovy	28/09/2016	24.045590	43.754190	Tamarindus indica	7	9	1	16
Andranovao camp Nord	06/09/2016	24.021250	43.739433	Delonix floribunda	4	5	0	9
Andranovao camp Nord	08/09/2016	24.021433	43.740667	Boscia longifolia	4	4	0	8
Andranovao camp Sud	07/09/2016	24.028483	43.744150	Commiphora	5	7	0	12
Grotte maike	29/09/2016	24.049650	43.757860	marchandii Tamarindus indica	4	4	0	8
Andranolovy	28/10/2016	24.045610	43.754220	Tamarindus indica	7	10	1	17
Andranovao camp Sud	04/10/2016	24.029500	43.742580	Delonix floribunda	4	8	0	12
Grotte maike	28/10/2016	24.049620	43.757940	Tamarindus indica	4	7	6	11
				Salvadora	-	-		
Andranolovy	27/11/2016	24.045800	43.754240	angustifolia	7	10	5	17
Andranovao camp Nord	04/11/2016	24.022820	43.739720	Boscia longifolia Didierea	2	4	3	6
Andranovao camp Sud	03/11/2016	24.028940	43.742780	madagascariensis	4	10	4	14
Grotte maike	28/11/2016	24.049660	43.757880	Tamarindus indica	4	9	5	13
Vintane	27/09/2016	24.043590	43.755360	Ficus sp.	6	8	0	14
Vintane	27/10/2016	24.043730	43.755370	Ficus sp.	7	9	0	16
Vintane	27/11/2016	24.044100	43.754800	Albizia mahalao	6	11	0	17
Andranolovy	25/04/2017	24.045570	43.754190	Tamarindus indica	6	8	2	14
Andranovao camp Sud	06/04/2017	24.028800	43.743130	Didierea madagascariensis	4	6	0	10
Grotte maike	25/04/2017	24.049740	43.757470	Tamarindus indica	4	5	0	9
Vintane	24/04/2017	24.043590	43.755460	Ficus sp.	6	7	0	13
Andranolovy	25/09/2017	24.045460	43.754270	Tamarindus indica	6	10	0	16
Grotte maike	26/09/2017	24.049690	43.757890	Tamarindus indica	6	4	0	10
Vintane	06/09/2017	24.043376	43.755580	Ficus sp.	6	8	0	14
Andranolovy	24/10/2017	24.045610	43.754200	Tamarindus indica	6	9	6	21
Andranolovy	26/10/2017	24.045590	43.754200	Ficus sp.	7	9	7	23
Grotte maike	25/10/2017	24.049640	43.757920	Tamarindus indica	5	8	2	15
Andranolovy	24/11/2017	24.045630	43.754220	Tamarindus indica	5	8	5	18
Grotte maike	24/11/2017	24.049740	43.757930	Tamarindus indica	2	6	2	10
Vintane	24/03/2018	24.043820	43.755370	Ficus sp.	4	6	2	12
Grotte maike	24/03/2018	24.049730	43.757920	Tamarindus indica	2	6	0	8
Andranolovy	25/03/2018	24.045510	43.754170	Tamarindus indica	7	8	2	17
Grotte maike	24/04/2018	24.049680	43.757870	Tamarindus indica	1	6	0	7
Vintane	25/04/2018	24.043650	43.755460	Ficus sp.	5	9	3	17
Andranolovy	25/04/2018	24.045720	43.754140	Tamarindus indica	6	7	3	16
Vintane	24/05/2018	24.043870	43.755420	Ficus sp.	6	8	0	14
Andranolovy	25/05/2018	24.045630	43.754220	Tamarindus indica	4	9	1	14
					-		<del>-</del>	

Sleeping site	Date	Latitude	Longitude	Sleeping tree	Male	Female	Juvenile	Total
Andranovao	08/05/2018	24.029560	43.742420	Delonix floribunda	6	13	2	21
Andranolovy	24/11/2018	24.045650	43.754140	Ficus sp.	4	7	3	14
Vintane	25/11/2018	24.043740	43.755230	Ficus sp.	5	7	4	16
Grotte maike	25/11/2018	24.049750	43.758030	Tamarindus indica	3	6	5	14