REVIEW

Elevation gradients of lemur abundance emphasise the importance of Madagascar's lowland rainforest for the conservation of endemic taxa

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ABSTRACT

1. Elevation gradients correlate with changes in several environmental conditions and are known to influence animal abundance. Animals in regions with a naturally limited extent of lowland rainforest are expected to have evolved adaptations to intermediate elevations that provided a stable environment during their evolution.

2. Since the lowland rainforest of Madagascar has a limited extent and suffers from increasing anthropogenic pressure, it is essential to understand how well species tolerate intermediate and high elevations. In this study, we aim to quantify the relationship between lemur abundance and elevation in the eastern rainforest of Madagascar.

3. We correlated abundance data on 26 lemur species (10 genera), including 492 records from 26 studies, with elevation. We analysed the consistency of correlations across species with a meta-analytical approach. We assessed the relationship between species' body mass and elevational gradients of abundance, and controlled for species' elevational range and median elevation. We then ran generalised linear mixed models to determine whether encounter rates were influenced by elevation, body mass, plant productivity, and anthropogenic disturbance.

4. Overall, the abundance of lemur species in Malagasy rainforests was negatively correlated with elevation, and species occupying broader elevational ranges showed stronger correlations. Body mass did not influence species' tolerance of high elevations. Even though several lemur species showed tolerance to the elevation gradient, the few remaining large patches of lowland rainforests host lemur species at greater abundances than other sites. Abundance across species was negatively related to body mass, elevation and seasonality in plant productivity, and positively related to plant productivity and anthropogenic disturbance.

5. Despite the ecological flexibility of many lemur species, the largest remnant patches of lowland rainforests host the highest levels of lemur abundance and are key to lemur

conservation. It is crucial to preserve this priority habitat both for biodiversity conservation and for our understanding of lemur adaptations.

Keywords: altitude, lowland rainforest, Madagascar, meta-analysis, primate

INTRODUCTION

The study of elevation gradients in relation to biodiversity patterns has received renewed interest in ecology, biogeography, and climate change research (Lomolino 2001, Körner 2007, McCain 2007, Malhi et al. 2010). High-elevation tropical ecosystems are of particular interest, since they may have represented essential refugia during drier periods in the tropics (Wilmé et al. 2006, Colwell et al. 2008, Malhi et al. 2010). Studying the effects of elevational gradients on animal distribution and populations can unveil species' niche tolerance and help us to understand their abilities to cope with environmental changes (Körner 2007). Many studies have been focused on species' diversity patterns along elevational gradients (e.g. Brown 2001, Heaney 2001, Lomolino 2001, Rahbek 2005, McCain 2007), while only few comparative studies have explored patterns of abundance in relation to elevation (e.g. Silva et al. 2001, Bateman et al. 2010). This relationship needs further investigation, since abundance is related to extinction risk, and understanding geographic patterns of animal abundance is key to informing conservation strategies (Brown et al. 1995, Sanderson 2006). Patterns of abundance are mainly the result of interactions between species' biological traits (e.g. those related to energetics), intra- and inter-specific interactions (e.g. territoriality and competition, respectively), environmental factors (e.g. resource availability and weather), and anthropogenic disturbance (Silva et al. 1997, Lomolino 2001, Benítez-López et al. 2017, Novosolov et al. 2017, Santini et al. 2018). Among species-specific characteristics, body mass and diet have been identified as major drivers of abundance in terrestrial vertebrates

(Silva et al. 1997, Santini et al. 2018), with large species and those at higher trophic levels living at lower abundance due to their higher energetic requirements and lower resource availability (Blackburn et al. 1993, Silva et al. 1997, Santini et al. 2018).

High elevation habitats tend to be more isolated than low elevations, and therefore generally suffer lower anthropogenic disturbance (Lomolino 2001). Furthermore, several environmental conditions are associated with elevational gradients (Brown 2001, Lomolino 2001, Körner, 2007, McCain 2007). Ambient temperature, atmospheric pressure and partial pressure of biologically important gases (e.g. oxygen and carbon dioxide) gradually decrease with an increase in elevation (Brown 2001, Körner 2007). Other environmental conditions, such as precipitation and plant productivity, do not follow a specific elevation trend but vary in different regions (Brown 2001, Körner 2007). In the tropics, optimal conditions for plant productivity and precipitation generally reach their maximum at intermediate elevations (around 800-1000 m above sea level - a.s.l.; Körner 2007, Propastin 2011, but the elevation varies among regions, e.g. it is 1500 m a.s.l. in the Philippines; Heaney 2001). Therefore, tropical species are usually expected to reach their peak abundance at intermediate elevations (Lomolino 2001).

Madagascar is a major hotspot of biodiversity and endemic species (Myers et al. 2000), many of which are now threatened with extinction (Schwitzer et al. 2014). Around 50% of Madagascar's eastern rainforests have been lost since the 1950s. Deforestation has increased rapidly in recent decades (Vieilledent et al. 2018), and lowland rainforests are particularly affected (Scales 2014). The lowland rainforest has a naturally limited extent in Madagascar since large portions of the eastern floodplains drifted away as a consequence of the break-up of the Indo-Madagascar subcontinent between 90 and 80 million years ago (Krause 2003, Wells 2003). Thus, lemurs have been hypothesised to have evolved adaptations to cope with intermediate elevations that represented a more stable environment and a larger expanse of forest than lowland rainforests during the Pleistocene (Messmer et al. 2000, Goodman & Ganzhorn 2004). In support of this hypothesis, the average intermediate elevation point for lemur species diversity (around 900 m a.s.l.) is higher than that for primates outside Madagascar (around 400 m a.s.l.; Goodman & Ganzhorn 2004, Lehman 2014). The large data set accumulated over the last decade on lemur abundance and distribution at rainforest sites and the easy access to contextual ecological data offer the opportunity to explore this hypothesis with more robust analyses. The eastern rainforest in Madagascar occupies a continuum from low to high elevations, and several lemur species occur over the entire elevational range while others are restricted to narrow geographic ranges (Goodman & Ganzhorn 2004, Wilmé et al. 2006). Considering the reduced area of lowland rainforest left on the island (Schwitzer et al. 2014), identifying the lemur species that have high abundance in lowland rainforest is imperative both for their conservation and for our understanding of their adaptations.

In this study, we aimed to quantify responses of lemur abundance to elevational gradients in the eastern rainforests of Madagascar. We considered different threats and constraints to make our predictions: surface effect and plant productivity for intermediate elevations, metabolic effects for small lemur species, and human impact for large lemur species. Considering that the optimal conditions for plant productivity usually occur at intermediate elevations in the tropics and lemur diversity is known to be higher at intermediate elevations, we hypothesised that the maxima of population abundance for most lemur species also occur at intermediate elevations (600-1200 m a.s.l.; Lehman 2014). We also hypothesised that small lemur species would show their maxima of abundance in lowland rainforests, since the ratio between energy expenditure and nutrient intake is disadvantageous for them at high elevations due to the increased costs of thermoregulation and locomotion in cool and harsh habitats (Caldecott 1980). Conversely, larger species, generally more threatened by anthropogenic activities, may show their maxima of abundance at high elevations which are less accessible to humans (Lomolino 2001, Körner 2007).

To test these hypotheses, we determined the effect sizes of the correlation coefficients between species encounter rates (a proxy of abundance) and elevation. This determination was achieved via a meta-analysis to identify the overall effect across all species and genera, and how these relationships are influenced by body mass. To investigate in more depth whether the species reached a peak of abundance at intermediate elevations, and test the influence of body mass, plant productivity and its seasonality, and anthropogenic disturbance, we also ran a linear model with both linear and quadratic terms. Specifically, we predicted:

1) No monotonic relationship between abundance and elevation for the lemur species that occur over the entire elevational range, since the best conditions for their survival are expected to be at intermediate elevations.

2) A positive effect of body mass on the correlation coefficient between abundance and elevation, reflecting the expectation that larger species with higher volume/surface ratios cope better with low temperatures due to the increase in heat conservation.

3) An effect of median elevation and elevational range on the effect sizes, because the relationship between elevation and abundance can be influenced by the elevational distribution of the species. In particular, species occupying broader elevational ranges were expected to show a weaker relationship between elevation and abundance than species showing limited elevational variation.

4) A positive influence of plant productivity; a negative influence of body mass, seasonality in plant productivity, and anthropogenic disturbance.

METHODS

Data collection

We collected population abundance estimates from the literature (including peer-reviewed and grey literature) for lemur species inhabiting the eastern rainforest of Madagascar. We excluded the littoral forests on sandy soil, since these habitats differ from rainforests (Bollen & Donati 2006). We used Google Scholar and Web of Science as search engines with the following research terms: abundance OR encounter rate OR density, AND lemur OR primate AND Madagascar, AND rainforest. We then excluded rainforest from the search in case any publications on lemur abundance in rainforests had been missed. We then inspected the papers and retained those that contained relevant data. We also searched other sources such as dissertations, book chapters, the International Union for Conservation of Nature's Species Survival Commission Primate Specialist Group newsletter (Lemur News), and the Fieldiana Zoology series (that included a large dataset on lemur encounter rates at different elevations).

We included a total of 26 publications in the meta-analysis. We used encounter rates (observed individuals per transect length) and not density estimates (estimated individuals per area) for analysis, since the former were more frequent in the literature. We excluded *Daubentonia madagascariensis* from the analysis since this lemur is very difficult to detect with line transects, and encounter rates are likely to be underestimated. Using the geographic coordinates of the 26 studies, we extracted average values for the Normalised Difference Vegetation Index (NDVI; proxy of plant productivity), the seasonality in plant productivity ($NDVI_{sd}$), and the Human Influence Index (HII; proxy of anthropogenic disturbance; Venter et al. 2016). NDVI variables were calculated starting from monthly layers between 1990 and 2015 with a resolution of 0.1 degree (~11 km) downloaded from https://neo.sci.gsfc.nasa.gov/. HII is a composite variable with a resolution of 30 arc-seconds (~1km) that integrates human population density, human land use and infrastructure, and human access.

Data analysis

We estimated the relationship between encounter rate and elevation for each lemur species using Spearman rank correlations. We transformed correlation coefficients to Fisher's z scores using the correlation sample size to obtain the effect size *z* [1] and variance *Vz* [2] for each correlation:

$$z = 0.5 \times \ln\left(\frac{1+r}{1-r}\right) \quad [1]$$

$$Vz = \frac{1}{n-3} \quad [2]$$

where *r* is the correlation coefficient and *n* is the sample size. To estimate the overall trend and agreement across species, we performed a meta-analysis on the *z* scores and their variance (Borenstein et al. 2009). Correlations with n < 5 were excluded from the analysis as they do not allow the estimation of variance. We ran a mixed-effect meta-analysis on the transformed effect size values and the associated variance to calculate a summary effect size, where species were treated as random effects. We tested the residual heterogeneity using the Q-statistic, where a significant Q test indicates that a significant amount of variability exists between the effect sizes. Then, to estimate the summary effect size per genus, we repeated the same meta-analysis including genera as fixed effects and removing the model's intercept (Schwarzer et al. 2015). We tested the difference between genera with the Tukey test. Finally, to test whether species body mass, the elevational range, and the median elevation affected the relationship between abundance and elevation, we used these three variables as moderators (covariates) in three meta-regressions. Body masses for all species in our dataset were collected from MADA (the Malagasy animal trait data archive) and were log10-transformed for the meta-regression (Razafindratsima et al. 2018). We tested the overall effect of fixed effects and moderators using the omnibus test. A significant omnibus test indicated that fixed effects and moderators contributed to explaining a significant part of the residual variance in the effect sizes. We used an alpha level of 0.05 to test significance. We also tested for phylogenetic signal in the residuals of the meta-analysis using Pagel's Lambda test (Freckleton et al. 2002) and the phylogeny from Herrera and Davalos (2016), and we did not find an effect (Lambda=6.611e^{-05}; p=1.000). The analysis was done using the 'metafor' package (Viechtbauer 2010) in R v. 3. 3.2 (R Core Team 2016).

To test whether lemur abundance and elevation had a quadratic relationship, we ran a Generalised Linear Mixed Model with a Poisson family. Firstly, we multiplied each encounter rate with the transect length to obtain the observation counts as response variable, and then we used transect length ($\log_{10}$) as an offset in the analysis (Benítez-López et al. 2017). We included body mass ($\log_{10}$), elevation ($\log_{10}$), and NDVI, NDVI_{sd}, and HII ($\log_{10}$) as fixed effects in the model, using both linear and quadratic effects. We used nested random effects with Family, Genus and Species levels to allow for different intercepts due to taxonomic-specific encounter rates. We then ran a full model selection and selected the best model based on the Akaike information criterion (Appendix S1). We tested for phylogenetic signal in the residuals of the model using Pagel's Lambda and found no significant effect (Lambda=0.280; p=0.214). Since the model including HII detected an effect that seemed likely to be spurious, we ran a second model without HII and considered this model for spatial predictions. As in the first model, we did not find a phylogenetic signal in this second model (Lambda=0.295; p=0.131). We predicted from the model only within a buffer of 0.5 degrees from our observations and using the digital elevation model in Robinson et al. (2014).

RESULTS

In total, we included 492 abundance data-points from 26 lemur species (10 genera) distributed throughout the extent of Madagascar's eastern rainforest in the meta-analysis (Appendix S2, Figure 1, Table 1). Overall, the abundance of lemur species in rainforests was negatively correlated with elevation, but a significant amount of residual heterogeneity existed between effect sizes, indicating a substantial variability between species (Figure 2, Table 2). Only a limited number of species showed significant correlation coefficients (Figure 2) and peaks of abundance at low elevations (Appendix S3). For the species *Avahi meridionalis*, *Avahi laniger*, *Eulemur albifrons*, *Eulemur collaris*, *Lepilemur fleuretae*, and *Microcebus tanosi* a significant negative correlation existed between abundance and elevation, while for *Lepilemur microdon* and *Propithecus candidus* there was a significant positive correlation (Figure 2). The meta-analysis using genera as fixed effects did not detect any significant correlation coefficients between abundance and elevation (Figure 3, Table 2). Similarly, the Tukey post-hoc test did not detect any significant difference between correlation coefficients per genus (Appendix S4). We found that species' body sizes were not significantly related to the correlation coefficients obtained via the meta-analysis (Appendix S5, Table 2). The correlation coefficients between lemur abundance and elevation were negatively related to the species' elevational range (Appendix S5, Table 2) and positively related to the species' median elevation (Appendix S5, Table 2).

The selected mixed effect model estimating the trend across species also showed a negative relationship between lemur encounter rates and elevation (Appendix S6, Figure 4). Furthermore, encounter rates were negatively related to species' body mass, positively related to NDVI and negatively related to $NDVI_{sd}$ (Appendix S7). When HII was included in the model, the relationship between lemur abundance and the other variables in the model remained the same, and HII was positively related to lemur abundance (Figure 4). We only report the spatial predictions for the model without HII, since the predictions based on the model with HII are likely to reflect a spurious effect (Appendix S8). The model predicted the highest lemur abundances to occur in the lowland rainforests of Makira-Masoala, Tsitongambarika, and in forest fragments at intermediate latitudes (Figure 5). We also tested the relationship between elevation and NDVI; it is described by a loess curve that peaks at low elevation (Appendix S9).

DISCUSSION

Elevation was significantly related to the abundance of lemurs. Within species, encounter rates were negatively correlated with elevation, and the average encounter rate for all species also decreased with increasing elevation. While we expected lemurs to reach their maxima of abundance at intermediate elevations, lowland rainforests appear to host higher lemur abundance than habitats at intermediate elevations. Our prediction was based on the observation that plant production should reach its maximum at intermediate elevation, where optimal values of mean temperature, around 20°C, and annual global radiation, around 6800 MJ/m^2, are expected in rainforests (White et al. 2000, Propastin 2011). Given the latitudinal extent of the eastern rainforest of Madagascar (from 14°10' to 24°57' S), the elevations at which conditions are optimal for plant productivity are likely to show large variation. An average temperature of 20°C can be found, for example, at an elevation of around 600 m a.s.l. in the Andohahela National Park (24°-25° S), and at around 950 m a.s.l. in the Marojejy National Park (14°-15° S; Karger et al. 2017a, b). In fact, plant productivity in our dataset is higher at low elevations (Appendix S9) and this figure is in accordance with the finding that the highest lemur abundance is found in lowland rainforests.

Our results indicate that the remnant lowland rainforests that have a low habitat disturbance host lemur species at higher abundances than other sites. For example, most of the lemur species (*Avahi meridionalis*, *Eulemur collaris*, *Lepilemur fleuretae*, and *Microcebus tanosi*) inhabiting one of the largest areas of lowland rainforest, the Tsitongambarika Protected Area in south-eastern Madagascar, showed higher abundances at low elevations. The other species that showed higher abundance at low elevations, *Eulemur* *albifrons*, also inhabits a large area of undisturbed lowland rainforests in north-eastern Madagascar, the Makira Protected Area. This species of *Eulemur* is also present at high densities in the other large area of lowland rainforest in Madagascar, the Masoala National Park (148 individuals/km^2; Sterling & Rakotoarison 1998). Among nocturnal species, *Avahi laniger* reached peak abundance in the lowland rainforest fragments of Antsahanadraitry, located at intermediate latitudes, and at Manompana, located in the north-east (Appendix S2).

Small fragments of lowland rainforests are of great value for conservation (Turner & Corlett 1996). Our results support this, and indicate that remnant lowland rainforests with low habitat disturbance may contain abundant lemurs. Nevertheless, lemur species that have their maxima of abundance in lowland rainforests may be particularly vulnerable to habitat degradation, since they are adapted to more stable ecological conditions (Green & Sussman 1990, Turner 1996, Myers et al. 2000, Gibson et al. 2011). For example, Sharma et al. (2014) found that primate specialists of lowland rainforests are reduced in abundance or extirpated in small fragments, while generalist species are more abundant there as a consequence of their ability to adapt to different environments. However, the tolerance of species to human disturbance may, in fact, vary considerably (Ewers & Didham 2006). Several lemur species are known to tolerate some levels of habitat degradation via shifts in activity patterns and dietary choices (Irwin et al. 2010, Donati et al. 2016, Sato et al. 2016). This tolerance may explain why we found a positive relationship between abundance and HII. Also, low levels of habitat disturbance may provide benefits, such as high food availability and higher food nutritional content (Ganzhorn 1995). Some species actually benefit from modified habitats, as previously reported in lemurs (e.g. Herrera et al. 2011, Eppley et al. 2017), in other primates (e.g. Zarate et al. 2014, Nekaris et al. 2017), and in animal species in general (Bhagwat et al. 2008).

Most lemur species are able to occupy the entire elevation gradient that, at least in the tropics, is strictly associated with a temperature gradient (Malhi et al. 2010) and with other environmental variables such as plant productivity. This tolerance to variation in elevation can be explained by the fact that lemurs exhibit several behavioural and physiological adaptations to cope with low temperatures and lean periods. For example, some cheirogaleids of the genera *Cheirogaleus* and *Microcebus* enter prolonged periods of torpor or hibernation during the cold, dry season when resource availability is low (Dausmann et al. 2009). These physiological responses to cold and harsh environments are exceptional in the tropics and are rarely shown in other tropical taxa (McKechnie & Mzilikazi 2011, Ruf & Geiser 2015). Larger lemur species cope with low temperatures by sun-basking (e.g. *Varecia*; Vasey 2002) or huddling in groups (*Eulemur*; Donati et al. 2011; *Hapalemur* Eppley et al. 2017). Huddling is a common strategy used by social mammals and birds to reduce energy expenditure (Gilbert et al. 2010). Other proposed adaptations to the harsh Malagasy environment include low basal metabolic rate (Wright 1999) and other flexible behaviours related to the energy minimiser strategy (Donati & Borgognini-Tarli 2006, Norscia et al. 2012, Campera et al. 2014). These adaptations allow lemurs to be more taxonomically diverse throughout a wider range of elevations than primates on other continents (Goodman & Ganzhorn 2004).

The only lemur species that was most abundant at high elevations was *Propithecus candidus*. This finding is in line with previous studies indicating that this species can inhabit several types of high-elevation habitats, including sclerophyllous forests and low ericoid bushes (Patel 2014). *Propithecus candidus* is also known for its thick pelage that may represent an adaptation for cold climates at high elevations (Lehman et al. 2005). This species can also be found at low elevations (235 m a.s.l.) in the Makira National Park at very low densities, although abundance has not been estimated (Patel & Andrianandrasana 2008). The highest abundance of *Propithecus candidus* was recorded in the Marojejy National Park, which represents a priority conservation site for this Critically Endangered lemur (Patel 2014).

We predicted a negative relationship between body mass and tolerance of high elevations, reflecting the ability of large animals to cope with cold environments (Blackburn et al. 1999). Yet, we found no significant relationship, suggesting that body mass was not an important factor explaining the elevation gradients of lemur abundance in the eastern rainforest. For example, the genus *Microcebus*, which includes the smallest lemurs in Madagascar ranging from 30 to 70 g in weight (Mittermeier et al. 2010), did not show higher abundances at low elevations. Only the abundance of *Microcebus tanosi* was significantly negatively related to elevation. The negative correlation coefficient between elevation and abundance was stronger for species present over a large elevation range, including lowland rainforests (Appendix S5). This finding contradicts our hypotheses, since the best conditions were expected at intermediate elevations (around 900 m a.s.l.) for most species. These results may be due to the fact that encounter rates were only available in two large portions of lowland rainforest, the Tsitongambarika Forest in the south-east and the Makira Forest in the north-east of Madagascar. Most of the lowland rainforests at intermediate latitudes have been cleared or reduced to small fragments where lemurs have been largely extirpated (Green & Sussman 1990, Vieilledent et al. 2018). Few remaining lowland forest fragments in central Madagascar can support populations of large lemurs (Ganzhorn et al. 2001), and even in larger fragments there has been an increase in human impacts. As a result, most of the encounter rates are from sites above 450 m a.s.l. We cannot exclude the possibility that some species have a larger elevational range not reflected by data on abundance in the literature. Nevertheless, the data considered for this analysis encompass all the elevation strata and we consider them representative for the eastern rainforest.

It is likely that the current distribution of many extant lemurs does not reflect their niche tolerance, but it is rather limited to areas of low anthropogenic impact where they were able to persist. A reduction of the elevational range of occurrence may have reduced the strength of the abundance – elevation relationship, thus masking a stronger dependence of species on low-elevation habitats. Indeed, the distortion of natural macroecological pattern is a common phenomenon that can limit our understanding of causal relationships in nature (Varela et al. 2009, Di Marco & Santini 2015, Santini et al. 2017). Other factors (e.g. plant productivity, competition; Herrera et al. 2018, Santini et al. 2018) may have contributed to lemur abundance patterns, although understanding the complexity of these interactions was beyond the scope of this study.

Although lemur species are well-known for their ecological, physiological, and behavioural flexibility, we found that their abundance was generally higher at lower elevations. Given the limited extent of undisturbed lowland rainforests in Madagascar, it is pivotal to promote conservation measures to maintain this habitat that hosts high abundances of several lemur species (Kremen et al. 1999, Campera et al. 2017). Rapid habitat degradation is occurring elsewhere in lowland rainforests (Myers et al. 2000, Gibson et al. 2011), so a similar analysis could be extended to other regions of the world where endemic taxa occur at different elevations, to determine their ability to occupy elevation gradients. Our results suggest that the lowland rainforest at intermediate latitudes in Madagascar may have contained large populations of lemurs, and that some of the most suitable areas for conservation may have already disappeared. Although there are no lemur species that are exclusively found in lowland forests and thus, strictly speaking, lemurs may be less vulnerable than other taxa to the disappearance of this habitat, losing this environment is not only important for conservation reasons. The eastern rainforest of Madagascar represents a continuum from low to high elevations, and the ability of the lemurs to use this elevational range has been hypothesised to explain the macroevolution of this group (Goodman & Ganzhorn 2004, Wilmé et al. 2006). The vanishing of the lowland habitats will thus hamper forever our ability to understand fully the adaptations and flexibility of this extraordinary group of primates.

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Table 1: Number of study locations (N; 492 in total), body mass (g), and expected and observed elevation range (m a.s.l.) for each of the 26 lemur species included in the meta-analysis. The data are derived from 26 publications. The expected elevation range includes all the locations in which the species is expected to be found based on species accounts, including sites where it was not encountered during transects, while the observed elevation range includes only the locations where the species was encountered. Body mass was retrieved from Razafindratsima et al. (2018), apart from *Microcebus tanosi* which was retrieved from Rasoloarison et al. (2013).

Species	**N**	**Body mass (g)**	**Elevation range (expected; m a.s.l.)**	**Elevation range (observed; m a.s.l.)**
Avahi laniger	15	1180	210–1550	210–1260
Avahi meridionalis	10	1213	178–1875	178–1500
Avahi peyrierasi	34	1034	180–1625	180–1625
Cheirogaleus crossleyi	19	292	638–1262	638–1262
Cheirogaleus major	24	468	178–1625	178–1625
Eulemur albifrons	11	1896	275–1875	275–1260
Eulemur albocollaris	6	2250	67–1625	67–1210
Eulemur collaris	13	2180	125–1875	125–1875
Eulemur fulvus	6	1633	905–1224	905–1224
Eulemur rubriventer	57	1978	180–1875	180–1625
Eulemur rufifrons	40	2151	180–1625	180–1625
Hapalemur aureus	6	1580	720–1625	810–1625
Hapalemur griseus	37	813	638–1283	638–1283
Hapalemur meridionalis	16	855	178–1875	178–1625
Hapalemur occidentalis	11	847	450–1875	450–1625
Indri indri	12	6593	500–1550	500–1224
Lepilemur fleuretae	9	890	178–1875	178–440
Lepilemur microdon	31	1105	638–1625	720–1625
Lepilemur seali	10	952	450–1625	520–1625
Microcebus mittermeieri	7	45	450–1625	450–1625
Microcebus rufus	33	44	638–1625	638–1625
Microcebus tanosi	11	52	178–1875	178–1875
Prolemur simus	8	2395	180–1625	180–1224
Propithecus candidus	10	5270	450–1875	520–1875
Propithecus edwardsi	37	5686	638–1625	638–1262
Varecia variegata	19	3524	180–1224	180–1224

Table 2. Results of the intercept-only meta-analysis, the meta-analysis using genera as fixed effects and the three metaregressions with body mass, median elevation and elevational range. SE = standard error; QE = statistic for the test of residual heterogeneity; QM= test statistic for the omnibus test of coefficients; P-values: * = p <0.05.

Model	**Term**	**Estimate (SE)**	**QE**	**QM**
Intercept-only	Intercept	-0.238 (0.010) *	76.426 *	
Genus as Fixed effects	*Avahi*	-0.423 (0.339)	64.945 *	7.215
	Cheirogaleus	-0.217 (0.399)		
	Eulemur	-0.460 (0.253)		
	Hapalemur	0.013 (0.307)		
	Indri	-0.389 (0.612)		
	Lepilemur	-0.135 (0.351)		
	Microcebus	-0.365 (0.356)		
	Prolemur	-0.384 (0.681)		
	Propithecus	0.143 (0.413)		
	Varecia	-0.066 (0.571)		
Body mass metaregression	Intercept	-0.308 (0.236)	76.669 *	0.138
	Body mass	0.002 (0.006)		
Median elevation metaregression	Intercept	-1.765 (0.488) ***	59.087	10.215 **
	Median elevation	0.150 e^{-2} (0.047 e^{-2}) **		
Elevational range metaregression	Intercept	0.455 (0.341)	70.192 *	4.447 *
	Elevational range	-0.053 e^{-2} (0.025 e^{-2}) *		

Figure 1: Map of Madagascar, showing the ?? sites included in the meta-analysis of the relationship between lemur encounter rate and elevation in the eastern rainforest of Madagascar.

Figure 2: Forest plot of effect sizes (Fisher's Z) for abundance in relation to elevation for each of the 26 lemur species and in summary (bottom bar), with 95% confidence intervals (horizontal bars). Overall, lemur abundance is negatively related to elevation. The size of the square for each species is proportional to the sample size (ranging from 6 to 57 samples for each species). The dashed line indicates zero (no relationship between abundance and elevation).

Figure 3: Forest plot of the effect sizes (Fisher's Z) for abundance in relation to elevation for each lemur genus estimated as fixed effects in the meta-analysis, with 95% confidence intervals (horizontal bars). The dashed line indicates zero (no relationship between abundance and elevation).

Figure 4: Results of the Generalised Linear Mixed Model with encounter rates (~abundance; ΔER) of lemurs in Madagascar's eastern rainforest as the dependent variable. BM: Body Mass; El: Elevation; NDVI: Normalised Difference Vegetation Index (proxy of plant productivity); NDVI_{sd}: proxy of seasonality in plant productivity; HII: Human Influence Index (proxy of anthropogenic disturbance).

Figure 5: Model predictions for encounter rates (?????) of lemurs in Madagascar's eastern rainforest from the Generalised Linear Mixed Model.

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SUPPORTING INFORMATION.

Additional supporting information may be found in the online version of this article at the publisher's website.

Appendix S1. Model selection for the Generalised Linear Mixed Models with encounter rates of lemurs in Madagascar's eastern rainforest as the dependent variable.

Appendix S2. List of data on the abundance of lemur species in the eastern rainforest in Madagascar included in the meta-analysis.

Appendix S3. Mean lemur abundance (encounter rates or densities) in elevation categories (every 400 m a.s.l.).

Appendix S4. Results of the Tukey post-hoc tests between lemur genera included in the meta-analysis.

Appendix S5: Metaregression between the correlation coefficient of the relationship between encounter rate and elevation and species body mass, elevational range, and median elevation.

Appendix S6: Model output of the Generalised Linear Mixed Models with encounter rates of lemurs in Madagascar's eastern rainforest as the dependent variable.

Appendix S7: Results of the Generalised Linear Mixed Model with encounter rates of lemurs in Madagascar's eastern rainforest as the dependent variable (excluding the Human Influence Index; HII).

Appendix S8: Model prediction for the Generalised Linear Mixed Model with encounter rates of lemurs in Madagascar's eastern rainforest as the dependent variable (including the Human Influence Index; HII).

Appendix S9: Relationship between elevation (in m a.s.l.) and the Normalised Difference Vegetation Index (NDVI) in Madagascar's eastern rainforest.