

This is a post-peer-review, pre-copyedit version of an article published in *International Journal of Primatology*. The final authenticated version is available online at: <https://doi.org/10.1007/s10764-021-00215-5>

A National-Level assessment of Lemur Hunting Pressure in Madagascar

Cortni Borgerson^{a,b,†*}, Steig E. Johnson^{c,†}, Emma Hall^d, Kerry A. Brown^d, Pamela R. Narváez-Torres^c, Be Jean Rodolph Rasolofoniaina^b, Be Noel Razafindrapaoly^b, Samuel D. Merson^c, Katharine E.T. Thompson^f, Sheila M. Holmes^g, Edward E. Louis Jr.^h, Christopher D. Golden^{b,i}.

†Contributed equally

*Corresponding Author

a.
Department of Anthropology
Montclair State University
1 Normal Ave
Montclair, NJ 07043 USA

b.
Madagascar Health and Environmental Research (MAHERY)
Maroantsetra 512, Madagascar

c.
Department of Anthropology and Archaeology
University of Calgary
2500 University Dr NW
Calgary, AB, T2N 1N4, Canada

d.
Department of Geography, Geology and the Environment, Centre for Earth and Environmental Science Research (CEESR), Kingston University,
Penrhyn Rd,
Kingston upon Thames KT1 2EE, United Kingdom

e.
Parks Australia
John Gorton Building
King Edward Terrace, Parkes
ACT 2600, Australia

f.
Department of Anthropology
Interdepartmental Doctoral Program in Anthropological Sciences (IDPAS)
Stony Brook University
100 Nicolls Rd
Stony Brook, NY 11794 USA

g.
Department of Wildlife, Fish, and Environmental Studies

Swedish University of Agricultural Sciences
Skogsmarksgränd
90183 Umeå, Sweden

h.

Grewcock's Center for Conservation and Research
Omaha's Henry Doorly Zoo and Aquarium
3701 S 10th St
Omaha, NE 68107, USA

i.

Department of Nutrition
Harvard T.H. Chan School of Public Health, Harvard University
677 Huntington Ave
Boston, MA 02115 USA

Abstract

Hunting is one of the greatest threats to nonhuman primates worldwide. Despite Madagascar's status as a primate mega-diversity country, a critical lack of information on the hunting of lemurs at the national scale persists. Here, we synthesize the current state of knowledge of the annual rates of household-level lemur hunting near ten protected areas, representing most ecoregions in Madagascar. We examine geographic and taxonomic variation in lemur hunting, including an analysis of hunting relative to species density, extinction risk, and intrinsic ecological characteristics of species. We found that lemurs are commonly hunted across Madagascar; the rural households in our study ate, on average, more than one lemur each year, or a median of 4.1% of the lemur species' population size where densities are known. However, this pressure varied significantly across sites and species, reaching its highest levels in the northeastern rainforest region. While hunting levels are concerning for numerous threatened species, hunting pressure was driven primarily by species availability, and among ecological traits, small body size was related to increased hunting; however, conservation status showed no such relationship. This first national-level assessment of hunting, including one-third of Madagascar's lemur species and more than a tenth of the world's primates, identifies regional variation and lemur taxa at acute risk from hunting—important steps toward developing targeted strategies to conserve one of the world's most threatened groups of vertebrates.

Keywords Bushmeat · Hunting · Lemurs · Madagascar · Primate · Wildlife

Introduction

Hunting for subsistence or commercial markets is among the greatest threats to nonhuman primates worldwide (Estrada *et al.* 2017). Wild mammals have long been an essential component of global food security (Booth *et al.* 2021). Yet, as human populations grow, the demand for natural resources also increases; wild meat now comprises more than one-fifth of all meat eaten in many sub-Saharan African nations (Smith 2016). This increase in hunting has contributed to high extinction risk in nearly two-thirds of the world's primate species (Estrada *et al.* 2017; IUCN 2020). The loss of primates also threatens to undermine forest regeneration processes, imperiling a wide variety of taxa, including humans (Effiom *et al.* 2013; Gardner *et al.* 2019; Peres *et al.* 2016). In spite of these known stressors and impacts, we still lack information on the hunting of primates in many biodiversity hotspots.

Madagascar is a primate mega-diversity country, and lemurs are one of the most threatened groups of vertebrates globally (Schwitzer *et al.* 2014). In Madagascar, hunting, along with habitat loss and climate change, are the main drivers of extinction risk for lemurs (IUCN 2020; Schwitzer *et al.* 2013). It is therefore crucial to obtain current, quantitative assessments of the putative risks to lemur populations, especially due to their disproportionate contribution to global primate diversity (Estrada *et al.* 2018) and to ecosystem functioning in Madagascar (Ganzhorn *et al.* 1999; Razafindratsima *et al.* 2018; Razafindratsima and Dunham 2014).

Relative to mainland Africa and South America (e.g., Duporge *et al.* 2020; Kumpel *et al.* 2010; Martins and Shackleton 2019; Stafford *et al.* 2017; van Velden *et al.* 2018), comprehensive assessment of hunting risk for lemurs across Madagascar has been limited. Evidence has begun to accumulate in the last decade that hunting, primarily for household-level subsistence, occurs at many locations throughout the island and that lemur species across the taxonomic range are targeted by hunters (Golden *et al.* 2022). Poverty, food insecurity, and malnutrition are important drivers of lemur hunting in Madagascar (Borgerson *et al.* 2016, 2019a; Merson *et al.* 2019; Reuter *et al.* 2016), and, where documented, hunting is unlikely to be sustainable (Borgerson *et al.* 2019a; Brook *et al.* 2019; Golden *et al.* 2019; Razafimanahaka *et al.* 2012). The historical depth of hunting pressure is also evidenced by cut marks on bones from both extinct and extant lemur genera dating from more than 2000 years ago (Perez *et al.* 2005). Lemurs may have been hunted for far longer, as recent finds reveal cut marks on elephant bird remains from 10,500 years ago (the earliest evidence of human presence in Madagascar) (Hansford *et al.* 2018). Hunting likely contributed to collapsing populations and the extinction of much of Madagascar's megafauna, including giant lemurs, by roughly 1000 years ago (Godfrey *et al.* 2019).

An understanding of which risk factors drive lemur hunting, including geography, conservation status, density, and the intrinsic characteristics of individual species, may aid the targeting of effective conservation strategies in Madagascar. Hunting pressure may contribute to the small or declining population size of many lemur species, key criteria for assessing extinction risk (IUCN 2020). In this case, species in more threatened categories (e.g., IUCN categories CR and EN) may have higher offtake levels. Alternatively, low-risk species may presumably be more abundant and therefore more frequent targets for hunters (Chaves *et al.* 2020; Dunn and Smith 2011; Fa *et al.* 2005; Martin *et al.* 2013; Sirén and Wilke 2016).

Intrinsic ecological traits of lemur species may also influence hunters' likelihood of encountering or preferring particular prey. Larger species may be both more conspicuous and more desirable, given the meat provided per unit effort (Isaac and Cowlishaw 2004; Jerzolimski and Peres 2003; Ripple *et al.* 2016; Stafford *et al.* 2017). Diet may also contribute to variation in hunting pressure. For example, larger daily and home ranges in many frugivores and omnivores may increase their encounter rates relative to folivores (Carbone *et al.* 2005; Milton and May 1976). Hunters in Madagascar target frugivores when they can predict their location at seasonally fruiting trees (Borgerson 2016); presumably it would be more difficult to predict where to target certain folivorous species. Furthermore, hunters may avoid folivores or prefer frugivores due to taste preferences (Koster *et al.* 2010). Lastly, activity patterns may be linked to variation in hunting risk, for example, when day-active species are more commonly seen and targeted by hunters. Indeed, hunting and other forms of anthropogenic disturbance are driving diurnal mammals worldwide to adopt more nocturnal habits (Gaynor *et al.* 2018). However, both the prevalence of passive hunting methods, such as snare trapping, and the knowledge of sleeping sites may leave nocturnal species equally susceptible.

Despite the growing body of evidence for hunting over space and time, there persists a lack of assessment of the hunting of lemurs at the national scale in Madagascar. There has been a concentration of quantitative research in the northeast (Borgerson 2015; Brook *et al.* 2019; Golden 2009), which may result in biased interpretations of which areas and species are especially prone to hunting risk. We aim to help fill the comparative, national-level knowledge gap for Madagascar's endemic primates by consolidating data on lemur-hunting levels across Madagascar and testing lemur species characteristics that may predict hunting pressure.

Here, we synthesize the current state of knowledge of the global levels of hunting risk for one-third of all lemur species (IUCN 2020). Specifically, we compare geographic variation in lemur hunting pressure among ten protected areas, and variation in annual offtake levels per household, both absolute and relative to species density, for 42 lemurs at the species and family levels, and describe the severity of hunting levels in terms of estimated offtake as a percentage of local population size. Further, we model how hunting levels relate to overall extinction risk and intrinsic ecological characteristics of species, including adult body mass, primary diet, and activity pattern; for a subset of sites, we also assess the effects of these predictors on offtake levels accounting for lemur species availability (i.e., density). This preliminary national assessment of lemur hunting builds on the growing body of site-based investigation into wildlife hunting in Madagascar, and may help to target lemur conservation strategies by identifying the taxa and regions at greatest risk from unsustainable hunting.

Methods

Study Sites and Species

We examined the hunting of lemurs surrounding ten protected areas in Madagascar (2009–2019; Fig. 1, Table I). These sites are broadly distributed and encompass a substantial amount of the cultural, climatic, ecological, and biological diversity for which Madagascar is well known (Goodman *et al.* 2018), and that can affect hunting

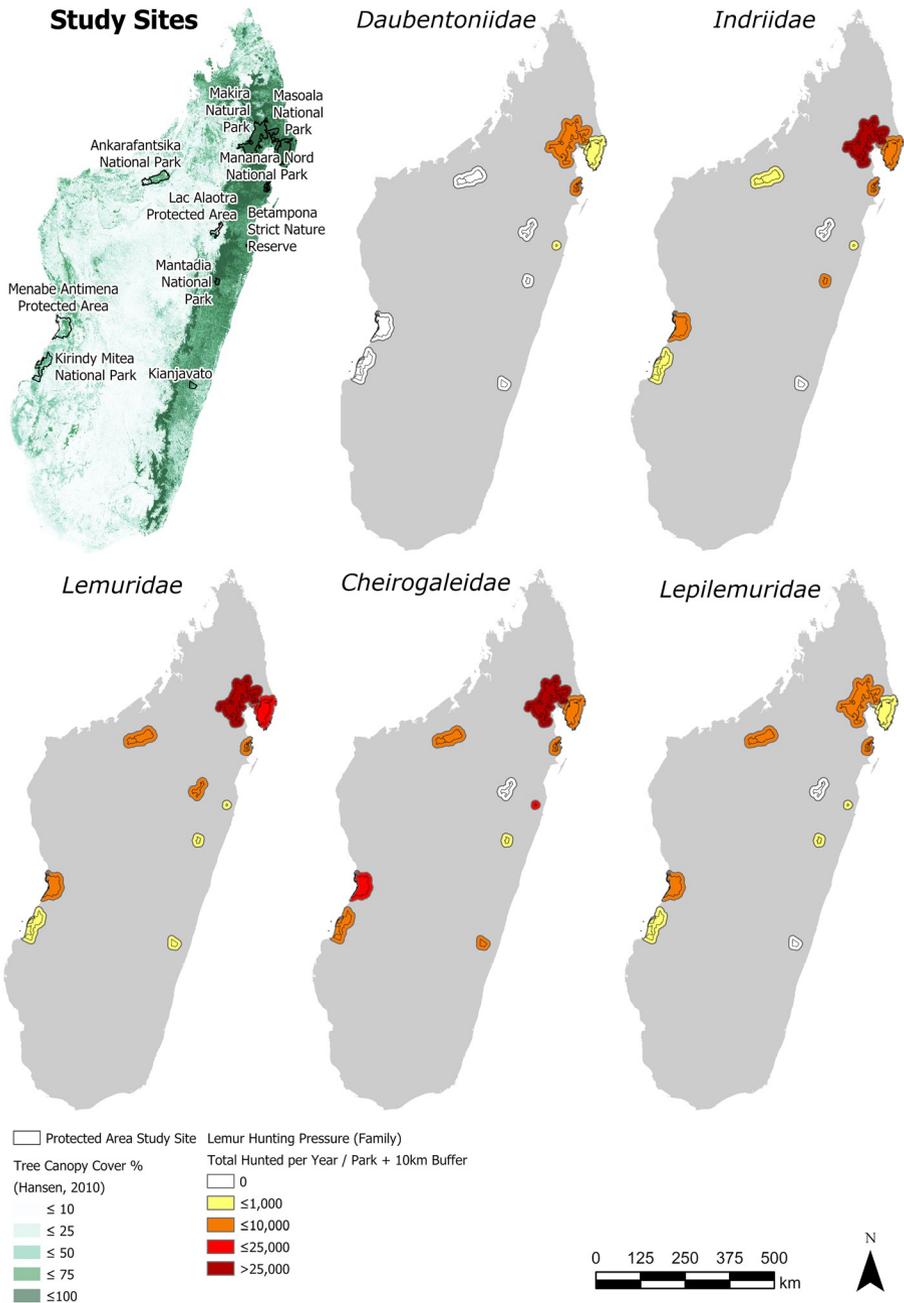


Fig. 1 Study sites and estimated hunting pressure (total number of individuals per year) by lemur family across ten protected areas in Madagascar (2009-2019).

behavior. We analyzed hunting data on 42 lemur species from all five families (Table II, Electronic Supplementary Material [ESM] Table SI). These species include all those present in our study sites. In the northeast of Madagascar, we investigated

Table 1 Size, forest cover, human population characteristics, and number of lemur species surveyed for the ten protected areas

Protected area	Area (km ²)	Area <10 km PA ^a (km ²)	Forest (%)	Forest <10 km PA (%)	Human population density (individuals per km ²) <10 km PA
Ankarafantsika	1365.13	2332.18	72	14	108.51
Betampona	22.40	504.87	99	31	81.92
Kianjavato	246.67	957.04	26	26	60.12
Kirindy Mitea	1562.21	2266.54	71	36	12.25
Lac Alaotra	424.77	1707.62	44	12	166.35
Makira	3721.79	6000.36	99	22	51.04
Mananara-Nord	241.56	1072.89	94	25	78.77
Mantadia	154.56	889.14	99	29	31.16
Masoala	2115.30	2553.42	99	26	56.65
Menabe Antimena	1895.33	1632.77	53	52	115.44

^a PA = protected area. All areas are terrestrial and exclude marine regions within the PA.

hunting of 18 species of lemur within three protected areas, the Masoala National Park, Makira Natural Park, and Mananara–Nord National Park, whose lowland and medium moist evergreen forests, littoral forests, mangroves, and high and low littoral thickets provide ecosystem services for local Malagasy of the primarily Betsimisaraka and Tsimihety ethnolinguistic groups. In the northwest, we collected data at Ankarafantsika National Park, which is home to dry deciduous and riparian forests as well as wooded grasslands, which provide for eight species of lemur and the Sakalava and Betsileo people. In central Madagascar, we assessed hunting of 16 lemur species within three protected areas, Lac Alaotra Protected Area, Betampona Strict Nature Reserve, and Mantadia National Park, in ecosystems characterized by lowland and medium moist evergreen forest, freshwater marshes, and wetlands, and home to the Betsimisaraka and Sihanaka people. In the southeast, we included the forests of Kianjavato (partly within the COFAV protected area) and, in the southwest, Kirindy Mitea National Park and the Menabe Antimena Protected Area. Kianjavato is characterized by lowland moist evergreen forests that provide for the Antaimbahoaka people and nine species of lemur. Kirindy Mitea National Park and the Menabe Antimena Protected Area are composed of dry deciduous forest, dry spiny thicket, littoral thicket, and mangroves which provide for nine species of lemur and the Sakalava–Masikoro and Sakalava–Vezo people. All sites also contained regional minority sociolinguistic ethnic groups and significant regions of agricultural and residential lands, as well as secondary grasslands, forests, and thickets (Goodman *et al.* 2018).

Rainfall, temperature, and seasons vary greatly across the sites. While the northeast might experience >3000 mm of precipitation a year (with 0 months of dryness, rainfall peaking in May–October) and a mean temperature range of 11–30°C (peaking in December–February), the southwest might instead receive <700 mm of rain (with 7 dry months and rainfall peaking in September–November) and a mean temperature range of 13–32°C (instead peaking in November–April) (Rakotondrafara *et al.* 2018).

For each of the 42 lemur species present at our study sites, we obtained data on conservation status (IUCN 2020) and ecological traits (adult body mass, diet, and activity pattern) from published sources (Mittermeier *et al.* 2010; Razafindratsima *et al.* 2018; Rowe and Myers 2016) (ESM Table SI). In a few cases, we were unable to ascertain the mouse lemur species (genus *Microcebus*) present. We adopted a conservative approach in terms of conservation status, using only data from the lower risk species that might be present at the site. This resulted in including values for *M. lehilahytsara* at Makira Natural Park and Masoala National Park (Poelstra *et al.* 2020) and *M. murinus* at Ankarafantsika National Park (Reuter *et al.* 2020). In two instances, the conservation status has not yet been evaluated (the newly described *Microcebus jonahi* at Mananara–Nord National Park (Schüßler *et al.* 2020), and the unknown *Microcebus* sp. at Lac Alaotra); we therefore excluded these taxa from analyses.

Household Surveys

Between 2009 and 2019, we conducted surveys of hunting in Malagasy by a native or fluent speaker of the regional dialect. We interviewed either the male or female heads of 4275 households in 172 communities to gather information on social, demographic, and behavioral characteristics of rural households (including lemur hunting and

consumption). Because Madagascar's seasonality affects hunting practices (Borgerson 2016; Golden *et al.* 2019), all surveys of hunting included recalls of the total number of each species of lemur they had caught during the prior year (Table II). This method has been shown to provide more accurate estimates of annual hunting rates than extrapolated recalls of the prior month because of the high seasonality, relatively low catch rates, and high saliency of lemurs from the hunters' perspective (Golden *et al.* 2013). We surveyed all households in small communities; in communities with >50 households, we either surveyed all households, or randomly selected study households using a grid system in each village, and either using a zig-zag method to bisect all quadrants,

Table II Estimated total number of individuals from 42 lemur species hunted per year (2009-2019) in ten protected areas and peripheral zones in Madagascar. Mean number of lemurs eaten per household per year^a are shown in parentheses

Lemur Species ^b	All Sites										
	Northern Madagascar				Central Madagascar			Southern Madagascar			
	Ankarafantsika National Park	Makira Natural Park ^c	Mananara-Nord National Park ^d	Masoala National Park ^e	Betampona Strict Nature Reserve ^f	Lac Alaotra Protected Area ^g	Montadia National Park ^h	Kianjavato	Kirindy Mita National Park ⁱ	Menabe Antimena Strictly Res. Area ^j	
	354,855 (1.26)	10,556 (0.18)	210,133 (5.25)	27,373 (1.48)	19,934 (0.62)	12,277 (1.16)	2,466 (0.03)	4,197 (0.34)	4,776 (0.32)	8,535 (1.75)	56,642 (1.52)
Chirogaleidae 126,347 (2.49)	201 (0.01)	46,398 (0.31)	41,406 (0.64)	3,279 (0.17)	1,578 (0.05)	0 (0)		35 (0.01)	135 (0.01)	4,322 (0.89)	94 (<0.01)
<i>Alouatta trichotis</i>	6,446 (0.33)										658 (0.02)
<i>C. medius</i>	658 (0.02)							0 (0)	0 (0)		
<i>M. jollyae</i>	3,740 (0.25)									3,740 (0.25)	
<i>M. jonahi</i>	5,086 (0.26)			5,086 (0.26)							
<i>M. lehilahytsara</i>	0 (0)							0 (0)			
<i>M. murina</i>	21,306 (0.48)									2,517 (0.52)	18,789 (0.44)
<i>M. simmonsii</i>	11,494 (1.08)					11,494 (1.08)					
<i>M. sp.</i>	29,653 (0.12)	135 (<0.01)	28,770 (0.44)		748 (0.02)		0 (0)				
<i>Mirza coquerelli</i>	282 (0.01)										282 (0.01)
<i>Platanus fuscifer</i>	83 (<0.01)				83 (<0.01)						
<i>P. pallescens</i>	0 (0)										0 (0)
Avahiidae 58,603 (0.43)	41,050 (0.18)		37,514 (0.58)	2,209 (0.11)	1,993 (0.06)	249 (0.02)	0 (0)	1,078 (0.17)			
<i>A. mooreorum</i>	1,993 (0.06)				1,993 (0.06)						
<i>A. occidentalis</i>	271 (<0.01)										
<i>A. peyrierasi</i>	0 (0)								0 (0)		
<i>Indri indri</i>	7,240 (0.05)		4,795 (0.07)	2,409 (0.13)		36 (<0.01)		0 (0)			
<i>Propithecus diademata</i>	261 (0.02)					0 (0)		263 (0.04)			
<i>P. coquerelli</i>	0 (0)	0 (0)									0 (0)
<i>P. verreauxi</i>	7,789 (0.12)									274 (0.06)	7,515 (0.18)
<i>P. candidus</i>	0 (0)										
Eulemuridae 122,208 (0.99)	49,466 (0.44)		38,134 (0.59)		11,296 (0.35)	36 (<0.01)			45 (<0.01)	438 (0.09)	2,912 (0.07)
<i>E. rufifrons</i>	3,395 (0.05)										
<i>E. fulvus</i>	6,818 (0.09)	6,418 (0.11)						400 (0.06)			
<i>E. rubriventer</i>	9,364 (0.05)		9,364 (0.14)				0 (0)		0 (0)		
<i>Haplolemur griseus</i>	864 (0.03)					249 (0.02)		209 (0.03)		406 (0.03)	
<i>H. occidentalis</i>	38,379 (0.18)		33,508 (0.51)	2,878 (0.15)	1,993 (0.06)		0 (0)				
<i>H. albobrunneus</i>	2,466 (0.03)						2,466 (0.03)				
<i>Prolemur simus</i>	395 (0.02)							35 (0.01)		360 (0.02)	
<i>Varecia rubra</i>	2,199 (0.03)		621 (0.01)		1,578 (0.05)						
<i>V. variegata</i>	8,657 (0.06)		4,851 (0.07)	3,681 (0.19)		0 (0)		35 (0.01)		90 (0.01)	
<i>Leontideus rosalia</i>	9,985 (0.15)		9,985 (0.15)								
<i>L. scottorum</i>	415 (0.01)				415 (0.01)						
<i>L. edwardsi</i>	1,624 (0.03)	1,624 (0.03)									
<i>L. rafiquadatus</i>	3,334 (0.13)									985 (0.2)	2,349 (0.05)
<i>L. mustelinus</i>	175 (0.02)					71 (0.01)		104 (0.02)			
<i>L. hollandorum</i>	4,283 (0.22)		4,283 (0.22)								
<i>Doubeumontia madagascariensis</i>	4,787 (0.03)	0 (0)	1,015 (0.02)	3,547 (0.18)	83 (<0.01)	142 (0.01)		0 (0)			

^a Modified from Golden *et al.* 2022; original data collected by CDG, CB, SEJ, BJRR, BNR, SDM, KETT, PRNT, and SMH.

^b Lemur illustrations copyright © 2018 by Joel Borgerson, all rights reserved.

^c Borgerson *et al.* 2019b; 419 households sampled.

^d Golden *et al.* 2014a; 1155 households sampled.

^e Golden *et al.* 2022; 287 households sampled.

^f Borgerson *et al.* 2019a; 387 households sampled.

^g Golden *et al.* 2014b; 298 households sampled.

^h Borgerson *et al.* 2018a; 485 households sampled.

ⁱ Merson *et al.* 2019; 362 households sampled.

^j Borgerson *et al.* 2018b; 336 households sampled.

^k Thompson *unpubl.data.*; 89 households sampled.

^l Merson *et al.* 2019; 456 households sampled.

selecting every second household, or by assigning a number to each household in each grid, and selecting a subset of households in all quadrants using a random number array.

Hunting Levels

We included two hunting measures for each lemur species: 1) mean number of individuals hunted per household per year and 2) total number of individuals per protected area per year. To estimate the latter, we multiplied the mean number of each lemur species eaten per household by the total number of households living within 10 km of the protected area (the maximum distance focal hunters walked from communities during a single day). To calculate the total number of households living within 10 km of each protected area, we used 1 km² gridded high-resolution satellite images of roofs from WorldPop (Lloyd 2016; Lloyd *et al.* 2017). For simplicity, we refer to the protected area and its associated 10 km periphery zone by the protected area name. We divided population size by the mean number of people per household within each region (Borgerson *et al.* 2018a,b, 2019a,b, *unpubl. data*; Golden *et al.* 2014b, 2019) to determine the total number of households surrounding each protected area. To estimate population density, we 'moved' households inside the protected area into the 10 km periphery, to ensure that we included these households in our analysis. We calculated the area of each protected area and its peripheral zone using shapefiles and data provided by Direction du Système des Aires Protégées (2017 and employed in Goodman *et al.* 2018), The World Database on Protected Areas (UNEP-WCMC and IUCN 2020), and Global Forest Watch (2019). To visualize geographic variation in hunting pressure, we used a Natural Jenks (Breaks) classification algorithm, standardized into five categories, to compare the total number of lemurs eaten within each lemur family within a 10 km radius of each protected area (ArcGIS 10.8.1).

Lemur Density and Population Size

To understand how lemur availability affects hunting pressure, we used distance sampling methods (Buckland *et al.* 1993; Buckland 2001), analyzed using Rdistance (McDonald *et al.* 2019), to assess the density of lemur species in northeastern Madagascar from 2012 to 2019 (Masoala National Park [CB, BNR, CDG], Makira Natural Park [CDG], and surrounding communities) and in Kianjavato from 2015 to 2016 (PRNT, SMH, SEJ). We calculated the densities of all lemur species that exceeded a minimum of 30 observations. The exception was *Prolemur simus* at Kianjavato ($N = 14$), which we included to provide information for all lemur species reported to be hunted at this site; however, the density estimate for this species should be treated with caution. We established a total of 213.5 km of transects (using a GPS): 176 km in Masoala, 20 km in Makira, and 17.5 km in Kianjavato. In Masoala, we sampled 34 transects (each 2 km in length) within forests adjacent to 17 communities. We walked each transect a minimum of 20 times per year, from 2012 until 2019. Two additional transects (total of 140 km in length, each walked twice in 2016) extended from the western border of the Masoala National Park through the interior, and ended at the eastern border, through the park's northern and southern regions. In Makira, we sampled 20 transects (each 1 km in length) within forests adjacent to 11 communities,

from 2012 until 2014. In Kianjavato, we sampled 35 diurnal transects and 22 nocturnal transects (each 0.5 km in length) in five forest fragments. We walked each transect 16–45 times during the day and 5–12 times at night in 2015 and 2016. We walked transect lines at a maximum rate of 1–1.5 km per hour. Each time we saw a lemur, we recorded the group size/composition, height (m), sighting angle, and the perpendicular distance (m) of the animal (or the center of the group of animals) from the transect line. To estimate the total population size of each species at each of the three sites, we summed the products of the species density and forest cover within the protected area and within the 10 km peripheral zones. We used this information to evaluate the severity of hunting pressure, to which, given uncertainty owing to estimation and extrapolation for both human and lemur population sizes, we report ordinal categories of concern based on the estimated percentage of the total population caught each year (Low = < 1%, Medium = 1 < 10%, High = 10 < 20%, Very High = ≥20%).

Statistical Analyses

We used linear mixed-effects models (LMMs) to determine relationships between annual offtake (mean number of lemurs hunted per household per year), offtake relative to density (annual offtake divided by the density of that species per km²), and four predictor variables: conservation status (IUCN category), mean adult body mass, primary diet, and activity pattern. We had data to calculate offtake relative to density for a subset of the original sites, which led to a reduction in sample size for this model (to 22). While Critically Endangered, Endangered, Vulnerable, and Least Concern species were all present in the annual offtake analysis, there were no species categorized as Least Concern in the sites where we calculated offtake relative to density. We treated diet as a binary variable (folivory vs. other primary diets), where folivory included diets primarily comprised of both leaves and bamboo. Activity pattern was also binary (nocturnal vs. day-active), with diurnal and cathemeral species included in the day-active category because of their activity overlap with mainly diurnal hunters. To reduce variance and to ensure that assumptions of a linear model were met, we log₁₀ transformed adult body mass, annual offtake, and annual offtake relative to species density. We assessed multicollinearity among predictor variables using variance inflation factor (VIF, values >5) and tolerance limit (values approximating 0) (Kutner *et al.* 2004); neither metric indicated a high correlation among predictors. For both models, we used site as a random factor in the mixed models to assume different baseline values (i.e., different intercepts) for the response variable at each location (Zuur *et al.* 2009). We derived the parameter estimate using the restricted maximum likelihood estimates (REML) and used a log ratio test to determine significance of the top models. We used the MuMIn package (Barton 2020) for model selection. We used the Akaike information criterion (AIC_c) for model development and ΔAIC (the change in AIC values relative to the best AIC model) for selecting optimal models, with a cutoff of Δ6 to include all models within the 95% confidence set (Harrison *et al.* 2018). We used the *lmer* function in the lme4 package (Bates *et al.* 2015) to fit LMMs. We report the top candidate model and models with ΔAIC_c <6 from the top model (Burnham and Anderson 2002).

Ethical Note

The Republic of Madagascar, Madagascar National Parks, Institutional Animal Care and Use (Protocols No. 2010-0010 at the University of Massachusetts Amherst, No. 2012-0028 and 2015-0002 at the Harvard T. H. Chan School of Public Health, No. 1183799 at Stony Brook University, and No. 2019-055 at Montclair State University), Animal Care Committee (No. BI11R-15 and AC15-0041 at the University of Calgary), and Human Subjects Institutional Review Boards (Protocols No. 2010-0595 at the University of Massachusetts Amherst, No. 13-1862 and 15-2230 at the Harvard T. H. Chan School of Public Health, No. SSD/CUREC1A/14-010 at Oxford University, No. 1183799 at Stony Brook University, and No. 18-19-1349 at Montclair State University) approved all research. We obtained oral informed consent from all participants, as well as each community's *chef fokontany* (local administrator). The authors declare that they have no conflict of interest and the anonymized datasets generated and/or analyzed during the current study are available from the corresponding author on reasonable request.

Results

Lemur hunting occurred in or near all protected areas surveyed (Table II). Across Madagascar, members of each household ate a mean of $1.10 \pm \text{SD } 1.11$ (median = 0.62) lemurs during the year prior to the survey (Table II), or a median 4.1% of lemur species' population sizes where densities are known (Table III). Hunting pressure, however, varied greatly among both species and protected areas (Tables II and III, Fig. 1).

Geographic Variation in Hunting Pressure

Of the ten sites, lemur hunting was lowest near the Lac Alaotra Protected Area, where people ate only one of five species of lemur (0.03 lemurs per household per year), and highest near the Makira Natural Park, where people consumed 11 of 12 species during the prior year (3.23 lemurs per household per year), and all species are eaten (Golden *et al.* 2014a). Total hunting pressure was highest near the protected areas of northeastern Madagascar, where a total of 20,000 to more than 200,000 lemurs may be eaten each year; total hunting pressure was also high near the Menabe Antimena Protected Area of southwestern Madagascar, where more than 50,000 lemurs may be eaten each year (Table II). Assuming an even distribution of hunting pressure per 1 km² of protected area and settled area within 10 km: >20 lemurs were eaten per 1 km² of land area at Betampona Strict Nature Reserve, Makira Natural Park, and Mananara–Nord National Park; 15–20 at Menabe Antimena Protected Area; 4–5 at Masoala National Park and Kianjavato; 2–3 at Ankarafantsika National Park, Kirindy–Mitea National Park, and Mantadia National Park; and 1–2 at Lac Alaotra Protected Area.

Taxonomic Variation in Hunting Pressure

The two most commonly eaten species of lemur were the Vulnerable *Eulemur albifrons* and *Cheirogaleus major*. Households consumed a mean of $0.31 \pm \text{SD } 0.22$ *E. albifrons* and $0.31 \pm \text{SD } 0.30$ *C. major* each year, for an extrapolated total of 49,466 *E. albifrons* and 46,398 *C.*

Table III Lemur densities and hunting pressure concern near three protected areas in Madagascar

 Lemur species ^a	IUCN status ^b	Makira Natural Park		Masoala National Park		Kianjavato	
		Density per km ²	Hunting pressure ^c	Density per km ²	Hunting pressure ^c	Density per km ²	Hunting pressure ^c
Cheirogalidae		172.17	Medium	116.36	Low	62.80	High
<i>Cheirogaleus major</i>	VU	57.84	High	66.94	Low	12.02	Medium
<i>Microcebus jollyae</i>	EN					50.78	Very High
<i>M. sp.</i>	-	114.33	Medium	49.42	Low		
Indriidae		53.61	High	51.64	Medium	9.39	Low
<i>Avahi laniger</i>	VU	47.96	High				
<i>A. mooreorum</i>	EN			51.64	Medium		
<i>A. peyrierasi</i>	VU					9.39	Low
<i>Indri indri</i>	CR	5.36	High				
<i>Propithecus candidus</i>	CR	0.29	Low				
Lemuridae		98.31	High	14.47	Medium	52.54	Medium
<i>Eulemur albifrons</i>	VU	69.3	High	43.39; 28.94 ^d	High		
<i>E. rufifrons</i>	VU					24.42	Low
<i>E. rubriventer</i>	VU					7.75	Low
<i>Hapalemur occidentalis</i>	VU	12.36	Very High	14.47	Medium		
<i>Prolemur simus</i>	CR					6.84 ^e	High
<i>Varecia rubra</i>	CR			15.14; 9.89	Medium		
<i>V. variegata</i>	CR	16.65	Medium			13.54	Medium
Lepilemuridae		-	-	34.5	Low		
<i>Lepilemur scottorum</i>	EN	-	-	34.5	Low		

^a Lemur illustration copyright © 2017 by Joel Borgerson, all rights reserved.

^b IUCN status: CR = Critically Endangered; EN = Endangered, VU = Vulnerable.

^c Defined categorically using the estimated percentage of the total population within the protected area and peripheral zone caught during the prior year: Low = < 1%, Medium = 1 < 10%, High = 10 < 20%, Very High = ≥ 20%.

^d Inside protected area; within peripheral zone.

^e Density calculated with $N = 14$ sightings (for all others, $N > 30$).

major eaten across all sites. The most commonly eaten Critically Endangered species of lemur were *Varecia variegata*, *Propithecus verreauxi*, and *Indri indri* (with an extrapolated total of 9364, 7789, and 7240 eaten per year, respectively, across sites) (Table II). People rarely ate lemurs of the genus *Phaner* across sites (<0.01 ± SD < 0.01 eaten per household per year).

Across all five extant families of lemurs (Cheirogaleidae, Daubentoniidae, Indriidae, Lemuridae, and Lepilemuridae), people ate cheirogaleids (especially *Cheirogaleus*) most frequently and in the greatest numbers (with a mean of 0.17 ± SD 0.31 eaten per household, or an extrapolated total of more than 125,000 cheirogaleids per year across the study sites) and people ate the monotypic Daubentoniidae least often (with a mean of 0.03 ± SD 0.07 eaten per household per year across sites) (Fig. 1). However, family-level pressure varied across the protected areas, with cheirogaleids eaten in greater number across all sites except the Masoala National Park, Ankarafantsika National Park, and Lac Alaotra Protected Area where lemurids were eaten most often (especially species within the genera *Eulemur*, *Hapalemur*, and *Varecia*) (Fig. 1).

Pressure as a Percentage of Population Size

We estimated the percentage of the lemur population size caught during the prior year at three sites where we had sufficient data to calculate most lemur densities (Kianjavato,

Makira Natural Park, and Masoala National Park) (Table III). While people caught a median 4.1% of each lemur's population size during the prior year, pressure varied greatly among both species and sites. Relative to population size, the most heavily targeted families of lemur were indriids and lemurids, with >10% of their population hunted annually. Among all Critically Endangered and Endangered species, the hunting levels of *Indri indri*, *Prolemur simus*, *Varecia rubra*, and *Microcebus jollyae* were highest relative to their population size.

Assessing Predictors of Annual Offtake and Offtake Relative to Species Diversity

The log ratio test indicated that the top candidate model for annual offtake was non-significant ($\chi_{(1, 86)} = 3.038$, $P = 0.081$; Table V) and included only adult body mass as a predictor (with higher levels of hunting of smaller species; Fig. 2b). The second candidate model was the intercept-only model (i.e., included no fixed factors) (Table IV). The top model that included adult body mass ($AIC_c = -208.4$, $W_i = 0.502$) was 1.1 times more likely to be the best explanation for variation in per household lemur hunting in Madagascar compared to the next best model ($AIC_c =$

Table IV Summary of model averaged estimates of fixed effects from LMMs on annual lemur offtake and offtake relative to species density (\log_{10}) in Madagascar (2009-2019)

Parameters	Estimate	SE	95% CI	<i>P</i>
Annual Offtake (\log_{10})				
Intercept	0.111	0.060	-0.01 to 0.23	0.063
IUCN status: Critically Endangered	Reference			
IUCN status: Endangered	0.013	0.024	-0.03 to 0.06	0.590
IUCN status: Vulnerable	0.022	0.018	-0.01 to 0.06	0.203
IUCN status: Least Concern	0.056	0.044	-0.03 to 0.14	0.203
Adult body mass (\log_{10})	-0.027	0.016	-0.06 to 0.00	0.086
Diet: Folivore	Reference			
Diet: Nonfolivore	0.004	0.015	-0.03 to 0.03	0.799
Activity pattern: Day-active	Reference			
Activity pattern: Nocturnal	-0.010	0.018	-0.05 to 0.03	0.576
Offtake Relative to Density (\log_{10})				
Intercept	0.411	0.333	-0.24 to 1.06	0.217
IUCN status: Critically Endangered	Reference			
IUCN status: Endangered	0.109	0.142	-0.17 to 0.39	0.444
IUCN status: Vulnerable	0.111	0.090	-0.07 to 0.29	0.218
Adult body mass (\log_{10})	-0.073	0.085	-0.24 to 0.09	0.392
Diet: Folivore	Reference			
Diet: Nonfolivore	-0.088	0.072	-0.23 to 0.05	0.222
Activity pattern: Day-active	Reference			
Activity pattern: Nocturnal	-0.169	0.099	-0.36 to 0.02	0.089

CI confidence interval, *SE* standard error.

Site identification was included as a random effect in the model.

Table V Top candidate models for response variables annual offtake (\log_{10}) per household and offtake relative to density

Model	AIC _c	Δ AIC _c	W_i	Parameters (direction of effect)	Significance ^a
Annual Offtake					
1	-208.4	0.00	0.502	Log adult body mass (-)	$\chi_{(1,86)}=3.038, P=0.081$
2	-208.2	0.20	0.455	Intercept-only	$\chi_{(6,86)}=12.510, P=0.051$
Offtake Relative to Density					
1	-8.00	0.00	0.879	Intercept-only	$\chi_{(5,22)}=5.574, P=0.350$
2	-2.00	5.99	0.044	Activity pattern (-)	$\chi_{(1,22)}=3.517, P=0.061$

AIC_c Akaike's information criterion (correction for small sample sizes), Δ AIC_c change in AIC values relative to the best AIC model, W_i Akaike weights.

We included site identification as a random effect in the model.

^a We conducted significance tests for the top candidate models using the likelihood ratio test.

-208.2, $W_i = 0.455$; Table IV). Primary diet, activity pattern, and IUCN threat category were not included in any of the top candidate models.

The top model for offtake relative to species density was the intercept-only model. Although it was not significant ($\chi_{(5, 22)} = 5.574, P = 0.350$; Table V), the top model (AIC_c = -8.00, $W_i = 0.879$) was 20 times more likely to be the best explanation for variation in lemurs caught per household relative to species density compared to the next best model (AIC_c = -2.00, $W_i = 0.044$; Table V). The second-best optimal model included only activity pattern as a predictor, where night-time activity had a non-significant negative effect on lemur offtake relative to density ($\chi_{(1, 22)} = 3.517, P = 0.061$; Table V).

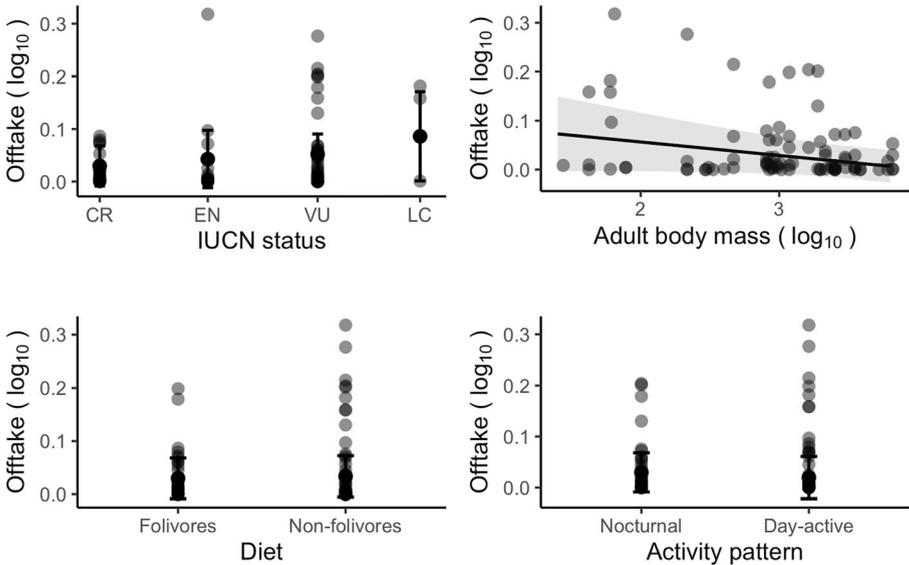


Fig. 2 Predicted probabilities for annual offtake per household (\log_{10}) for lemur species at ten study sites and four predictor variables: conservation status (IUCN category), mean adult body mass (\log_{10}), primary diet, and activity pattern (2009-2019). Error bars show 95% CI and shaded gray area in adult body mass (\log_{10}) shows 95% CI.

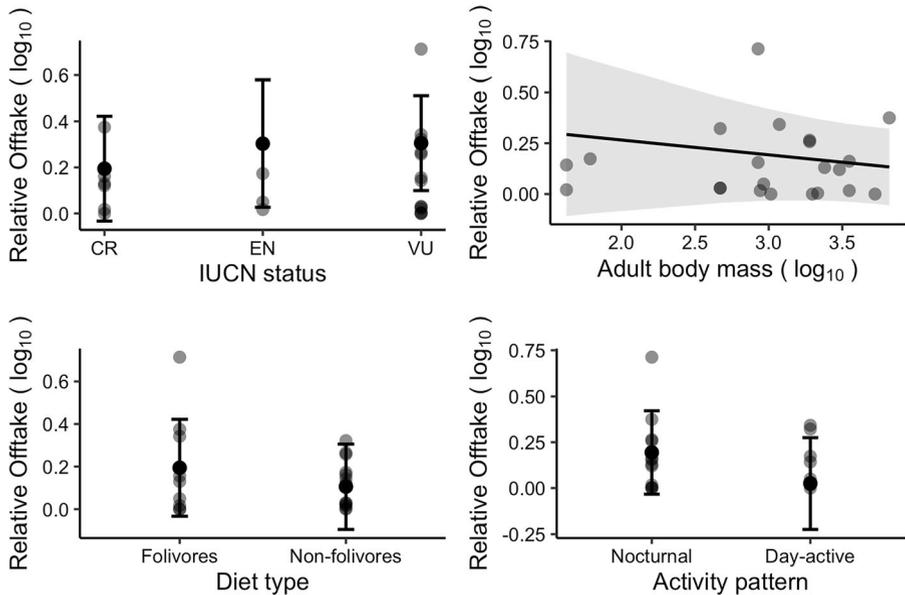


Fig. 3 Predicted probabilities for offtake relative to species density per household (\log_{10}) for lemur species at each study site and four predictor variables: conservation status (IUCN category), mean adult body mass, primary diet, and activity pattern (2009-2019). Error bars show 95% CI and shaded gray area in adult body mass (\log_{10}) shows 95% CI.

Discussion

Our findings suggest that lemur hunting is common across Madagascar. Households near the protected areas we surveyed eat, on average, one lemur each year. Such rural subsistence consumption in Madagascar scales up to significant pressure at the site and national levels. However, this pressure varied significantly across sites and species.

People ate 2000 to over 200,000 lemurs during the prior year near each of the ten protected areas we studied. In terms of geographic variation, the focus of previous research on lemur hunting in northeastern Madagascar (e.g., Borgerson 2015, 2016; Borgerson *et al.* 2019a; Brook *et al.* 2019; Golden 2009; Golden *et al.* 2011, 2014a) does not appear to have biased interpretations of which areas and species are especially prone to hunting risk, and instead reflects the region's higher comparative hunting pressure. The northeast contains the country's largest protected area (Makira Natural Park), largest national park (Masoala National Park), and largest remaining contiguous forests in Madagascar (Goodman *et al.* 2018). The region is also more rural than much of Madagascar, with the lowest connectivity (i.e., highest travel time to the nearest urban center) within the country (Rice *et al.* 2020), while still sustaining moderate population densities. Thus, high hunting levels in this region may reflect a larger, comparatively intact ecosystem which is, at least in the short term, more capable of sustaining both people and lemurs. This would be consistent with the high levels of species diversity in the lemur hunting within this region as well; people ate 94.4% of 18 lemur species during the prior year near northeastern protected areas, compared to only 69.0% of 32 lemur species present elsewhere. However, the severity of hunting remains high for many of the lemur species within these protected areas (e.g., *Eulemur albifrons*). Crucially, our data set lacks sites from the far south of Madagascar, a region where food insecurity is especially acute (Noromiarilanto *et al.* 2016).

Among lemur families, hunters targeted daubentoniids least often and caught cheirogaleids and lemurids in the greatest quantities, while indriids and lemurids were the most heavily targeted relative to their population size. However, there was significant variation in hunting pressure within each lemur family. For example, Cheirogaleidae contained some of the most and least commonly eaten lemur species in Madagascar; while people ate *Cheirogaleus major* often, they almost never ate *Phaner* species across sites. Of Critically Endangered species, current hunting pressure on *Indri indri*, *Prolemur simus*, and *Propithecus verreauxi* is especially concerning, with a high proportion of their population hunted annually across protected areas where densities are known. Such hunting potentially exacerbates other major threats to these species, such as habitat loss and fragmentation (IUCN 2020; Schwitzer *et al.* 2013)—a devastating combination for species highly sensitive to environmental disturbance and/or with slow life histories (Baden *et al.* 2019; Richard *et al.* 2002).

Understanding what lemur characteristics drive hunting can help conservation authorities and managers target species most threatened by heavy hunting pressure and infer which species may be hunted most heavily in regions for which we have no data. While studies have found that many hunters preferentially target larger primates (Isaac and Cowlshaw 2004; Ripple *et al.* 2016; Stafford *et al.* 2017), we found that lemurs with smaller body sizes were more likely to be caught and eaten across Madagascar. However, it is likely that hunters did not prefer small body size itself, but rather that smaller lemurs were more abundant within the landscape: once we controlled for species density, body size no longer significantly contributed to the model. This finding is consistent with other studies which have found that smaller, more abundant species are far more likely to be hunted than larger, rare species (Chaves *et al.* 2020; Martin *et al.* 2013; Sirén and Wilkie 2016). Such species may be found in or near agricultural settlements allowing for opportunistic capture, thus reducing the effort required to actively or passively trap the animal (Smith 2005). Therefore, higher availability of small species can increase their desirability even if larger more 'optimal' returns on their investment exist in the area (Chaves *et al.* 2020). Most hunting occurred adjacent to the more species-rich protected areas, a pattern that increases hunters' chances of catching more abundant species, as seen in other countries (Bachmann *et al.* 2020). In contrast to body size, activity pattern emerged as a marginally significant predictor of hunting pressure when controlling for species abundance. Specifically, day-active (diurnal and cathemeral) species had higher relative offtake levels. This finding may again highlight the importance of opportunism, with increased likelihood of encountering or detecting lemurs that are moving or feeding when hunters are also active.

While hunting levels appear to be most strongly linked to a species' current abundance in the environment, we lack sufficient longitudinal data to test whether past hunting might have already pushed species into higher extinction risk categories. Higher hunting pressure on some species in the past may have reduced their availability and thus current levels of annual offtake are low. This could mask a preference, for instance, for larger prey species. In the most serious cases, such hunting may have already resulted in local or global extinctions. The disappearance of many large-bodied lemur species during the Holocene might be an especially salient example. Hunters targeted these species (Perez *et al.* 2005), and it is likely that hunting pressure preceded habitat loss as the primary threat (Godfrey and Irwin 2007). It is clear that body size

once affected extinction risk in Madagascar, as no lemur species larger than 10 kg persist today (Godfrey *et al.* 2019).

Although hunters commonly targeted some particularly threatened taxa, such as Critically Endangered *Indri*, *Prolemur*, and *Varecia*, we found no evidence that extinction risk predicted hunting levels. This contrasts with evidence in other countries, where hunters can prize rarity and disproportionately target threatened species (Hall *et al.* 2008). The much greater prevalence of subsistence over market-based hunting in Madagascar, driven by poverty and immediate family or community needs (Borgerson *et al.* 2016, 2019a; Golden *et al.* 2014a, 2019; Jenkins *et al.* 2011; Merson *et al.* 2019), may explain the lack of effect of conservation status. There was relatively low variability in IUCN threat categories; indeed, >95% of lemurs are classed in as Critically Endangered, Endangered, or Vulnerable (IUCN 2020) and we had no Least Concern species in our sample comparing offtake relative to density. This underscores the risk that high hunting pressure poses for virtually all lemur species. Similarly, neither diet nor activity pattern predicted higher annual offtake, and activity pattern contributed modestly to offtake relative to species density. These findings suggest that the opportunistic and passive trapping methods commonly used in rural Madagascar may discriminate less among species which differ in these traits (Borgerson 2016; Golden 2009). Future research might focus on social, economic, and cultural aspects of hunting communities across Madagascar as potential drivers of variation in relative hunting pressure among lemur species that we observed in a subset of protected areas.

Our broad-scale geographic and species-level coverage of lemur hunting pressure underscore regions and taxa of special concern, and we identify important gaps that should be addressed in order to develop comprehensive conservation strategies that account for hunting. In particular, we highlight the need for current density estimates of lemur species across Madagascar, additional research in Madagascar's far south, and a better understanding of the role of hunter preference in hunting pressure. Information on the density of lemur species is especially crucial. Hunting relatively few individuals can have devastating effects on especially rare taxa (Estrada *et al.* 2017; Hall *et al.* 2008; Ripple *et al.* 2016). For many lemur species, we continue to lack the current density estimates which are essential for both understanding the effects of hunting on lemur populations and for evaluating the conservation status of these lemur species. Because data on the densities of lemur species within many protected areas are currently lacking, we were only able to assess whether lemurs are being caught at high or low rates relative to their local availability at three of the ten sites. Efforts to collect data on both hunting and densities of lemur species are urgently needed to inform both conservation statuses, as well as to target and measure the effects of strategies which aim to reduce hunting pressure. Such combined studies of the annual rates of hunting, and how this hunting affects local lemur densities, are especially needed within southern Madagascar, where a gap in the hunting literature within Madagascar remains. Our study includes two southern sites (Kianjavato in southeastern Madagascar and Kirindy Mitea in south-central western Madagascar), which may not be representative of larger southern protected areas, such as Andohahela, Tsimanampetose, or Ranomafana National Parks. Furthermore, direct knowledge of hunters' prey preferences and their variation across Madagascar are needed. Culture and perceived attributes can have the most significant effect on hunters' selection of target species (Chaves *et al.* 2020; de Araujo Lima Constantino *et al.* 2021; van Vliet 2018; van

Vliet and Mbazza 2011). Diets in Madagascar are especially deficient in fat (Golden *et al.* 2019), and many heavily targeted species are known for their significant seasonal deposits of fat; the two most frequently hunted species (*Eulemur albifrons* and *Cheirogaleus major*) are targeted when at their fattest (Borgerson 2016). Understanding such causes for lemur choice can aid in targeting interventions appropriately, such as increasing the availability and affordability of sustainable alternative foods including poultry and insects.

This investigation suggests that lemur hunting is ubiquitous but varies markedly by region and taxonomic group. Hunting is overall highest in the northeast, and in the diverse Cheirogaleidae and Lemuridae families. However, given their relatively low population densities, current hunting pressure may have the most severe consequences for indriids and lemurids. Abundant lemurs are eaten most often, while the ecological traits we measured appear to have little influence on which species are targeted more frequently. This first national-scale study of lemur hunting is an important step toward developing targeted strategies to conserve one of the world's most threatened groups of vertebrates.

Acknowledgments We would like to extend our deepest gratitude to the communities in which we work. Without them, this research would have been impossible. We would also like to thank the editor, Joanna M. Setchell; the organizers of this special issue, Alejandro Estrada and Paul Garber, and two anonymous reviewers; Steven M. Goodman for kindly providing protected area shapefiles; Marina B. Blanco for her expert advice on taxonomy; Richard J. Bankoff for his support in estimating densities within Rdistance; and the Republic of Madagascar and Madagascar National Parks for their continued support and permission to conduct research. This research was funded by grants from the National Geographic Society Conservation Trust (C135–08, C280–14, C021–17, and 55616C-20), the Margot Marsh Biodiversity Foundation, Primate Action Fund, the National Science Foundation SBE-IBSS Postdoctoral Research Fellowship (1513638), the National Science Foundation Graduate Research Fellowship Program (2015213765), the Natural Sciences and Engineering Research Council of Canada, Global Wildlife Conservation, Lemur Conservation Action Fund (5095.005-0175), Primate Conservation Inc, Rowe Wright Grant (46), and International Union for the Conservation of Nature, Save our Species (IUCN-SOS 2018A-117).

References

- Bachmann, M. E., Junker, J., Mundry, R., Nielsen, M. R., Haase, D., et al. (2019). Disentangling economic, cultural, and nutritional motives to identify entry points for regulating a wildlife commodity chain. *Biological Conservation*, 238, 108177. <https://doi.org/10.1016/j.biocon.2019.07.022>.
- Bachmann, M. E., Nielsen, M. R., Cohen, H., Haase, D., Kouassi, J. A. K., et al (2020). Saving rodents, losing primates: Why we need tailored bushmeat management strategies. *People and Nature*, 2, 889–902. <https://doi.org/10.1002/pan3.10119>.
- Baden, A. L., Mancini, A. N., Federman, S., Holmes, S. M., Johnson, S. E., et al (2019). Anthropogenic pressures drive population genetic structuring across a Critically Endangered lemur species range. *Scientific Reports*, 9(1), 16276. <https://doi.org/10.1038/s41598-019-52689-2>.
- Bartoń, K. (2020). MuMIn: Multi-model inference. *R package version, 1*(43), 17 <https://CRAN.R-project.org/package=MuMIn>.
- Bates, D., Mächler, M., Bolker, B., & Walker, S. (2015). Fitting linear mixed-effects models using lme4., 67(1), *Journal of Statistical Software*, 1–Journal of Statistical Software48. <https://doi.org/10.18637/jss.v067.i01>.

- Booth, H., Clark, M., Milner-Gulland, E.J., Amponsah-Mensah, K., Antunes, A.P., et al (2021). Investigating the risks of removing wild meat from global food systems. *Current Biology*. <https://doi.org/10.1016/j.cub.2021.01.079>.
- Borgerson, C. (2015). The effects of illegal hunting and habitat on two sympatric endangered primates. *International Journal of Primatology*, 36(1), 74–93. <https://doi.org/10.1007/s10076-015-9812-x>.
- Borgerson, C. (2016). Optimizing conservation policy: The importance of seasonal variation in hunting and meat consumption on the Masoala peninsula of Madagascar. *Oryx*, 50(3), 405–418. <https://doi.org/10.1017/S0030605315000307>.
- Borgerson, C., Johnson, S. E., Louis, E. E., Holmes, S. M., Anjaranirina, E. J. G., et al (2018b). The use of natural resources to improve income, health, and nutrition within the forests of Kianjavato, Madagascar. *Madagascar Conservation & Development*, 13(1), 45–52. <https://doi.org/10.4314/mcd.v13i1.6>.
- Borgerson, C., McKean, M. A., Sutherland, M. R., & Godfrey, L. R. (2016). Who hunts lemurs and why they hunt them. *Biological Conservation*, 197, 124–130. <https://doi.org/10.1016/S0006320716300556>.
- Borgerson, C., Razafindrapaoly, B., Rajoana, D., Rasolofoniaina, B. J. R., & Golden, C. D. (2019a). Food insecurity and the unsustainable hunting of wildlife in a UNESCO World Heritage site. *Frontiers in Sustainable Food Systems: Land, Livelihoods, and Food Security*, 3, 99. <https://doi.org/10.3389/fsufs.2019.00099>.
- Borgerson, C., Randrianasolo, J. F., Andraina, T. R., Anjaranirina, E. J. G., Randriamady, H. J., et al (2019b). Wildlife hunting in complex human-environmental systems: How understanding natural resource use and human welfare can improve conservation in the Ankarafantsika National Park, Madagascar. *Madagascar Conservation & Development*, 14(1), 37–45. <https://doi.org/10.4314/mcd.v14i1.7>.
- Borgerson, C., Vonona, M. A., Vonona, T., Anjaranirina, E. J. G., Lewis, R., et al (2018a). An evaluation of the interactions among household economies, human health, and wildlife hunting in the Lac Alaotra wetland complex of Madagascar. *Madagascar Conservation & Development*, 13(1), 25–33. <https://doi.org/10.4314/mcd.v13i1.5>.
- Brook, C. E., Herrera, J., Borgerson, C., Fuller, E., Andriamahazoarivosoa, P., et al (2019). Population viability and bushmeat harvest sustainability for Madagascar lemurs. *Conservation Biology*, 33(1), 99–111. <https://doi.org/10.1111/cobi.13151>.
- Buckland, S. T. (2001). *Introduction to distance sampling: Estimating abundance of biological populations*. London: Oxford University Press.
- Buckland, S. T., Anderson, D. R., Burnham, K. P., & Laake, J. L. (1993). *Distance sampling: Estimating abundance of biological populations*. London: Chapman and Hall.
- Burnham, K. P., & Anderson, D. R. (2002). *Model selection and multimodel inference: A practical information-theoretic approach* (2nd ed.). New York: Springer Science+Business Media.
- Carbone, C., Cowlishaw, G., Isaac, N. J. B., Rowcliffe, J. M., & Raymond, B. H. (2005). How far do animals go? Determinants of day range in mammals. *The American Naturalist*, 165(2), 290–297. <https://doi.org/10.1086/426790>.
- Chaves, L. S., Alves, R. R. N., & Albuquerque, U. P. (2020). Hunters' preferences and perceptions as hunting predictors in a semiarid ecosystem. *Science of the Total Environment*, 726, 138494. <https://doi.org/10.1016/j.scitotenv.2020.138494>.
- de Araujo Lima Constantino, P., Valente-Neto, F., Nunes, A. V., & Campos-Silva, J. V. (2021). Culture still matters: Conservation implications of hunting by ethnolinguistic groups in Southwestern Amazonia after centuries of contact. *Biodiversity Conservation*. <https://doi.org/10.1007/s10531-020-02099-y>.
- Direction du Système des Aires Protégées. (2017). Shapefiles of the protected areas of Madagascar.
- Dunn, M. A., & Smith, D. A. (2011). The Spatial Patterns of Miskitu Hunting in Northeastern Honduras: Lessons for Wildlife Management in Tropical Forests. *Journal of Latin American Geography*, 10(1), 85–108.
- Duporge, I., Hodgetts, T., Wang, T., & Macdonald, D. W. (2020). The spatial distribution of illegal hunting of terrestrial mammals in sub-Saharan Africa: A systematic map. *Environmental Evidence*, 9(1), 15. <https://doi.org/10.1186/s13750-020-00195-8>.
- Effiom, E. O., Nuñez-Iturri, G., Smith, H. G., Ottosson, U., & Olsson, O. (2013). Bushmeat hunting changes regeneration of African rainforests. *Proceedings of the Royal Society B: Biological Sciences*, 280(1759). <https://doi.org/10.1098/rspb.2013.0246>.
- Estrada, A., Garber, P. A., Mittermeier, R. A., Wich, S., Gouveia, S., et al (2018). Primates in peril: The significance of Brazil, Madagascar, Indonesia and the Democratic Republic of the Congo for global primate conservation. *PeerJ*, 6. <https://doi.org/10.7717/peerj.4869>.
- Estrada, A., Garber, P. A., Rylands, A. B., Roos, C., Fernandez-Duque, E., et al (2017). Impending extinction crisis of the world's primates: Why primates matter. *Science Advances*, 3(1). <https://doi.org/10.1126/sciadv.1600946>.

-
- Fa, J. E., Ryan, S. F., & Bell, D. J. (2005). Hunting vulnerability, ecological characteristics and harvest rate of bushmeat species in afro-tropical forests. *Biological Conservation*, 121(2), 167–176. <https://doi.org/10.1016/j.biocon.2004.04.016>.
- Ganzhorn, J. U., Fietz, J., Rakotovo, E., Schwab, D., & Zinner, D. (1999). Lemurs and the regeneration of dry deciduous forest in Madagascar. *Conservation Biology*, 13, 794–804. <https://doi.org/10.1046/j.1523-1739.1999.98245.x>.
- Gardner, C. J., Bicknell, J. E., Baldwin-Cantello, W., Struebig, M. J., & Davies, Z. G. (2019). Quantifying the impacts of defaunation on natural forest regeneration in a global meta-analysis. *Nature Communications*, 10(1), 4590. <https://doi.org/10.1038/s41467-019-12539-1>.
- Gaynor, K. M., Hojnowski, C. E., Carter, N. H., & Brashares, J. S. (2018). The influence of human disturbance on wildlife nocturnality. *Science*, 360(6394), 1232–1235. <https://doi.org/10.1126/science.aar7121>.
- Global Forest Watch. (2019). World Resources Institute. www.globalforestwatch.org (accessed August 1, 2020).
- Godfrey, L. R., & Irwin, M. T. (2007). The evolution of extinction risk: Past and present anthropogenic impacts on the primate communities of Madagascar. *Folia Primatologica*, 78(5–6), 405–419. <https://doi.org/10.1159/000105152>.
- Godfrey, L. R., Scroton, N., Crowley, B. E., Burns, S. J., Sutherland, M. R., et al (2019). A new interpretation of Madagascar's megafaunal decline: The “subsistence shift hypothesis”. *Journal of Human Evolution*, 130, 126–140. <https://doi.org/10.1016/j.jhevol.2019.03.002>.
- Golden, C. D. (2009). Bushmeat hunting and use in the Makira Forest, north-eastern Madagascar: A conservation and livelihoods issue. *Oryx*, 43(3), 386–392. <https://doi.org/10.1017/S0030605309000131>.
- Golden, C. D., Bonds, M. H., Brashares, J. S., Rasolofoniaina, B. J. R., & Kremen, C. (2014a). Economic valuation of subsistence harvest of wildlife in Madagascar. *Conservation Biology*, 28, 234–243. <https://doi.org/10.1111/cobi.12174>.
- Golden, C. D., Desisto, C., Borgerson, C., & Randriamady, H. J. (2022, in press). Hunting and the consumption of wildlife on Madagascar. In S. M. Goodman (Ed.), *The new natural history of Madagascar*. Princeton, NJ: Princeton University Press.
- Golden, C. D., Fernald, L. C. H., Brashares, J. S., Rasolofoniaina, B. J. R., & Kremen, C. (2011). Benefits of wildlife consumption to child nutrition in a biodiversity hotspot. *Proceedings of the National Academy of Sciences of the USA*, 108, 19653–19656. <https://doi.org/10.1073/pnas.1112586108>.
- Golden, C. D., Rabehatonina, J. G. C., Rakotosoa, A., & Moore, M. (2014b). Socio-ecological analysis of natural resource use in Betampona Strict Natural Reserve. *Madagascar Conservation & Development*, 9, 83–89. <https://doi.org/10.4314/mcd.v9i2.4>.
- Golden, C. D., Vaitla, B., Ravaoliny, L., Vonona, M. A., Anjaranirina, E. G., et al (2019). Seasonal trends of nutrient intake in rainforest communities of north-eastern Madagascar. *Public Health Nutrition*, 22(12), 2200–2209. <https://doi.org/10.1017/S1368980019001083>.
- Golden, C. D., Wrangham, R. W., & Brashares, J. S. (2013). Recall accuracy for wildlife consumption. *Animal Conservation*, 16, 597–603. <https://doi.org/10.1111/acv.12047>.
- Goodman, S. M., Raherilalao, M. J., & Wohlhauser, S. (2018). *The terrestrial protected areas of Madagascar: Their history, description, and biota*. Antananarivo Madagascar: Association Vahatra.
- Hall, R. J., Milner-Gulland, E. J., & Courchamp, F. (2008). Endangering the endangered: The effects of perceived rarity on species exploitation. *Conservation Letters*, 1(2), 75–81. <https://doi.org/10.1111/j.1755-263X.2008.00013.x>.
- Hansford, J., Wright, P. C., Rasoamiaramanana, A., Pérez, V. R., Godfrey, L. R., et al (2018). Early Holocene human presence in Madagascar evidenced by exploitation of avian megafauna. *Science Advances*, 4(9), eaat6925. <https://doi.org/10.1126/sciadv.aat6925>.
- Harrison, X. A., Donaldson, L., Correa-Cano, M. E., Evans, J., Fisher, D. N., et al (2018). A brief introduction to mixed effects modelling and multi-model inference in ecology. *PeerJ*, 6, e4794. <https://doi.org/10.7717/peerj.4794>.
- Isaac, N. J. B., & Cowlshaw, G. (2004). How species respond to multiple extinction threats. *Proceedings of the Royal Society Series B: Biological Sciences*, 271, 1135–1141. <https://doi.org/10.1098/rspb.2004.2724>.
- IUCN. (2020). The IUCN Red List of Threatened Species. www.iucnredlist.org (accessed August 18, 2020).
- Jenkins, R. K., Keane, A., Rakotoarivelo, A. R., Rakotomboavonjy, V., Randrianandrianina, F. H., et al (2011). Analysis of patterns of bushmeat consumption reveals extensive exploitation of protected species in eastern Madagascar. *PLoS ONE*, 6(12), e27570. <https://doi.org/10.1371/journal.pone.0027570>.
- Jerozolinski, A., & Peres, C. A. (2003). Bringing home the biggest bacon: a cross-site analysis of the structure of hunter-kill profiles in Neotropical forests. *Biological Conservation*, 111(3), 415–425.

- Koster, J. M., Hodgen, J. J., Venegas, M. D., & Copeland, T. J. (2010). Is meat flavor a factor in hunters' prey choice decisions? *Human Nature*, *21*(3), 219–242. <https://doi.org/10.1007/s12110-010-9093-1>.
- Kumpel, N. F., Milner-Gulland, E. J., Cowlshaw, G., & Rowcliffe, J. M. (2010). Assessing sustainability at multiple scales in a rotational bushmeat hunting system. *Conservation Biology*, *24*(3), 861–871. <https://doi.org/10.1111/j.1523-1739.2010.01505.x>.
- Kutner, M. H., Nachtsheim, C. J., & Neter, J. (2004). *Applied linear regression models*, 4th ed. (pp. 495, 497). McGraw-Hill Irwin.,
- Lloyd, C. (2016). WorldPop Archive global gridded spatial datasets. Version Alpha 0.9. Harvard Dataverse (Dataset). <https://dataverse.harvard.edu/dataverse/WorldPop> (accessed July 1, 2020).
- Lloyd, C., Sorichetta, A., & Tatem, A. (2017). High resolution global gridded data for use in population studies. *Scientific Data*, *4*, 170001. <https://doi.org/10.1038/sdata.2017.1>.
- Martin, A., Caro, T., & Kiffner, C. (2013). Prey preferences of bushmeat hunters in an east African savannah ecosystem. *European Journal of Wildlife Research*, *59*, 137–145. <https://doi.org/10.1007/s10344-012-0657-8>.
- Martins, V., & Shackleton, C. M. (2019). Bushmeat use is widespread but under-researched in rural communities of South Africa. *Global Ecology and Conservation*, *17*, e00583. <https://doi.org/10.1016/j.gecco.2019.e00583>.
- McDonald, T., Carlisle, J., McDonald, A., Nielson, R., Augustine, B., et al (2019). <https://cran.r-project.org/web/packages/Rdistance/index.html>.
- Merson, S. D., Dollar, L. J., Johnson, P. J., & Macdonald, D. W. (2019). Poverty not taste drives the consumption of protected species in Madagascar. *Biodiversity Conservation*, *28*, 3669–3689. <https://doi.org/10.1007/s10531-019-01843-3>.
- Milton, K., & May, M. L. (1976). Body weight, diet and home range area in primates. *Nature*, *259*(5543), 459–462. <https://doi.org/10.1038/259459a0>.
- Mittermeier, R. A., Louis, J. E. E., Richardson, M., Schwitzer, C., Langrand, O., et al (2010). *Lemurs of Madagascar* (3rd ed.). Arlington, VA: Conservation International.
- Noromiarilanto, F., Brinkmann, K., Faramalala, M. H., & Buerkert, A. (2016). Assessment of food self-sufficiency in smallholder farming systems of south-western Madagascar using survey and remote sensing data. *Agricultural Systems*, *149*, 139–149. <https://doi.org/10.1016/j.agsy.2016.09.005>.
- Peres, C. A., Emilio, T., Schiatti, J., Desmouliere, S. J. M., & Levi, T. (2016). Dispersal limitation induces long-term biomass collapse in overhunted Amazonian forests. *Proceedings of the National Academy of Sciences of the USA*, *113*(4), 892–897. <https://doi.org/10.1073/pnas.1516525113>.
- Perez, V. R., Godfrey, L. R., Nowak-Kemp, M., Burney, D. A., Ratsimbazafy, J., & Vasey, N. (2005). Evidence of early butchery of giant lemurs in Madagascar. *Journal of Human Evolution*, *49*(6), 722–742. <https://doi.org/10.1016/j.jhevol.2005.08.004>.
- Poelstra, J., Salmons, J., Tiley, G. P., Schüller, D., Blanco, M. B., et al (2020). Cryptic patterns of speciation in cryptic primates: microendemic mouse lemurs and the multispecies coalescent. *Systematic Biology*, *70*(2), 203–218. <https://doi.org/10.1093/sysbio/syaa053>.
- Rakotondrafara, M. L., Randriamarolaza, L. Y. A., Rasolonjatovo, H., Rakotomalala, & C. L. Razanakakiniana. (2018). In S. M. Goodman, M. J. Raheerilalao, & S. Wohlhauser (Eds.), *The terrestrial protected areas of Madagascar: Their history, description, and biota* (pp.199–206). Antananarivo Madagascar: Association Vahatra.
- Razafimanahaka, J. H., Jenkins, R. K. B., Andriafidison, D., Randrianandrianina, F., Rakotomboavonjy, V., et al (2012). Novel approach for quantifying illegal bushmeat consumption reveals high consumption of protected species in Madagascar. *Oryx*, *46*(4), 584–592. <https://doi.org/10.1017/S0030605312000579>.
- Razafindratsima, O. H., & Dunham, A. E. (2014). Assessing the impacts of nonrandom seed dispersal by multiple frugivore partners on plant recruitment. *Ecology*, *96*(1), 24–30. <https://doi.org/10.1890/14-0684.1>.
- Razafindratsima, O. H., Yacoby, Y., & Park, D. S. (2018). MADA: Malagasy animal trait data archive. *Ecology*, *99*(4), 990–990. <https://doi.org/10.1002/ecy.2167>.
- Razafindratsima, O. H., Gentles, A., Drager, A. P., Razafimahaimodison, J.-C. A., Ralazampirenena, C. J., & Dunham, A. E. (2018). Consequences of lemur loss for above-ground carbon stocks in a Malagasy rainforest. *International Journal of Primatology*, *39*(3), 415–426. <https://doi.org/10.1007/s10764-018-0042-x>.
- Reuter, K. E., Blanco, M., Ganzhorn, J. & Schwitzer, C. (2020). *Microcebus murinus*. *The IUCN Red List of Threatened Species* 2020: e.T163314248A115567306. 10.2305/IUCN.UK.2020-2.RLTS.T163314248A115567306.en (accessed August 2020).

-
- Reuter, K. E., Randell, H., Wills, A. R., & Sewall, B. J. (2016). The consumption of wild meat in Madagascar: Drivers, popularity and food security. *Environmental Conservation*, 43(3), 273–283. <https://doi.org/10.1017/S0376892916000059>.
- Rice, B. L., Annappagada, A. V., Baker, R. E., Bruijning, M., Dotse-Gborgbortsi, W., et al (2020). High variation expected in the pace and burden of SARS-CoV-2 outbreaks across sub-Saharan Africa. *medRxiv*. <https://doi.org/10.1101/2020.07.23.20161208>.
- Richard, A. F., Dewar, R. E., Schwartz, M., & Ratsirarson, J. (2002). Life in the slow lane? Demography and life histories of male and female sifaka (*Propithecus verreauxi verreauxi*). *Journal of Zoology*, 256, 421–436. <https://doi.org/10.1017/S0952836902000468>.
- Ripple, W. J., Abernethy, K., Betts, M. G., Chapron, G., Dirzo, R., et al (2016). Bushmeat hunting and extinction risk to the world's mammals. *Royal Society Open Science*, 3(10), 160498. <https://doi.org/10.1098/rsos.160498>.
- Rowe, N., & Myers, M. (2016). *All the world's primates*. Charlestown, RI: Pogonias Press.
- Schüßler, D., Blanco, M. B., Salmona, J., Poelstra, J., Andriambelason, J. B., et al (2020). Ecology and morphology of mouse lemurs (*Microcebus* spp.) in a hotspot of microendemism in northeastern Madagascar, with the description of a new species. *American Journal of Primatology*, e23180. <https://doi.org/10.1002/ajp.23180>.
- Schwitzer, C., Mittermeier, R. A., Davies, N., Johnson, S., Ratsimbazafy, J., et al (Eds.). (2013). Lemurs of Madagascar: A strategy for their conservation 2013–2016. Bristol: IUCN SSC Primate Specialist Group, Bristol Conservation and Science Foundation, and Conservation International.
- Schwitzer, C., Mittermeier, R. A., Johnson, S. E., Donati, G., Irwin, M., et al (2014). Averting lemur extinctions amid Madagascar's political crisis. *Science*, 343, 842–843. <https://doi.org/10.1126/science.1245783>.
- Sirén, A. H., & Wilkie, D. S. (2016). The effects of ammunition price on subsistence hunting in an Amazonian village. *Oryx*, 50, 47–55. <https://doi.org/10.1017/S003060531400026X>.
- Smith, D. A. (2005). Garden game: Shifting cultivation, indigenous hunting and wildlife ecology in western Panama. *Human Ecology*, 33, 505–537. <https://doi.org/10.1007/s10745-005-5157-Y>.
- Smith, M. (2016). Nutrient Supplies by Food and Country (2011). Harvard Dataverse, V3. <https://doi.org/10.7910/DVN/UZW5S3>.
- Stafford, C. A., Preziosi, R. F., & Sellers, W. I. (2017). A pan-neotropical analysis of hunting preferences. *Biodiversity Conservation*, 26, 1877–1897. <https://doi.org/10.1007/s10531-017-1334-8>.
- UNEP-WCMC, & IUCN. (2020). Protected planet. The world database on protected areas (WDPA)/the global database on protected areas management effectiveness (GD-PAME). July 2020, Cambridge, UK: UNEP-WCMC and IUCN. www.protectedplanet.net (accessed July, 2020).
- van Vliet, N. (2018). “Bushmeat crisis” and “cultural imperialism” in wildlife management? Taking value orientations into account for a more sustainable and culturally acceptable wildmeat sector. *Frontiers in Ecology and Evolution*, 6, 1–6. <https://doi.org/10.3389/fevo.2018.00112>.
- van Vliet, N., & Mbazza, P. (2011). Recognizing the multiple reasons for bushmeat consumption in urban areas: A necessary step toward the sustainable use of wildlife for food in central Africa. *Human Dimensions of Wildlife*, 16, 45–54. <https://doi.org/10.1080/10871209.2010.523924>.
- van Velden, J., Wilson, K., & Biggs, D. (2018). The evidence for the bushmeat crisis in African savannas: A systematic quantitative literature review. *Biological Conservation*, 221, 345–356. <https://doi.org/10.1016/j.biocon.2018.03.022>.
- Zuur, A., Ieno, E. N., Walker, N., Saveliev, A. A., & Smith, G. M. (2009). *Mixed effects models and extensions in ecology with R*. New York: Springer Science+Business Media.

