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Limestone cliff-face and cave use by wild ring-tailed lemurs (*Lemur catta*) in southwestern Madagascar

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ABSTRACT

Ring-tailed lemurs live in a range of habitats in southwestern Madagascar. To date, much of the knowledge of ring-tailed lemur ecology, biology and behavior come from riverine gallery forests sites. Recent years have seen an expansion of comprehensive research on this resilient species, including areas of limestone spiny forest along Madagascar's southwestern coast. This work is documenting newly discovered behaviors by this species. The regular use of cliff-faces and embedded crevices and caves by ring-tailed lemurs in southwestern Madagascar are reported here. Cave use by several anthropoid primates has been explained as a thermoregulatory behavior. It is suggested that cliff-face and cave use by these ring-tailed lemurs serves several purposes, including resource acquisition, thermoregulation, and as an anti-predator avoidance strategy in the absence of suitable large sleeping trees. Observations indicate that the limestone boundaries of the Mahafaly Plateau and their associated xerophytic scrub forests warrant further conservation attention, given the presence of behavioral variation and increasing threats to this endangered primate species.

RÉSUMÉ

Lemur catta occupe divers habitats dans le Sud-ouest de Madagascar. L'écologie, la biologie et le comportement de *Lemur catta* sont actuellement mieux connus des populations vivant dans les forêts riveraines et les zones environnantes. Pour mieux comprendre cette espèce de lémurien, les recherches ont été étendues à d'autres habitats dont les forêts épineuses du plateau calcaire qui est situé le long du littoral Sud-ouest de Madagascar. Dans cette étude nous rapportons les comportements récemment découverts de *Lemur catta* qui utilise les falaises et les grottes dans le Sud-ouest de Madagascar. L'utilisation des grottes par la plupart des primates hominoïdes est liée à un avantage thermorégulateur offert par ce milieu. Dans notre cas, l'exploitation de falaises et de grottes par *Lemur catta* semble être associée à un mécanisme permettant d'échapper aux prédateurs et à l'absence de grands arbres qui devaient servir de dortoirs. De sorte que les falaises et les forêts épineuses du plateau calcaire Mahafaly ont besoin d'une conservation particulière car nos résultats de suivis montrent que les changements de comportement du lémurien emblématique de cette région trouve vraisemblablement son origine dans la dégradation de l'environnement de cette espèce.

INTRODUCTION

Ring-tailed lemurs (*Lemur catta*) are a resilient primate species, inhabiting a wide range of habitats across southern and southwestern Madagascar that includes areas of heavy human disturbance (e.g., Sauther et al. 1999, Gould 2006, Jolly et al. 2006). Spanning a range from the southernmost point in Madagascar (Cap Sainte Marie), across the spiny forests and dry deciduous riverine forests of the Atsimo-Andrefana Region, through the high-altitude Andringitra Massif and surrounding highlands, ring-tailed lemurs live within a range of challenging environments in terms of temperature variation, droughts, cyclones and differing levels of anthropogenic change (Goodman et al. 2006, LaFleur 2012). *Lemur catta* is also the most terrestrial of all living lemurs, and exploits a wide range of resources, depending on the habitat (e.g., Sauther et al. 1999, Goodman et al. 2006, Gould 2007). To date, most of what is known about this species' biology, ecology, and behavior comes from long-term studies (> 25 years) at two riverine gallery sites, the Bezà Mahafaly Special Reserve and Berenty Private Reserve (Gould 2007). Only recently has information on this species been available from more xeric spiny forest areas, including along the limestone plateau of Madagascar's southwestern region (Sauther and Cuozzo 2008, Kelley 2011, Cuozzo and Sauther 2012, LaFleur 2012). In this paper, the use of caves and cliff fissures by ring-tailed lemurs at two sites, Tsimanampesotse National Park and the Tsinjoriake New Protected Area, both located in southwestern Madagascar, is described in detail for the first time, and possible ecological functions of this behavior discussed.

Cave use is rare among primates, but has been previously reported among continental African and Asian anthropoid primates, including chimpanzees, baboons, and langurs. A variety of hypotheses have been put forth regarding this behavior,

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many positing thermoregulation as a key reason (Pruetz 2001, 2007, Huang et al. 2003, McGrew et al. 2003, Barrett et al. 2004, Workman 2010). For example, cave use among chimpanzees in southeastern Senegal looks to be an "opportunistic" behavior in response to high temperatures (Pruetz 2007: 318). Explanations for cave use by primates also include access to water, obtaining nutrients through geophagy and predator avoidance (McGrew et al. 2003).

Among Madagascar's strepsirhine primates, only anecdotal observations of cave use have been previously reported. Ring-tailed lemurs at Andrahomana cave, in southern Madagascar have been seen resting and feeding during the daytime in this cave (Vasey et al. 2013). At Isalo National Park, on the southern edge of Madagascar's central highlands, ring-tailed lemurs were observed entering caves to lick the soil as well as using caves during the day and at night (Dinets, pers. com). Finally, a single report from northern Madagascar describes crowned lemurs (*Eulemur coronatus*), using a cave to drink water (Wilson et al. 1989).

Early reports by Perrier de la Bâthie (1927) described ring-tailed lemurs using the vertical cliff-faces of the Andringitra Massif, central Madagascar. A more recent study of these high-altitude (ranging above 2,000 meters) *L. catta* on the Andringitra Massif, near the northern boundary of this species' range in south-central Madagascar, has documented the use of fissures and overhangs in the granitic outcrops as sleeping sites (Goodman et al. 2006). Goodman et al. (2006) hypothesize that i) caves serve as shelter in response to cold temperatures at this altitude, and/or ii) caves and rock overhangs may be a way of avoiding predation by the endemic fossa (*Cryptoprocta ferox*). Gould (pers. comm.) has recently observed a small *L. catta* troop (n = 4) that uses a small cave in the Ambalavao region of the highlands, in the same region as the Andringitra Massif. This population lives in habitat with no forest cover due to slash-and-burn agriculture, and survives on anthropogenic resources such as crops and fruit trees. This example of ring-tailed lemur cave use is likely a result of human action rather than ecological adaptations such as thermoregulation or predator avoidance, and is similar to langur cave use described by Li and Rogers (2005), where these monkeys use caves and limestone karst as a refuge in response to deforestation and expanding cultivation. In fact, all of the scattered, fragmented *L. catta* populations in this highland region may be using the granitic slopes, massifs and caves as a refuge, as the surrounding areas are void of continuous forest, subject to frequent intentional burning (e.g., Goodman and Langrand 1996), and are marked by vast expanses of cultivated land (Cameron and Gould 2013). Data on ring-tailed lemur cliff-face and cave use in areas of continuous forest, but without the large sleeping trees present in riverine gallery forest areas such as Bezà Mahafaly Special Reserve and Berenty Private Reserve, would add to current anecdotal reports from this and other species and provide valuable data to interpret and explain this behavior beyond it being a response to anthropogenic effects.

METHODS

As part of the authors' long-term collaborative research on the ecology, biology and behavior of ring-tailed lemurs in southwestern Madagascar, research has been carried out along the western edge of the Mahafaly Plateau, Atsimo-Andrefana Region. Data presented here are based on a cumulative 11 months of direct observations, supplemented with data from camera traps. The authors have spent varying amounts of time at Tsimanampesotse National Park (E43°46'–43°50', S24°03'–24°12') ranging from several weeks to seven months: May/June 2006 (MLS, FPC, IAJY); May/June 2007 (MLS, FPC, IAJY); June 2008 (MLS, FPC, IAJY, MML); September 2010 through April 2011 (MML); August 2013 (ML). During the seven-month behavioral study, camera traps monitored daily lemur activity as well as predator behavior. Tsimanampesotse is a 42,000 ha National Park representing the western most escarpment of the limestone Mahafaly Plateau and is constructed of Cenozoic limestone (DuPuy and Moat 1998). A highly seasonal habitat, most rainfall occurs between December and February with annual rainfall rarely exceeding 500mm (Donque 1975, APAAT Protected Areas Report: http://bioval.jrc.ec.europa.eu/APAAT/pa/2307/), although during this same time period during this research rainfall was only 400mm (LaFleur 2012). Temperature also varies dramatically with daytime highs of well over 40°C, although mean daily temperatures range between 22.5°C and 35.8°C (LaFleur 2012). The area is also affected by high winds, frequent droughts and cyclones (Andriatsimietry et al. 2009, LaFleur 2012). At Tsimanampesotse census data on five groups are available from 2006, 2007 and 2010–11: Vintany (n = 12–20 adults), ILove (n = 9–13 adults), Akao (n = 9–15 adults), Capture Be (n = 14 adults) and Miandry (n = 12 adults). For this report the focus is on three lemur troops that have been regularly observed, Vintany, ILove and Akao, including during the above-mentioned continuous seven-month study. Standard focal sampling methods were used during this study (LaFleur 2012). The Vintany and ILove troops inhabit an area above saline Lac Tsimanampesotse, in the limestone spiny forest on the western edge of the Mahafaly Plateau. Akao spends parts of its time along the eastern edge of Lac Tsimanampesotse, as well as ascending the western edge of the escarpment. Tsimanampesotse contains dry spiny forest with open-canopied dwarf flora of the Euphorbiaceae, Didiereaceae, Bombaceae, and Fabaceae families as well as areas of semi-deciduous trees (LaFleur 2012, Jacky Youssouf, unpub. data). To characterize the habitat at Tsimanampesotse in 2007 three areas encompassing the lemur groups have been evaluated using seven transects covering a total of 300x10 meters for each of the three areas.

Most recently (2012), the authors expanded their work to include an area north of Tsimanampesotse and the Onilahy River mouth/Saint Augustin Bay, in the Tsinjoriake New Protected Area, between 15km and 25km south of Toliara (E43°45'36", S23°26'53"). This newly protected area encompasses approximately 25,000 ha of limestone cliffs and southwestern dry spiny forest thicket as well as coastal mangroves. A total of 12 20x50 m vegetation transects were carried out to characterize the lemur's habitats. During a brief previous survey in 2007 by the University of Brighton, *Lemur catta* were reported to sleep in trees near a cave area and within nearby crevices (Scott et al. no date). In April 2012 members of the research team carried out an intensive month long study of ring-tailed lemurs at Tsinjoriake that included daily census, habitat analyses and behavioral ecology (Ravelohasindrazana 2013, Ravoavy 2013). LALR and JFR also conducted interviews and administered questionnaires to 30 community members regarding their use of resources in the area. Eight ring-tailed lemur groups were observed using focal sampling within two locations during April 2012. These were: Ambanilia troops; Mailaka (n = 5), Ekipa (n = 11), Fetry (n = 3), Tsy misaraky (n = 2), and Antsifotse troops; Troop 1 (n = 2), Troop 2 (n = 3), Troop 3 (n = 4) and Troop 4 (n =5). In July/August 2013, a second preliminary ecological survey was conducted, including the use of camera traps, of *Lemur catta* and their habitats at two locations in the Tsinjoriake Protected Area, one in the Binabe area including the Grotte (or cave) of Binabe and the Grotte Ambanilia area where the Sarodrano Peninsula meets the mainland, north of the mouth of Onilahy River.

RESULTS

During each of the seven time periods spent observing *Lemur catta* at Tsimanampesotse and/or Tsinjoriake, at least some troops within these larger populations regularly, and for the ILove troop at Tsimanampesotse exclusively, used cliff-face crevices and/or small caves as sleeping sites at night (Figure 1). This was true during the continuous seven-month study of this troop from September 2010 through April 2011. Of interest, not all troops at these localities exhibit this behavior. At Tsimanampesotse the Vintany troop regularly sleeps in a large cluster of *Ficus* sp. trees at the top of a vertical limestone depression, where these lemurs sometimes descend to drink water. The Akao troop at Tsimanampesotse was never seen using cliff-face areas as sleeping sites; rather, they regularly slept in a stand of introduced Australian pines (*Casuarina equisetifolia*) along the eastern lake margin. Vegetation transects revealed that there were very few large (> 10 cm DBH) *Ficus* sp. or *Tamarindus indica* trees available for sleeping (20 of 225 trees measured), and the majority of these are found near limestone sinks that may also contain steep cliff-faces and/or caves.

At Tsinjoriake, of the eight troops observed, four commonly used one of three caves for sleeping at night (Grotte Binabe: Troops 2 and 4; Grotte Binakely: Troop 3; Grotte Ambanilia: Ekipa Troop). During the 2013 visit to the area no direct observations of the lemurs using Grotte Ambanilia were made, but fresh *L. catta* fecal material near the entrance was found, indicating they were still using this cave as resting or sleeping sites.

In addition to their use as nightly sleeping sites, larger caves within limestone sinks/depressions commonly contained pools of water that were used by lemurs as drinking sites at both Tsimanampesotse (Figure 2, cf. Video 1) and Tsinjoriake (at Grotte Sarodrano and Grotte Binabe). The larger caves were also used as 'day caves' during the hot season apparently to cool off at Tsimanampesotse. At Tsimanampesotse members of ILove group also lick the limestone walls around the caves and fissures (cf. Video 2). Large trees in the area, those greater than 10 cm in DBH (*Ficus marmorata*, *Poupartia sylvatica*, *Tamarindus indica* and *Noronhia* sp.), are limited to coastal mangrove forest and a small gallery forest as well as within the immediate vicinity of large limestone caves that contain pools of water. The majority of the vegetation is dwarfed, with heights less than 2.5m (cf. Zafisamimanana 2012, Ravelohasindrazana 2013, Ravoavy 2013). Thus, four of the eleven troops observed at both locations used cliff-face crevices and/or caves as sleeping sites and most troops were also observed using large caves as drinking sources and/or potentially as refugia from excessive heat along the western edges of the limestone Mahafaly Plateau. These data greatly expand the knowledge of ring-tailed lemur cave use in Madagascar, which to date has been primarily anecdotal.

DISCUSSION

Cave use by non-human primates has been linked to thermoregulation, predator avoidance, and/or resource access, as well as refugia in response to human actions such as deforestation (e.g., Pruetz 2001, 2007, Huang et al. 2003, McGrew et al. 2003, Goodman 2006, Workman 2010). Similar to the langurs of Southeast Asia discussed earlier (Huang et al. 2003, Workman 2010), ring-tailed lemur cave use in the Andringitra and Tsaranoro region much further north of Tsimanampesotse and Tsinjoriake is likely linked to deforestation, given only remnant forests exist in these areas (Goodman and Langrand 1996, Cameron and Gould 2013). As the areas in which observations of cliff-face and cave use display intact forests, at least until recently, it is unlikely that cave use in this region is a direct response to deforestation.

FIGURE 1. The ILove troop lemurs on cliff-face, about to enter small sleeping caves at Tsimanampesotse National Park. Arrow denotes one of the sleeping caves.

FIGURE 2. The ILove troop drinking water from the Grotte Mitoho at Tsimanampesotse. Photo by Violaine Pellicheroo, with permission from the author.

Large caves with pools of fresh water do provide important sources of drinking water during the day at both study sites, especially since these are available year round (LaFleur 2012). In addition, at Tsinjoriake there are also limestone seeps along the edges of the coastal Mangrove forests which make fresh water available during low tide, and which are used by some lemur troops (e.g., Ekipa troop). Goodman et al. (2006) put forth the interesting question of whether ring-tailed lemurs can exist in areas without fresh water and suggest that, especially in spiny forests, they may meet their water needs from their diet and/or from dew that collects on plants overnight. At a highly anthropogencially altered habitat in the Cap Sainte-Marie region of southern Madagascar, Kelley (2011) reports only one instance of ring-tailed lemurs drinking water and suggests the lemurs there also receive their water requirements from their foods, particularly the introduced *Opuntia* sp. Nevertheless, the fact that lemurs living within the spiny forest habitats of Tsimanampesotse and Tsinjoriake do seek out and use fresh water resources support the hypothesis that access to water may be significant, and that pools of fresh water within such caves or fresh water emanating from limestone seeps are an important aspect of their ecology in these intact spiny forests. It is also possible that, like at Isalo National Park, the lemurs may practice geophagia by ingesting soil within cave environs. To date this has not been observed within the actual caves but has been seen in other areas (LaFleur 2012). However, as noted above, in August 2013, MML observed ring-tailed lemurs licking the walls of limestone cliffs where they sleep at Tsimanampesotse. As water precipitates out of the limestone and dries it may provide access to minerals for these lemurs. This licking behavior, along with geophagia, has been widely noted among ring-tailed lemurs living in gallery forest sites (e.g., Jolly 1966, Loudon et al. 2006).

Cave use in this region may also be a way to stay cool during the hot wet season as well as to stay warm during the cool dry season (at Tsimanampesotse temperatures range from 10.4° C to 41.9° C but can be even hotter or cooler in more open areas (LaFleur 2012)). While some ring-tailed lemurs likely use day caves to escape the extreme heat, as observed for Fongoli chimpanzees (Pruetz 2001, 2007), it is important to distinguish between day and night use of caves, as different pressures (e.g., predation, ambient temperatures) likely vary throughout the day. At Tsimanampesotse, the ILove troop used the small cliff-face crevices and caves for sleeping without exception during all the observations, and at all times of the year, from the scorching Austral summer, where temperatures regularly range above 40°C to the cool late Austral fall and early winter when temperatures can fall as low as the single digits °C (LaFleur 2012). In addition, for the troops studied at Tsimanampesotse only the ILove troop used caves and fissures for night sleeping, while neither the Vintany nor the Akao troops did. As the ILove and Vintany troops live only several hundred meters from each other on top of the western escarpment of the Mahafaly Plateau, they experience similar temperature conditions, and thus would be expected to respond to these stressors in a similar way, given the availability of numerous limestone depressions and cliff-faces in Vintany's range. Similarly, the Akao troop used a large stand of *Casuarina equisetifolia* at the eastern edge of the Lac Tsimanampesotse, along a marshy area each night throughout the observations in May/June 2006. During that period, temperatures at night dropped near the single digits °C, with high humidity. Thus, these lemurs sleep under quite cold conditions, yet have never been observed using caves along the escarpment as night sleeping sites, despite their daily use of this escarpment area for foraging. There are also a variety of behavioral responses to temperature challenges. At Tsimanampesotse during periods of excessively high temperatures (at or greater than 40°C) the lemurs spent considerable time resting in the shade and licking their hands and feet to cool off (LaFleur 2012). During especially cold mornings the ILove troop left its caves at daylight and formed 'lemur balls' on the limestone surface above their sleeping caves until the sun was high enough to allow individual sunning. Similarly, at Tsinjoriake the lemurs visited the mangroves during the hottest period of the day, where they could rest and feed in the shade of these larger trees, but did not use these trees to sleep overnight. Thus, thermoregulation alone is unlikely to be the primary reason for sleeping at night in caves and fissures.

As noted by Anderson (1998), primates spend about half of their lives within sleeping sites, and where primates choose to sleep is thus an important aspect of their behavioral ecology. Numerous studies have indicated that sleeping sites appear to be selected to provide some safety from predation (cf. reviews in Anderson 1998, Bitetti et al. 2000, Cui et al. 2006, Cheyne et al. 2012). Especially critical is a sleeping site that allows early predator detection or provides difficult access for an approaching predator. For example, both talapoin and tufted capuchin monkeys choose sleeping areas where approaching predators create noise and vibrations (Gautier-Hion 1970, Zhang 1995). Sympatric Kloss's gibbons (*Hylobates klossi*) and Mentawi langurs (*Presbytis potenziana*) on Siberut Island, Indonesia, both use tall emergent sleeping trees, but the gibbons preferentially select trees with few large lianas. Human hunters, who use the large lianas to climb into the trees, are thus able to kill far more langurs than gibbons (Tenaza and Tilson 1985, Cheyne et al. 2012). Habitat structure is especially essential for understanding variation in anti-predation behavior (Enstam 2007). For example, patas monkeys on continental Africa live in open savannas with few large sleeping trees and thus individuals have a dispersed sleeping pattern with one individual sleeping in a tree. Within the same habitat, African vervets will sleep in tall trees within riverine forest habitats and thus all individuals may sleep in one tree (Enstam 2007). Hamadryas baboons (*Papio hamadryas*) living in the highlands of Ethiopia, are especially relevant here: their habitat has few sleeping trees, but they solve this dilemma by sleeping on sheer cliff-faces (Kummer 1968).

Goodman et al. (2006) were the first to suggest that the use of limestone crevices and/or overhangs on vertical cliff-faces as night sleeping sites by ring-tailed lemurs could be an anti-predator strategy, specifically in response to endemic fossa (*Cryptoprocta ferox*). Thus, another possible explanation for cave use among the studied lemurs is that using crevices and caves as night sleeping sites at Tsimanampesotse and Tsinjoriake may provide some safety from night-active predators within a habitat with a relative paucity of large trees for suitable sleeping sites. Studies of ring-tailed lemurs in gallery forests document that this species either chooses sleeping trees that are tall and have broad dense canopies that are large enough to accommodate the entire troop, or stands of tall trees that allow all individuals to sleep near one another (Sauther et al. 1999). In over 25 years of study at the Bezà Mahafaly Special Reserve, ring-tailed lemurs have never been observed to use any night sleeping sites other than large trees, even when troop size exceeds 20 individuals (MLS, pers. observ.). Given the variety of known lemur predators at Bezà Mahafaly Special Reserve, including *Cryptoprocta ferox*, wild cats, feral dogs and a diversity of avian raptors (Sauther 1989, Gould and Sauther 2007) use of such sleeping trees may be an anti-predator strategy, especially as ring-tailed lemurs also exhibit predation sensitive foraging strategies (Gould and Sauther 2007). That ring-tailed lemurs seek out safe night sleeping sites is also supported at other sites. For example, two troops of ring-tailed lemurs studied in the Cap Sainte-Marie region of southern Madagascar used stands of introduced *Opuntia* sp. as night sleeping areas, despite there being remnant stands of larger trees in traditionally protected sacred forests (Kelley 2011). Here, remnant stands of sacred forests are very small in area and widely dispersed, and ring-tailed lemurs were never observed to use these as night sleeping areas except in one instance, where the lemurs slept in a hedge of *Opuntia* sp. near one of these sacred forests.

At Tsimanampesotse *Ficus* sp., *Tamarindus indica* and *Casuarina equisetifolia* are the only trees large enough to provide potential sleeping trees for a lemur troop. *Ficus* sp. and *T. indica* are rare. Only 20 of the 255 trees on our transects with a DBH > 10 cm were these species, and these were typically found near the caves that form in limestone depressions. *C. equisetifolia* is only found along the marshy banks of Lac Tsimanampesotse. Unlike the degraded areas of Cap Sainte Marie (Kelley 2011), there are no hedges of *Opuntia* sp. at Tsimanampesotse. One habitat difference between the Vintany, Akao and ILove troops at Tsimanampesotse is that both Vintany and Akao troops have access to trees tall and large enough to accommodate an entire ring-tailed lemur troop and are thus suitable as sleeping sites. It is also important to note that the stand of *C. equisetifolia* trees used by the Akao lemurs is surrounded by thick marsh ferns of *Acrostichum aureum* at the base of the trees, which are difficult and noisy to move through, thus likely inhibiting terrestrial predator access to these trees. Also, these lemurs have been observed to use the plants to avoid avian predators, by quickly descending from the *Casuarina equisetifolia* into the ferns. The ILove troop sleeps in the cliff-face crevices/caves that border a deep limestone depression despite there being a few large *T. indica* and *Ficus* sp. trees in their range. In August 2013, a new troop was observed in a different area at Tsimanampesotse using a large cave as their nightly sleeping site. Around this cave are a number of large *Ficus sp.* trees, yet this group does not use them as night sleeping sites. While a long-term study of ring-tailed lemur cave use is needed, these observations indicate caves are viewed as acceptable and, in some areas with larger trees, even as preferred night sleeping sites. Recent observations also indicate that ring-tailed lemurs may perceive sleeping caves as important refugia from nocturnal predators but not necessarily diurnal ones. In one case, as the ILove troop was entering their caves and crevices in the evening, one individual started alarm calling at a raptor flying over the caves. All lemurs quickly came out of the cave and scanned the area for the hawk. This is similar to anti-predator behaviors exhibited by Bezà Mahafaly gallery forest ring-tailed lemurs, which will orient towards avian prey and often mob them (Sauther 1989).

Both, the fossa (*Cryptoprocta ferox*) as well as wild cats (*Felis silvestris*) have been documented to occur at Tsimanampesotse and fecal analyses indicate fossa prey on ring-tailed lemurs here (LaFleur 2012). While fossa are adept climbers, they are not able to climb high canopy trees very well, due to their large size (Hawkins 2003). At Tsimanampesotse the camera trap data indicate that fossa can scale narrow tall trees, thus rendering these types of trees useless as safe sleeping sites. Also, the only known successful predation of a lemur during the 2010–2011 study period was on an infant in the Vintany group, whose body was found beneath this troop's sleeping tree, a large broad *Ficus* sp. The infant clearly showed two large canine puncture wounds on the neck (LaFleur 2012). Thus at Tsimanampesotse, given that access to sleeping caves and crevices requires scaling a vertical cliff-face, it likely does provide safety from night-active fossa and nocturnal wild cat predation and this may explain why some lemur troops use caves even though larger trees may be nearby.

Further evidence of cave use for predator avoidance is seen at Tsinjoriake. Important predators include packs of village dogs as well as fossa. At this site there are only a few areas that contain large trees. This includes the mangrove forest and a small gallery forest as well as areas directly next to Grotte Binabe and Grotte Binakely. Within both the mangrove forest and the small gallery forest the majority of trees have a DBH of < 10 cm (mangrove: 92 %; gallery forest: 64 %, Ravelohasindrazana 2013). There are large trees (> 10 cm DBH) around Grotte Binabe, but these are few in number and are found only directly next to the cave. At the Grotte of Binabe and Binakely the lemurs regularly uses cliff-face crevices and caves for sleeping that would be difficult for fossa and wild cats to scale. Similarly, the Ekipa troop uses a group of caves that are located on the side of a limestone cliff that vertically drops precipitously into the ocean. The situation for the Ekipa troop is, however, slightly more complex. Earlier observations (Scott et al. no date) noted that, in addition to this cave, this group also used a stand of *Tamarindus indica* trees by a hotel for sleeping. Work by the research team in April 2012 also noted this. However, in June 2012, one month of camera trapping in this area showed no images of lemurs there. Most recently, in July/August 2013, the local research guide informed the research team that the Ekipa troop is no longer using these tamarind trees due to a large and growing pack of domestic dogs in the area, which apparently blocks the terrestrial access route to this fragmentary stand of trees. Thus, the Ekipa troop appears to now exclusively use the cave located on the limestone cliffs for sleeping, presumably to avoid these introduced predators. Given the long coexistence of *L. catta* and endemic predators in southwestern Madagascar, it is suggested that cliff-face and cave use is a natural part of the *L. catta* behavioral repertoire and is then available when needed, such as in the highland region in response to human actions (i.e., deforestation).

This novel behavior by ring-tailed lemurs expands the knowledge of primate cave use, previously reported in detail only for anthropoid primates, and when viewed through the lens of human evolution provides a broader context to interpret cave use by human ancestors (e.g., McGrew et al. 2003, Pruetz 2007). These data also aid the interpretation of cave use in primate paleobiology. For example, a recent study found fecal pellets in Anjohikely Cave in northern Madagascar, attributed to extinct

Archaeolemur (Vasey et al. 2013), suggesting that this large, semi-terrestrial lemur may have used the cave for shelter and nutrients. A clearer understanding of cave use in extant lemurs could thus expand the understanding of the paleoecology of this extinct species. The ongoing collaborative work on these ring-tailed lemur populations will allow the testing of various hypotheses regarding primate cave use.

Tsimanampesotse is one of the only protected areas of Cenozoic limestone habitats on the Mahafaly Plateau (DuPuy and Moat 1998). These authors also noted the importance of other areas of the Mahafaly Plateau, specifically along the escarpment edge towards Saint Augustin, which today encompasses the new Tsinjoriake Protected Area. However, we are just beginning to understand the ecology of ring-tailed lemurs in spiny forest habitats (e.g., Kelley 2011, LaFleur 2012) as most studies of ring-tailed lemurs have been in gallery forest habitats (Sauther 1999, Gould 2007). Given the importance of limestone caves for safe shelter, nutrition and drinking sites among ring-tailed lemurs it is essential that these habitats remain intact. However, the limestone cliffs and southwestern dry spiny forest thicket as well as coastal mangroves of southwestern Madagascar are currently under intense human pressure, including the development of limestone mining operations such as Gulf Industrial Limited's Soalara Limestone Project near the mouth of the Onilahy River. Ring-tailed lemurs, recently classified as an endangered species by the International Union for the Conservation of Nature (IUCN) Species Survival Commission (SSC), are threatened by deforestation and habitat degradation throughout southwestern Madagascar. Tsimanampesotse can now be added as a habitat undergoing extensive anthropogenic change. As recently as August, 2013 trees were being actively harvested as cattle forage, construction materials, and for carving pirogues. Based on the discovery of forest traps and communications with local people, ring-tailed lemurs are also now actively hunted in the area. Until now, poaching of ring-tailed lemurs (and other mammals) in southwestern Madagascar has remained relatively rare, due to widespread traditional taboos. However, rapid social change, along with the well-established existing black-market trade in radiated tortoises (*Astrochelys radiata*) and the demand for alternative or luxury bushmeat in Madagascar's cities have resulted in a niche for harvesting ring-tailed lemurs. Similarly, Tsinjoriake is especially affected by its close location to the large city of Toliara. For example, questionnaires indicate that 14 of the 39 tree species used by ring-tailed lemurs are also used to produce charcoal in the area including *Tamarindus indica* and *Ficus* sp. (Ravelohasindrazana, 2013, Ravoavy, 2013). The questionnaires also indicate that adult ring-tailed lemurs are hunted by humans (using dogs) as a food resource. Infant ring-tailed lemurs become pets and are sold in Toliara for between 3,000 and 4,000 Malagasy Ariary (about $US1.36–1.81) while smoked ring-tailed lemurs sell for 4,000–5,000 Malagasy Ariary ($US1.77–2.21). One of the biggest threats to this protected area is the collection of firewood to fuel the production of bricks at Ankoronga. It is estimated that the production of bricks in the village consumes 1,200–1,500 cart-loads of dead wood per month (Andriamahafaly 2010). The Tsinjoriake New Protected Area has recently been established as a community-based ecological reserve (initially developed under the auspices and guidance of the *Programme Germano-Malgache pour l'Environnement Coopération Allemande* / GIZ, a European NGO that provided funds for local development of this reserve. GIZ/GTZ also laid the groundwork for local community development). The continued support of the Tsinjoriake reserve and community development project now rests on local Malagasy researchers, scientists and community developers, who are responsible for obtaining funds to fully implement the project. Towards this end, JY and the University of Toliara are working with GIZ/GTZ and the local community TAMIA to facilitate community development and training to enable sustainable development and energy use at Tsinjoriake.

These areas have rarely been included in long-term lemur (and other faunal) research and conservation. Although not as speciose (in terms of lemurs) as rainforest habitats, with only *Lemur catta* and *Microcebus griseorufus* observed by the authors, these coastal areas are rich in endemic plant, bird and reptile species and do hold important information for understanding lemur evolution and the presence of unique lemur traits (e.g., LaFleur 2012). As such, they deserve immediate conservation attention.

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REFERENCES

Anderson, J. R. 1998. Sleep, sleeping sites and sleep-related activities: Awakening to their significance. American Journal of Primatology 46, 1: 63–75.

Andriamahafaly, M. N. 2010. Plan d'Aménagement et de Gestion de la Nouvelle Aire Protégée Communautaire de Tsinjoriake, Toliara, 135pp. Unpubl. Report.

Andriatsimietry, R., Goodman, S. M., Razafimahatratra, E., Jeglinski, J. W. E., Marquard, M., and Ganzhorn, J. U. 2009. Seasonal variation in the diet of *Galidictis grandidieri* Wozencraft, 1986 (Carnivora: Eupleridae) in a sub-arid zone of extreme south-western Madagascar. Journal of Zoology 279, 4: 410–415. (doi:10.1111/j.1469-7998.2009.00633.x)

Barrett, L., Gaynor, D., Rendall, D., Mitchell, D. and Henzi, S. P. 2004 Habitual cave use and thermoregulation in chacma baboons (*Papio hamadryas ursinus*). Journal of Human Evolution 46, 2: 215–222. (doi:10.1016/j.jhevol.2003.11.005)

Cameron, A. and Gould, L. 2013. Fragment-Adaptive behavioural strategies and intersite variation in the ring-tailed lemur (*Lemur catta*) in South-Central Madagascar. In: Primates in Fragments. Developments in Primatology: Progress and Prospects. L. K. Marsh and C. A. Chapman (eds.), pp 227–243. Springer, New York, NY. (doi:10.1007/978-1-4614-8839-2_16)

Cheyne, S. M., Höing, A., Rinear, J. and Sheeran, L. K. 2012. Sleeping site selection by Agile gibbons: The influence of tree stability, fruit availability and predation risk. Folia Primatologica 83: 299–311. (doi:10.1159/000342145)

Cui, L.-W., Quan, R.-C. and Xiao, W. 2006. Sleeping sites of black-and-white snub nosed monkeys (*Rhinopithecus bieti*) at Baima Snow Mountain, China. Journal of Zoology 270, 1:192–198. (doi:10.1111/j.1469-7998.2006.00137.x)

Cuozzo, F.P. and Sauther, M.L. 2012. The dental ecology of ring-tailed lemurs (*Lemur catta*). In: Leaping Ahead: Advances in Prosimian Biology. J. C. Masters, M. Gamba, M. and F. Génin (eds.), pp 157–163. Springer, New York, NY.

Di Bitetti, M. S., Luengos, E. M., Baldovino M. C. and Benesovsky V. 2000. Sleeping site preferences in tufted capuchin monkeys (*Cebus apella nigritus*). American Journal of Primatology 50, 4: 257–274. (doi:10.1002/(SICI)1098-2345(200004)50:4<257::AID-AJP3>3.0.CO;2-J)

Donque, G. 1975. Contribution à l'Étude du Climat de Madagascar. Nouvelle Imprimerie des Arts Graphiques, Tananarive.

Du Puy, D. J. and Moat, J. F. 1998. Vegetation mapping and classification in Madagascar (using GIS): implications and recommendations for the conservation of biodiversity. In: Chorology, Taxonomy and Ecology of the African and Madagascan Floras. C. R. Huxley, J. M. Lock and D. F. Cutler D.F. (eds.), pp 97–117. Royal Botanic Gardens, Kew.

Enstam, K. L. 2007. Effects of habitat structure on perceived risk of predation and anti-predator behavior of vervet (*Crecopithecus aethiops*) and patas (*Erythrocebus patas*) monkeys. In: Predation in Primates. S. Gursky S. and A. Nekaris (eds.), pp 308–338. Cambridge University Press, Cambridge.

Gautier-Hion, A. 1970. L'organisation sociale d'une bande de talapoins (*Miopithecus talapoin*) dans le nord-est du Gabon. Folia Primatologica 12, 2: 116–141. (doi:10.1159/000155285)

Goodman, S. M. and Langrand, O. 1996. A high mountain population of the ring-tailed lemur (*Lemur catta*) on the Andringitra Massif, Madagascar. Oryx 30, 4: 259–268. (doi:10.1017/S003060530002175X)

Goodman, S. M., Rakotoarisoa, S. V. and Wilmé, L. 2006 The distribution and biogeography of the Ringtailed lemur (*Lemur catta*) in Madagascar. In: Ringtailed Lemur Biology Developments in Primatology: Progress and Prospects. A. Jolly, N. Koyama, H. Rasamimanana. and R. W. Sussman (eds.), pp 3–15. Kluwer Academic/Plenum, NY.

Gould, L. 2007. *Lemur catta* ecology: What we know and what we need to know. In: Lemurs: Ecology and Evolution. L. Gould and M. L. Sauther (eds.), pp 257–276. Springer, New York, NY.

Gould, L. and Sauther, M. L. 2007. Anti-predator strategies in a semi-terrestrial diurnal prosimian, the ring-tailed lemur (*Lemur catta*), at the Beza Mahafaly Special Reserve, Madagascar. In: Predation in Primates. S. Gursky S. and A. Nekaris, A. (eds.), pp 275–288. Cambridge University Press, Cambridge.

Hawkins, C. E. 2003. *Cryptoprocta ferox*, Fossa. In: The Natural History of Madagascar. S. M. Goodman and J. P. Benstead (eds.), pp 1360–1363. The University of Chicago Press, Chicago.

Huang, C., Wei, F., Li, M., Li, Y. and Sun, R. 2003 Sleeping cave selection, activity pattern and time budget of white-headed langurs. International Journal of Primatology 24, 4:813–824. (doi:10.1023/A:1024628822271)

Jolly, A. 1966. Lemur Behavior. The University of Chicago Press, Chicago.

Jolly, A., Sussman, R. W., Koyama, N. and Rasmimanana, H. (eds.). 2006. Ringtailed Lemur Biology. Springer, New York, NY.

Kelley, E. A. 2011. *Lemur catta* in the Region of Cap Sainte-Marie, Madagascar: Introduced Cacti, Xerophytic Didiereaceae-*Euphorbia* Bush, and Tombs. Unpublished Ph.D. Thesis. Washington University, St. Louis, MO.

Kummer, H. 1968. Social organization of hamadryas baboons. The University of Chicago Press, Chicago.

LaFleur, M. 2012. Ecology of Ring-tailed Lemurs (*Lemur catta*) at the Tsimanampetsotsa National Park, Madagascar: Implications for Female Dominance and the Evolution of Lemur Traits. Unpublished Ph.D. Thesis. University of Colorado-Boulder. Published online at http://vetmeduni.academia.edu/MarniLaFleur

Li, Z. and Rogers, M. E. 2005. Are limestone hills a refuge or essential habitat for whiteheaded langurs in Fusui, China? International Journal of Primatology 26, 2: 437–452. (doi:10.1007/s10764-005-2932-y)

Loudon, J. E., Sauther, M. L. Fish, K. D., Hunter-Ishikawa, M. and Jacky Youssouf, I. 2006. One reserve, three primates: applying a holistic approach to understand the interconnections among ring-tailed lemurs (*Lemur catta*), Verreaux's sifaka (*Propithecus verreauxi*), and humans (*Homo sapiens*) at Beza Mahafaly Special Reserve, Madagascar. Ecological and Environmental Anthropology 2, 2: 54–74. Published online at http://www.uga.edu/eea

McGrew, W. C., McKee, J. K. and Tutin, C. E. G. 2003. Primates in caves: two new reports of *Papio* spp. Journal of Human Evolution 44, 4: 521–526. (doi:10.1016/S0047-2484(03)00042-3)

Perrier de la Bâthie, H. 1927. Le Tsaratanana, l'Ankaratra el l'Andringitra. Mémoires de l'Académie Malgache 3: 1–71.

Pruetz, J. D. 2001. Use of caves by savanna chimpanzees (*Pan troglodytes verus*) in the Tomboronkoto region of southeastern Senegal. Pan Africa News 8, 2: 26–28.

Pruetz, J. D. 2007. Evidence of cave use by savanna chimpanzees (*Pan troglodytes verus*) at Fongoli, Senegal: implications for thermoregulatory behavior. International Journal of Primatology 48: 316-319. (doi:10.1007/s10329-007-0038-1)

Ravelohasindrazana, L. A. L. 2013. Etude de la population *Lemur catta* de la NAP Tsinjoriake site d'Antsifotse. Mémoire de fin d'étude en vue de l'obtention du diplôme de Licence Professionnelle en Biodiversité et Environnement (5^{e} promotion). Option: Biologie Animale. Université de Toliara, Faculté de Science.

Ravoavy, J. F. 2013. Etude de la Population de *Lemur catta* (*Maki*), dans la Nouvelle Aire Protégée Tsinjoriaky, Région Sud-Ouest de Madagascar. Mémoire en vue de l'obtention du Diplôme de Licence Professionnelle en Biodiversité et Environnement. Université de Toliara, Faculté de Science.

Sauther, M. L. 1989. Antipredator behavior in troops of free-ranging *Lemur catta* at Beza Mahafaly special reserve, Madagascar. International Journal of Primatolology 10, 6: 595–606. (doi:10.1007/BF02739366)

Sauther, M. L., Sussman, R. W. and Gould, L. 1999. The socio-ecology of the ring-tailed lemur: thirty-five years of research. Evolutionary Anthropology 8, 4:120–132. (doi:10.1002/(SICI)1520-6505(1999)8:4<120::AID-EVAN3>3.0.CO;2-O)

Sauther, M. L. and Cuozzo, F. P. 2008. Somatic variation in living, wild ring-tailed lemurs (*Lemur catta*). Folia Primatologia 79: 55–78. (doi:10.1159/000108589)

Scott, D., Annael, O., Mbohoahy, T., Raharinirina, N. L., Smith, M., Tanteliniaina, S., Thompson, S. and Tsagnangara, C. No Date. University of Brighton (UOB) Spiny Forest Research Expedition 2007/2008 Final Report. Unpubl. report to University of Brighton.

Tenaza, R. and Tilson R. 1985. Human predation and Kloss›s gibbon (*Hylobates klossii*) sleeping trees in Siberut Island, Indonesia. American Journal of Primatology 8, 4: 299–308. (doi:10.1002/ajp.1350080405)

Vasey, N., Burney, D. A. and Godfrey, L. 2013. Coprolites associated with *Archaeolemur* remains in North-western Madagascar suggest dietary diversity and cave use in a subfossil prosimian. In: Leaping Ahead: Advances in Prosimian Biology. J. Masters, M. Gamba and F. Génin (eds.), pp 149–156. Springer New York, NY.

Video 1: <http://www.youtube.com/watch?v=8qnBWSMqF_I&feature=youtu.be>

Video 2: <http://www.youtube.com/watch?v=mf_DSTCDyfI&feature=youtu.be>

Wilson, J. M., Stewart, P. D., Ramangason, G.-S., Denning, A. M. and Hutchings, M. S. 1989. Ecology and conservation of the crowned lemur, *Lemur coronatus*, at Ankarana N. Madagascar. Folia Primatologica 52, 1–2: 1–26.

Workman, C. 2010. The foraging ecology of the Delacour's langur (*Trachypithecus delacouri*) in Van Long Nature Reserve, Vietnam. Unpublished Ph.D. Thesis. Duke University. http://dukespace.lib.duke.edu/dspace/bitstream/handle/10161/2457/D_Workman_Catherine_a_201005.pdf?sequence=1

Zhang, S.-Y. 1995. Sleeping habits of brown capuchin monkeys (*Cebus apella*) in French Guiana. American Journal of Primatology 36, 4: 327–335. (doi:10.1002/ajp.135036040)

Zafisamimanana, L. M. 2012. Cartographie de l'Occupation du Sol dans la NAP Tsinjoriake. Unpubl. Report.

SUPPLEMENTARY MATERIAL.

AVAILABLE ONLINE ONLY.

Video clip showing Ilove troop lemurs at Tsimanampesotse scaling vertical limestone cliff and entering sleeping caves. Video by Michelle Sauther.

FIGURE S1. Lemur from the Akao troop in *Casuarina equisetifolia* tree on lake margin (A) and within the marshy ferns of *Acrostichum aureum* at the base of these trees (B) at Tsimanampesotse National Park, 2006.

FIGURE S2. Lemurs from the Grotte de Binabe troop on the cliff-face at Tsinjoriake Protected Area.

FIGURE S3. Cave above Sarodrano peninsula, where the "Ekipa" troop sometimes sleeps.

FIGURE S4. Spiny forest habitat at Tsinjoriake. The arrow is pointing at a tree that is 2 m. tall.

FIGURE S5. ILove troop ring-tailed lemurs huddling in a "lemur ball" on limestone rocks after leaving sleeping caves at Tsimanampesotse National Park.