9 The effects of the lunar cycle, temperature, and rainfall on the trapping success of wild brown mouse lemurs (*Microcebus rufus*) in Ranomafana National Park, southeastern Madagascar

Anja M. Deppe, Andrea Baden, and Patricia C. Wright

Introduction

Micromammals are notoriously difficult to observe because of their small size, and their cryptic, and often nocturnal lifestyle (Halle and Stenseth, 2001). Therefore, live trapping methods are commonly employed to determine distribution, estimate population densities, and infer animal activity (Gentry *et al.*, 1965; Vickery and Rivest, 1991; Atsalis, 2000; Caro *et al.*, 2001; Radespiel *et al.*, 2001; Schwab and Ganzhorn, 2004; Halle 2006; Prugh and Brashares, 2010). Because trapping is an indirect method of studying animal behavior, results should be interpreted cautiously (Prugh and Brashares, 2010), and should take into account a number of biotic and abiotic factors (Prugh and Golden, 2014). Factors that can affect activity and therefore capture rates of small mammals include predator behavior (Hilton *et al.*, 1999; Michalski and Norris, 2011; Cozzi *et al.*, 2012; Falcy and Danielson, 2013), and the temporal and spatial availability of food and shelter (Kotler *et al.*, 1993; Caro *et al.*, 2001; Davidson and Morris, 2001; Kelt *et al.*, 2004). In addition, possible affects of season, temperature, rainfall, and the lunar cycle must be considered (Kotler *et al.*, 1991; Daly *et al.*, 1992; Sutherland and Predavec, 1999; Stokes *et al.*, 2001; Michalski and Norris, 2011; Maestro and Marinho,2014; Prugh and Golden, 2014).

Small mammals may reduce activity during extreme temperatures (either hot or cold) due to thermoregulatory demands (Gentry and Odum, 1957; Vickery and Bider, 1981; Falcy and Danielson, 2013). Cold is especially dangerous to small mammals because of their susceptibility to hypothermia. This might explain why old-field mice (*Peromyscus polionotus*) were less frequently captured during cold than warm

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nights (Gentry and Odum, 1957), and why common voles (*Microtus arvalis*) reduced activity with decreasing temperature (Lehman and Sommersberg, 1980). Some small mammals (Lyman, 1983), including small primates such as mouse lemurs (*Microcebus*) and dwarf lemurs (*Cheirogaleus*), may become completely inactive for periods of time, undergoing hibernation (dwarf lemurs) or periods of torpor (Genin et al., 2005; Blanco and Godfrey, 2014). Mouse lemurs may be in an inactive, torpid state for days, weeks, or even months during the austral winter (Ortmann *et al.*, 1997; Schmid, 2000).

Rain may increase or decrease animal activity. Insectivorous mice and shrews, for example, became more active during rainy nights, possibly because the rain increased insect activity or entered their below-ground shelters (Gentry *et al.*, 1965; Jahoda, 1970; Doucet and Bider, 1974; Vickery and Bider, 1981; Vickery and Rivest, 1991; Stokes *et al.*, 2001; Maestri and Marinho, 2014). Rain can have a negative effect on the activity of small mammals. For example, wet fur exacerbates heat loss, which might explain why common voles ceased activity when rain coincided with low temperatures (Lehman and Sommersberg, 1980). Rain also increases background noise and reduces visibility, making the detection of predators and prey more difficult (Vickery and Rivest, 1991; Hilton *et al.*, 1999; Maestri and Marinho, 2014). Rain further makes it more difficult to observe animals (personal observation), and can thereby affect the human observer's perception of activity.

Lunar illumination is also known to influence animal activity (Gursky, 2003). Moon phases and associated variations in lunar brightness can affect the hunting success of visually oriented predators such as owls, carnivores, and snakes (Dice, 1945; Vermeij, 1982; Clarke, 1983; Bearder *et al.*, 2002; Cozzi *et al.*, 2012; Lillywhite and Brischoux, 2012). A reduction in travel and foraging during moonlit nights has been observed in rodents (Kotler *et al.*, 1991; Bowers *et al.*, 1993; Hughes *et al.*, 1994; Plesner *et al.*, 1995), and particularly in species that live in habitats with no or little cover (Prugh and Golden, 2014) such as deserts (Daly *et al.*, 1992; Price *et al.*, 1994; Upham and Hafner, 2013), meadows (Bouliska, 1995), or secondary forests (Michalski and Norris, 2011). This might be explained by a higher (perceived) predation risk during lunar illumination. Rodents in desert and meadow habitats may be particularly vulnerable because visual predators can detect them more easily, and aerial predators further benefit from an unobstructed attack path. The avoidance of moonlight (lunar phobia) has further been observed in primates (Erkert, 1989; Bearder *et al.*, 2006; Starr *et al.*, 2012; Rode-Margono and Nekaris, 2014), and bats (Fenton *et al.*, 1977; Morrison, 1978; Lang *et al.*, 2006). In bats, moonlight avoidance may, however, be an adaptation to the lunar phobic behavior of their insect prey rather than an antipredation behavior (Erkert, 1974).

An increase in activity during bright nights (lunar philia) has been recorded in a range of animals including rodents (Sutherland and Predavec, 1999; Kotler, 1984), wallabies (Blumstein *et al.*, 2000), primates (Bearder *et al.*, 2002; Gursky, 2003; Eppeley *et al.*, 2015), and carnivores (Cozzi *et al.*, 2012). Lunar philia has been linked to enhanced prey or predator detection in visually oriented species (Bearder *et al.*, 2002; Gursky, 2003; Prugh and Golden, 2014), and to the reduction of feeding competition with dominant, lunar phobic, species (Upham and Hafner, 2013). Lunar philic behavior appears to be particularly common in nocturnal primates including owl monkeys (*Aotus*), galagos (*Galago*), and tarsiers (*Tarsius*), as well as cathemeral lemurs (Erkert, 1974, 1989; Charles-Dominique, 1977; Erkert and Gröber, 1986; Wright, 1989; Nash, 1986, 2007; Donati *et al.*, 2001; Bearder *et al.*, 2002; Gursky, 2003; Fernandez-Duque and Erkert, 2006; Eppeley *et al.*, 2015). Because primates are visually oriented (Kirk and Kay, 2004; Tetreault *et al.*, 2004), they probably benefit from enhanced predator detection during bright nights (Charles-Dominique, 1977; Gursky, 2003; Bearder *et al.*, 2006). Insectivorous or carnivorous species like tarsiers, lorises (*Nycticebus*), and mouse lemurs may further benefit from enhanced visual prey detection (Gursky, 2003; Starr *et al.*, 2012). However, there is also evidence that some nocturnal primates, including lorises and mouse lemurs, may be lunar neutral or lunar phobic, which could be an effect of food availability, vulnerability to predation, or temperatures during the study period (Erkert, 1989; Bearder *et al.*, 2006; Starr *et al.*, 2012; Rode-Margono and Nekaris, 2014).

The purpose of this study was to test the hypothesis that abiotic factors, specifically temperature, rainfall, and the lunar cycle, affect activity patterns and capture rates of the brown mouse lemur (*Microcebus rufus*) in the Talatakely trail system area in Ranomafana National Park (RNP). The brown mouse lemur is a small-bodied (45 g), nocturnal primate found in the southeastern rainforests of Madagascar (Atsalis, 2000), which forages mostly solitarily for fruit, nectar, and insects (Atsalis, 1999a). Mouse lemurs are endemic to Madagascar and inhabit a variety of habitats including rainforest, dry forest, spiny forest, plantations, and human dwellings (Kappeler and Rasoloarison, 2003). Due to their small body size, mouse lemurs across all habitat types are subject to high predation rates (Goodman *et al.*, 1993; Goodman, 2003a). Predators include diurnal and nocturnal raptors (Goodman *et al.*, 1993; Karpanty, 2006; Karpanty and Wright, 2007), viverrids (Hawkins, 2003; Dollar *et al.*, 2007), and snakes (Cadle, 2003; Raxworthy, 2003).

Little is known about predation rates for the brown mouse lemur at our study site. The diurnal raptors found in RNP include the Henst's goshawk (*Accipiter henstii*), the Madagascar buzzard (*Buteo brachypterus*), and the Madagascar harrier hawk (*Polyboroides radiatus*), and predation rates are low at an estimated 4.5% annually (Karpanty, 2006). Carnivorous mammals in RNP that are known to eat mouse lemurs are the diurnal ring-tailed mongoose (*Galidia elegans*; Goodman, 2003b; Deppe *et al.*, 2008), and the cathemeral fosa (*Cryptoprocta ferox*; Dollar *et al.*, 2007). There is no evidence that the nocturnal broad-striped mongoose (*Galidictis fasciata*; Goodman, 2003c) or the nocturnal Malagasy civet (*Fossa fossana*; Kerridge *et al.*, 2003) prey on mouse lemurs, but little is known about these largely terrestrial predators. Owls are one of the most effective predators (Vermeij, 1982), and while they are highly visual, they are able to locate prey in complete darkness by acoustic cues alone (Payne, 1971; Konishi, 1973). In the dry forest, owls appeared to be by far the most dangerous predator to mouse lemurs and were estimated to take nearly a third of the gray mouse lemur population annually (Goodman *et al.*, 1993). Owl species present in RNP are the small Madagascar scops owl (*Otus rutilus*), the medium-sized Madagascar red owl (*Tyto soumagnei*), and the large Madagascar long-eared owl (*Asio madagascariensis*; Hawkins and Goodman, 2003). We do not know owl predation rates at our site, but long-term trap-recapture data suggest that overall, predation rates for the brown mouse lemur are well below those found in gray mouse lemurs (unpublished data). Snakes include various smaller colubrid species, but the large nocturnal Madagascar tree boa (*Sanzinia madagascariensis*) is probably the most dangerous to brown mouse lemurs (Cadle, 2003; Raxworthy, 2003).

Like many mouse lemur species (Ortmann *et al.*, 1997; Schmid, 2001), the brown mouse lemur appears to undergo periods of inactivity (torpor) during the often cold and lean austral winter (personal observation), where temperatures may reach lows of 4°C (Wright and Andriamihaja, 2002). Anecdotal evidence further suggested that brown mouse lemurs decrease activity with increasing rainfall. Based on our observations and what has been found for other primate species, we predicted that brown mouse lemurs are more active, and more likely to be trapped, during warm nights than cold ones, dry nights than rainy nights, and during bright nights than dark nights. We applied an indirect measure, live-trap rates, assuming that a higher trap rate reflects higher general activity.

Methods

We present data gathered over a 4-year period (2004–2007) during Madagascar's austral spring (September–December), resulting in a total of 228 trap nights during which 6718 baited traps yielded 1795 captures. We focus only on data collected during the austral spring because brown mouse lemurs were generally absent from traps during the austral winter (June–August) and fall (March–May), possibly because of inactivity due to low temperatures and high food availability, respectively (Harcourt, 1987; Atsalis, 1999a). During January and February, frequent storms and cyclones prevented research.

Study site

Fieldwork was conducted in Talatakely, a well-established trail system of ~ 9 ha in Ranomafana National Park. The park, established in 1991, comprises 43,500 ha of continuous rainforest located in southeastern Madagascar at 21°16′S latitude and 47°20′E longitude (Wright, 1992; Wright and Andriamihaja, 2002). Elevations range from 500 to 1500 m, and annual rainfall is 4000 mm (RNP/Centre ValBio, unpublished data), most of which falls during the austral summer months from December to March. Based on RNP/Centre ValBio records, temperatures range from lows in June–September (4–12°C) to highs in December–February (30–32°C). Our data were collected in the spring when temperatures ranged from 10 to 20°C at night and 15 to 25°C during the day.

Data collection

Capture–mark–recapture techniques were employed as part of a long-term collaborative project to monitor the behavioral ecology of brown mouse lemur populations within the Talatakely trail system (Blanco and Meyer, 2009). Animals were captured nightly using Sherman live traps (30 × 8 × 10 cm; H.B. Sherman Traps, Inc., Tallahassee, FL, USA). Following standard protocol (Harcourt, 1987; Atsalis, 1999a; Blanco, 2008), traps were set at 25–50 m intervals in pairs along opposing pre-existing trails. Each trap was situated at least 5 m off-trail and fixed to a sturdy, horizontal substrate at ~1.5 m above the ground. Traps were baited with a piece of fresh banana and opened nightly at 1700 hours during 4–5 consecutive nights per week. Traps were checked and re-collected at 2100 hours, because our experience has shown that brown mouse lemurs are most likely to enter the traps within the first 2 h of nightfall. All captured lemurs were brought to the Centre ValBio research station where, with the exception of a few days where the chip scanner was not available, individuals were sexed and identified, or if unknown, marked with AVID microchips for later re-identification (Avid Identification Systems, Inc., Norco, CA, USA). Animals were then released between 2300 and 0100 hours the same night of capture to minimize disturbance. Individuals were released at the site of their original capture. Because the same lemurs were commonly recaptured every night, approximately 30 traps were rotated among 60 fixed locations along the trail to minimize the dependence on provisioning. All methods and procedures complied with protocols approved by the Stony Brook University Institutional Animal Care Committee and adhered to the legal requirements of Madagascar.

Data analysis

Nightly capture success, or trap rate, was calculated by dividing the number of captured individuals by the number of total traps opened that night. Data were found to be non-normally distributed using a Kolmogorov–Smirnov goodness-of-fit test and, for this reason, non-parametric statistics were used. We used a non-parametric Mann–Whitney *U* test to test for differences in trap rates between males and females.

Moon phases were determined using a lunar calendar and were divided into four main categories: full moon (defined as the night of full moon, plus two days prior to and following full moon, i.e., 5 days), new moon (defined as the night of new moon, plus two days prior to and following, i.e., 5 days), waning (the 10 days between full and new moon), and waxing (the 10 days between new and full moon). To test whether moon phase was related to trap rate, we used a non-parametric Kruskal–Wallis test followed by pairwise Mann–Whitney *U* comparisons with Bonferroni corrections.

Rainfall and temperature data were extracted from the CVB database. We tested for relationships between trap rate and both minimum nightly temperature and total nightly rainfall using Spearman's rho correlations. We excluded maximum

Table 9.1 Details of annual and total trapping effort during the study period 2004–2007 for the Talatakely trail system in Ranomafana National Park. The trap rate (in %) states the likelihood of a brown mouse lemur entering a trap, and is calculated by dividing the total number of individuals captured by the total number of traps set during that period.

Trap period	Trap nights	Traps	Captures	Males	Females	Trap rate (%)
Sep–Dec 2004	55	2051	380	269	111	18.5
Oct–Dec 2005	52	1393	364	194	170	26.1
Sep–Nov 2006	49	1246	416	278	138	33.4
Sep–Dec 2007	72	2028	635	471	164	31.3
Total	228	6718	1795	1212	583	26.7

Table 9.2 Total number of brown mouse lemur captures by month, sex, and male to female capture ratio. The trap rate is the capture likelihood (total number of individuals caught divided by the total number of traps set) in percent for both sexes combined.

Month	All	Female	Male	Male:female	Trap rate (%)
September	384	16	368	23.0	19
October	895	315	580	1.8	31
November	452	215	237	1.1	29
December	64	37	27	0.73	21

temperatures measured for each day because low temperatures were most relevant to night-active brown mouse lemurs and because there was a strong correlation between daily maximum and minimum temperatures. Statistical analysis was conducted using SPSS 15.0. The alpha level was set *a priori* at 0.05 unless otherwise noted.

Results

We captured a total of 1795 brown mouse lemurs (68% males, 32% females) during a total of 228 trap nights (Table 9.1). Capture likelihood was highest in October and November (Table 9.2). Males were captured significantly more often than females (Mann–Whitney $U = 13{,}930$, $p < 0.001$; Table 9.2). Overall trap rates differed significantly across lunar phases ($H = 11.16$, $p = 0.011$; Figure 9.1). Animals were significantly more likely to be captured during full moon nights than during any other phase (Full × Waxing, $p = 0.023$; Full × New, $p = 0.026$; Full × Waning, $p = 0.030$). Rainfall and minimum temperature varied across months (Table 9.3). We found a significant negative relationship between trap rate and both rainfall (Spearman's rho = −0.187, $p < 0.001$) and minimum nightly temperature (−0.146, $p = 0.029$), such that trap rates increased with decreasing rainfall and decreasing temperatures.

Table 9.3 Monthly average (and ranges) of minimum temperatures and rainfall for the Talatakely trail system in Ranomafana National Park during the study period 2004–2007.

Month	Min. temp (°C)	Rainfall (mm)
September	13.6 (10–17)	7.0 (0–42)
October	14.7 (9–19)	4.7 (0–54)
November	16.9 (10–21)	6.1 (0–58)
December	19.3 (11–22)	13.7 (0–60)
Average	15.5 (9–22)	6.3 (0–60)

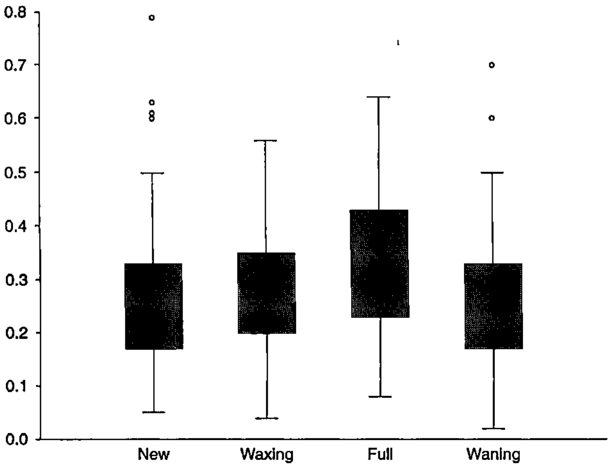

Figure 9.1 Brown mouse lemur trap rate by lunar phase. Box plots represent median ± range. Traps rates were significantly higher during full moon than any other lunar phase.

Discussion

We analyzed trapping data collected over a four-year period in RNP to assess whether rainfall, minimum temperature, or the lunar cycle affected the likelihood of capturing brown mouse lemurs in live traps. We assumed the capture rates were a proxy for general activity, and predicted that activity might vary due to changes in predation risk, foraging efficiency, and thermoregulatory demands. We found that brown mouse lemurs were most likely to be captured during nights around a full moon, and dry nights with lower temperatures. Overall, more than twice as many males than females were captured.

Lunar illumination has been hypothesized to enhance to detection of live prey as well as predators (Gursky, 2003). It has been proposed that visually oriented prey species such as primates may benefit from bright nights because their increased ability to detect predators lowers predation risk, while less-visual species such as rodents may experience an increase in predation risk by visually oriented predators (Gursky, 2003; Bearder *et al.*, 2006; Prugh and Golden, 2014; Rode-Margono and Nekaris,2014; Eppeley *et al.*, 2015). While our prediction was met in that the only moon phase that positively affected capture likelihood was the full moon category, the effect was not very strong (p-values between 0.023 and 0.03). It is thus unclear whether brown mouse lemurs are lunar philic like so many other primates (e.g., Gursky, 2003; Eppeley *et al.*, 2015). We will next discuss how moonlight might affect brown mouse lemur behavior. It is important to note that while our site had been selected logged in the 1980s, the forest has since recovered, with most areas having a closed canopy. In combination with frequent cloud cover, this might make moonlight penetration negligible on many nights. An effect of cover was observed in the paca (*Cuniculus paca*), a Neotropical rodent. Lunar illumination had little effect on pacas inhabiting a dense canopy primary rainforest (Michalski and Norris, 2011), whereas pacas inhabiting a more open canopy secondary forest avoided moonlight, presumably because of a higher (perceived) predation risk (Emmons *et al.*, 1989; Harmsen *et al.*, 2011). Differences in canopy cover may also explain why gray mouse lemurs reduced activity with increasing illumination (Erkert, 1989). Gray mouse lemurs inhabit a more open canopy dry forest habitat, and may thus experience a higher predation risk by visual predators (Goodman *et al.*, 1993). However, the gray mouse lemurs tested were captive animals with no need to avoid predators or to forage, so the behavior observed in the study (Erkert, 1989) may not accurately reflect the behavior of wild individuals.

It is, however, conceivable that brown mouse lemurs benefit from illumination by an enhanced ability to detect food or predators. Brown mouse lemurs commonly hunt flying and crawling insects such as moths and beetles, and even though they rely on hearing to detect insects (Görlitz and Siemers, 2007), their ability to catch them may increase with increasing illumination. Flowers were common during our trapping period, and moonlight may make them easier to detect. The largest benefit from lunar illumination might, however, be derived from an increased ability to detect predators. Brown mouse lemur predation rates by nocturnal predators are not known for our site, but nocturnal predators present include the fosa (*C. ferox*), the Madagascar tree boa (*S. madagascariensis*), and owls (*O. rutilus*, *T. soumagnei*, *A. madagascariensis*; Goodman, 2003a; Raxworthy, 2003). The large fosa (7–12 kg) probably poses little threat to the small agile brown mouse lemurs during the night, and is extremely rare at our site (Wright, personal observation). While owl hunting success increases with illumination, they can hunt in complete darkness, relying on acoustic signals alone (Konishi, 1973; Clarke, 1983), which enables them to be active across all moon phases. In the rainforest, owls are camouflaged ambush hunters that pounce on their prey from perches, and thus the likelihood to detect an owl may not be affected by levels of illumination. Moreover, predator recognition experiments suggest that owl recognition is not well developed in the brown mouse lemur (Deppe and Wright, 2007), maybe because owls appear to be relatively rare at our site (Wright, personal observation). In contrast, the ability to detect snakes might increase with increasing illumination. For example, while the Madagascar tree boa is a very well-camouflaged predator that is difficult to detect even during the daytime (Deppe, personal observation), experiments suggest that brown mouse lemurs visually recognize snakes (Deppe 2005, 2006). Future studies increasing sample sizes, including more seasons, and expanding experiments may shed more light on how the brown mouse lemur responds to the lunar illumination.

There is increasing evidence that behavioral responses to lunar illumination are variable within species, and may change in response to season, food availability, age, habitat characteristics, and predator presence (e.g. Lockard and Owings, 1974; Kotler, 1984; Emmons *et al.*, 1989; Sutherland and Predavec, 1999; Harmsen *et al.*, 2011; Starr *et al.*, 2012; Upham and Hafner, 2013; Prugh and Golden, 2014; Rode-Margono and Nekaris, 2014). The gray slender loris (*N. lydekkerianus*), for example, was found to be largely lunar neutral, but sometimes vocalized and foraged more for insects during bright nights (Bearder *et al.*, 2006). The Javan slow loris (*N. javanicus*) tended to reduce activity during cold nights, regardless of illumination, suggesting that thermoregulatory considerations affected activity more than moonlight (Rode-Magonos and Nekaris, 2014).

Our prediction that brown mouse lemurs would be more likely to be captured during warmer nights was not met because capture likelihood increased with decreasing temperature. This was surprising because small mammals are susceptible to hypothermia (Falcy and Danielson, 2013), and tend to reduce activity when its cold (e.g., Lehman and Sommersberg, 1980; Rode-Margono and Nekaris, 2014). During the austral winter, June through August, when temperatures may reach lows of 4°C, mouse lemurs, especially females, may enter an inactive state of torpor to conserve energy (Ortmann *et al.*, 1997; Schmid, 2000; Genin *et al.*, 2005). The torpor behavior of the brown mouse lemur is not well understood, but low capture rates suggest prolonged torpor in this species as well (Harcourt, 1987; Atsalis, 1999b; Table 9.2; unpublished data). The seeming preference for cold temperatures found in our study is thus surprising. However, trapping took place in the early evening, where temperatures were well above nightly minimum temperatures. So while it is possible that brown mouse lemurs reduced activity during the coldest parts of the night, this would not be reflected in our study. The austral spring tends to be warm and dry, especially from October on (Table 9.3), but we do not believe it is hot enough to have thermoregulatory consequences, especially after sundown. Moreover, by far the most brown mouse lemurs were captured during October and November. It is important to note that our *p*-value of 0.029 was relatively high. We do not think that during our study period temperature had an effect on trapping success, but that our result was confounded by other factors, such as insect or predator activity, or sample size.

Rain may increase or decrease animal activity by increasing insect activity, flooding underground shelters, lowering visibility, and increasing background noise (Gentry *et al.*, 1965; Jahoda, 1970; Doucet and Bider, 1974; Vickery and Bider, 1981; Vickery and Rivest, 1991; Hilton *et al.*, 1999; Stokes *et al.*, 2001; Maestri and Marinho, 2014). As expected, rainfall negatively affected capture rates, where captures decreased with increasing rainfall. Brown mouse lemurs may prefer dry nights because detecting prey and predators might be easier. Rainfall, particularly heavy rain, increases background noise and lowers visibility, and may thus negatively affect the ability to see or hear predators and insects. While small mammals have been recorded to increase activity during light rain as a result of increased insect activity (Doucet and Bider, 1974; Vickery and Bider, 1981; Cresswell and Harris, 1988), heavy rain might have negative effects. Flying insects in particular stay out of the rain, and the background noise probably makes it more difficult for brown mouse lemurs to acoustically locate insect prey (Görlitz and Siemers, 2007). Rain may also have thermoregulatory consequences because wet fur exacerbates heat loss (Jahoda, 1970, 1973), and the small brown mouse lemur may avoid rain to conserve energy. One limitation of our finding is that because the rainfall was collected over a 24-h period, we do not know whether it actually rained during trapping hours. However, there is anecdotal evidence that trap rates were low during heavy rain (Deppe, personal observation). In addition, there is often a marked increase in frequency and severity of rainfall in December, which likely contributes to the low trap rates during that time (Deppe, personal observation; Table 9.3).

In summary, our findings suggest that during the months of September–December, brown mouse lemurs are more likely to be captured during full moon nights, dry nights, and lower nightly minimum temperatures. No link has been established between trapping success and activity (Prugh and Brashares, 2010), so it is important to keep in mind that trapping success may not accurately reflect general activity. Nonetheless, the more an animal is moving about, the more likely it is to encounter a trap. However, brown mouse lemurs quickly learn the trap locations and become very "trap happy", where in some cases individuals return to the same trap every night. These individuals might not necessarily be generally active, but may go straight to a known trap for banana. It is also important to note that October and November are the prime mating months at our site. Both males and females are highly active, conspicuous, sometimes travel in groups, and may even be active in broad daylight (Deppe, personal observation). These activity patterns are specific to the mating season, and because half of our data were collected during that time, our findings may not extend to other times of the year. It would be informative to examine whether trapping during other seasons reveals different results with regard to the lunar cycle, rainfall, and temperature. We acknowledge the limitations of this study, particularly its indirect nature of assessing activity. Future studies should aim to include additional seasons and the employment of radiotelemetry techniques or observations to obtain more direct information about brown mouse lemur activity cycles.

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References

Atsalis S. 1999a. Seasonal fluctuations in body fat and activity levels in a rain-forest species of mouse lemur, *Microcebus rufus*. *International Journal of Primatology* 20:883–910.

Atsalis S. 1999b. Diet of the brown mouse lemur (*Microcebus rufus*) in Ranomafana National Park, Madagascar. *International Journal of Primatology* 20:193–229.

Atsalis S. 2000. Spatial distribution and population composition of the brown mouse lemur (*Microcebus rufus*) in Ranomafana National Park, Madagascar, and its implications for social organization. *American Journal of Primatology* 51:61–78.

Bearder S, Nekaris KA, Buzell A. 2002. Dangers in the night: are some nocturnal primates afraid of the dark? In LE Miller (ed.), *Eat or Be Eaten: Predator Sensitive Foraging Among Primates* (pp. 21–43). Cambridge University Press, Cambridge.

Bearder S, Nekaris KA, Curtis DJ. 2006. A re-evaluation of the role of vision in the activity and communication of nocturnal primates. *Folia Primatologica* 77:50–71.

Blanco MB. 2008. Reproductive schedules of female *Microcebus rufus* at Ranomafana National Park, Madagascar. *International Journal of Primatology* 29:323–338.

Blanco MB, Godfrey LR. 2014. Hibernation patterns of dwarf lemurs in the high altitude forest of eastern Madagascar. *Developments in Primatology: Progress and Prospects* pp. 23–42.

Blanco MB, Meyer JS. 2009. Assessing reproductive profiles in female brown mouse lemurs (*Microcebus rufus*) from Ranomafana National Park, southeast Madagascar, using fecal hormone analysis. *American Journal of Primatology* 71:439–446.

Blumstein DT, Daniel JC, Griffin, AS, Evans CS. 2000. Insular tammar wallabies (*Macropus eugenii*) respond to visual but not acoustic cues from predators. *Behavioral Ecology* 11:528–535.

Bouliska A. 1995. Interactions between predation risk and competition: a field study of kangaroo rats and snakes. *Ecology* 76:165–178.

Bowers MA, Jefferson JL, Kuebler, MG. 1993. Variation in giving-up densities of foraging chipmunks (*Tamias striatus*) and squirrels (*Sciurus carolinensis*). *Oikos* 66:229–236.

Cadle JE. 2003. Colubridae, snakes. In SM Goodman, JP Benstead (eds.), *The Natural History of Madagascar* (pp. 997–1004). University of Chicago Press, Chicago.

Caro TM, Brock R, Kelly M. 2001. Diversity of mammals in the Bladen Nature Reserve, Belize, and factors affecting their trapping success. *Mammalian Biology* 66:90–101.

Charles-Dominique P. 1977. *Ecology and Behaviour of Nocturnal Primates.* Columbia University Press, New York.

Clarke JA. 1983. Moonlight's influence on predator/prey interactions between short-eared owls (*Asio flammeus*) and deermice (*Peromyscus maniculatus*). *Behavioral Ecology and Sociobiology* 13:205–209.

Cozzi G, Broekhuis F, McNutt JW, Turnbull LA, MacDonald DW, Schmid B. 2012. Fear of the dark or dinner by moonlight? Reduced temporal partitioning among Africa's large carnivores. *Ecology* 93:2590–2599.

Cresswell WJ, Harris S. 1988. The effects of weather conditions on the movement and activity of badgers (*Meles meles*) in a suburban environment. *Journal of Zoology, London* 216:187–194.

Daly M, Behrends PR, Wilson MI, Jacobs LF. 1992. Behavioural modulation of predation risk: moonlight, avoidance and crepuscular compensation in a nocturnal rodent, *Dipodomys merriami*. *Animal Behaviour* 44:1–9.

Davidson DL, Morris DW. 2001. Density-dependent foraging effort of deer mice (*Peromyscus maniculatus*). *Functional Ecology* 15:575–583.

Deppe AM. 2005. Visual predator recognition and response in wild brown mouse lemurs (*Microcebus rufus*) in Ranomafana National Park, Madagascar. *American Journal of Primatology* 66(Suppl 1):97–98.

Deppe AM. 2006. Visual snake recognition in wild brown mouse lemurs (*Microcebus rufus*). *American Journal of Primatology* 68(Suppl 1):34.

Deppe AM, Wright PC. 2007. Owl recognition via visual, olfactory, and auditory sensory cues in a small nocturnal primate, *Microcebus rufus*, in Ranomafana National Park, Madagascar. Prosimian Congress, Ithala, p. 43.

Deppe AM, Randriamiarisoa M, Kasprak AH, Wright PC. 2008. Predation on the brown mouse lemur (*Microcebus rufus*) by a diurnal carnvivore, the ring-tailed mongoose (*Galidia elegans*). *Lemur News* 13:17–18.

Dice LR. 1945. Minimum intensities of illumination under which owls can find dead prey by sight. *The American Naturalist* 784:385–415.

Dollar L, Ganzhorn J, Goodman SM. 2007. Primates and other prey in the seasonally variable diet of *Cryptoprocta ferox* in the dry deciduous forest on western Madagascar. In A Gursky, KAI Nekaris (eds.), *Primate Anti-predator Strategies* (pp. 63–76). Springer, New York.

Donati G, Lunardini A, Keppeler PM, Borgognini Tarli SM. 2001. Nocturnal activity in the cathemeral red-fronted lemur (*Eulemur fulvus rufus*), with observations during a lunar eclipse. *American Journal of Primatology* 53:69–78.

Doucet CJ, Bider JR. 1974. The effects of weather on the activity of the masked shrew. *Journal of Mammalogy* 55:348–363.

Emmons LH, Sherman P, Bolster D, *et al.* 1989. Ocelot behaviour in moonlight. In KH Redford, JF Eisenberg (eds.), *Advances in Neotropical Mammalogy* (pp.233–242). Sandhill Crane Press, Gainesville.

Eppely TM, Ganzhorn JU, Donati G. 2015. Cathemerality in a small, folivorous primate: proximate control of diel activity in *Hapalemur meridionalis*. *Behavioral Ecology and Sociobiology* April: DOI 10.1007/s00265-015-1911-3.

Erkert HG. 1974. Der Einfluss des Mondlichtes auf die Aktivitätsperiodik nachtaktiver Säugetiere. *Oecologia* 14:269–287.

Erkert HG. 1989. Lighting requirements of nocturnal primates in captivity: a chronological approach. *Zoo Biology* 8:179–191.

Erkert HG, Gröber J. 1986. Direct modulation of activity and body temperature of owl monkeys (*Aotus lemurinus griseimembra*) by low light intensities. *Folia Primatologica* 47:171–188.

Falcy MR, Danielson B. 2013. A complex relationship between moonlight and temperature on the foraging behavior of the Alabama beach mouse. *Ecology* 94:2632–2637.

Fenton MB, Boyle NG, Harrison TM, Oxley D J. 1977. Activity patterns, habitat use, and prey selection by some African insectivorous bats. *Biotropica* 9:73–85.

Fernandez-Duque E, Erkert HG. 2006. Cathemerality and lunar periodicity of activity rhythms in owl monkeys of the Argentinian Chaco. *Folia Primatologica* 77:123–138.

Genin F, Schilling A, Perret M. 2005. Social inhibition of seasonal fattening in wild and captive gray mouse lemurs. *Physiology & Behavior* 86:185–194.

Gentry JB, Odum EP. 1957. The effect of weather on the winter activity of old-field rodents. *Journal of Mammalogy* 38:72–78.

Gentry JB, Golley FB, McGinnis JT. 1965. Effect of weather on captures of small mammals. *The American Midland Naturalist* 75:526–530.

Goodman SM. 2003a. Predation on lemurs. In SM Goodman, JP Benstead (eds.), *The Natural History of Madagascar* (pp. 1221–1228). University of Chicago Press, Chicago.

Goodman SM. 2003b. Carnivora: *Galidia elegans*, ring-tailed mongoose, *Vontsira mena*. In SM Goodman, JP Benstead (eds.), *The Natural History of Madagascar* (pp.1351–1354). University of Chicago Press, Chicago.

Goodman SM. 2003c. *Galidictis*, broad striped mongoose, *Vontsira fotsy*. In SM Goodman, JP Benstead (eds.), *The Natural History of Madagascar* (pp. 1355–1357). University of Chicago Press, Chicago.

Goodman SM, O'Connor S, Langrand O. 1993. A review of predation on lemurs: implications for the evolution of social behavior in small, nocturnal primates. In PM Kappeler, JU Ganzhorn (eds.), *Lemur Social Systems and their Ecological Basis* (pp. 51–66). Plenum Press, New York.

Görlitz H, Siemers, BM. 2007. Sensory ecology of prey rustling sounds: acoustical features and their classification by wild grey mouse lemurs. *Functional Ecology* 21:143–153.

Gursky S. 2003. Lunar philia in a nocturnal primate. *International Journal of Primatology* 24:351–367.

Halle S. 2006. Polyphasic activity patterns in small mammals. *Folia Primatologica* 77:15–26.

Halle S, Stenseth NC. 2001. *Activity Patterns in Small Mammals: An Ecological Approach.* Springer, New York.

Harcourt C. 1987. Brief trap/retrap study of the brown mouse lemur (*Microcebus rufus*). *Folia Primatologica* 49:209–211.

Harmsen B, Foster R, Siver SC, Ostro LET, Doncaster CP. 2011. Jaguar and puma activity patterns in relation to their main prey. *Mammalian Biology* 76:320–324.

Hawkins CE. 2003. *Cryptoprocta ferox*, fossa, *Fosa*. In SM Goodman, JP Benstead (eds.), *The Natural History of Madagascar* (pp. 1360–1363). University of Chicago Press, Chicago.

Hawkins CE, Goodman SM. 2003. Introduction to the birds. In SM Goodman, JP Benstead (eds.), *The Natural History of Madagascar* (pp. 1019–1044). University of Chicago Press, Chicago.

Hilton GM, Ruxton GD, Cresswell W. 1999. Choice of foraging area with respect to predation risk in redshanks: the effects of weather and predator activity. *Oikos* 87:295–302.

Hughes JJ, Ward D, Perrin MR. 1994. Predation risk and competition affect habitat selection and activity of Namib desert gerbils. *Ecology* 75:1397–1405.

Jahoda JC. 1970. The effects of rainfall on the activity of *Onychomys leucogaster breviauritus*. *American Zoologist* 10:326.

Jahoda JC. 1973. The effect of the lunar cycle on the activity pattern of *Onchomys leucogaster breviauritus*. *Journal of Mammalogy* 54:544–549.

Kappeler PM, Rasoloarison RM. 2003. *Microcebus*, mouse lemurs. In SM Goodman, JP Benstead (eds.), *The Natural History of Madagascar* (pp. 1310–1315). University of Chicago Press, Chicago.

Karpanty S. 2006. Direct and indirect impacts of raptor predation on lemurs in southeastern Madagascar. *International Journal of Primatology* 27:239–261.

Karpanty S, Wright PC. 2007. Predation on lemurs in the rainforest of Madagascar by multiple predator species: observations and experiments. In A Gursky, KAI Nekaris (eds.), *Primate Anti-predator Strategies* (pp. 77–99). Springer, New York.

Kelt DA, Meserve PL, Nabors LK, Forister ML, Gutierrez JR. 2004. Foraging ecology of small mammals in semiarid Chile: the interplay of biotic and abiotic factors. *Ecology* 85:383–397.

Kerridge FJ, Ralisoamalala RC, Goodman SM, Pasnick SD. 2003. In SM Goodman, JP Benstead (eds.), *The Natural History of Madagascar* (pp. 1363–1365). University of Chicago Press, Chicago.

Kirk EC, Kay RF. 2004. The evolution of high visual acuity in the anthropoidea. In CF Ross, RF Kay (eds.), *Anthropoid Origins: New Visions* (pp. 539–602). Kluwer, New York.

Konishi M. 1973. Locatable and nonlocatable acoustic signals from barn owls. *The American Naturalist* 107:775–785.

Kotler BP. 1984. Risk of predation and the structure of desert rodent communities. *Ecology* 65:689–701.

Kotler BP, Brown, JS, Hasson O. 1991. Factors affecting gerbil foraging behavior and rates of owl predation. *Ecology* 7:22249–22260.

Kotler BP, Brown JS, Mitchell WA. 1993. Environmental factors affecting patch use in two species of gerbilline rodents. *Journal of Mammalogy* 54:256–260.

Lang AB, Kalko EKV, Roemer H, Bockholdt C, Dechmann DKN. 2006. Activity levels of bats and katydids in relation to the lunar cycle. *Behavioral Ecology* 146:659–666.

Lehmann U, Sommersberg CW. 1980. Activity patterns of the common vole, *Microtus arvalis*–automatic recording of behaviour in an enclosure. *Oecologia* 47:61–75.

Lillywhite HB, Brischoux F. 2012. Is it better in the moonlight? Nocturnal activity of insular cottonmouth snakes increases with lunar light levels. *Journal of Zoology* 286:194–199.

Lockard RB, Owings DH. 1974. Seasonal variation in moonlight avoidance by bannertail kangaroo rats. *Journal of Mammalogy* 55:189–193.

Lyman C. 1983. *Hiberation and Torpor in Mammals and Birds*. Academic Press, London.

Maestri R, Marinho JR. 2014. Singing in the rain. Rainfall and moonlight affect daily activity patterns of rodents in a Neotropical forest. *Acta Theriologica* 59:427–433.

Michalski F, Norris D. 2011. Activity pattern of *Cuniculus paca* (Rodentia: Cuniculidae) in relation to lunar illumination and other abiotic variables in the southern Brazilian Amazon. *Zoologia* 28:701–708.

Morrison DW. 1978. Lunar phobia in a neotropical fruit bat, *Artibeus jamaicensis* (Chiroptera: Phyllostomidae). *Animal Behaviour* 26:852–855.

Nash LT. 1986. Influence of moonlight level on traveling and calling patterns in two sympatric species of *Galago* in Kenya. In D Taub, F King (eds.), *Current Perspectives in Primate Social Dynamics* (pp. 357–367). Van Norstrand, New York.

Nash LT. 2007. Moonlight and behavior in nocturnal and cathemeral primates, especially *Lepilemur leucopus*: illuminating possible anti-predator efforts. In S Gursky, KAI Nekaris (eds.), *Primate Anti-predator Strategies* (pp. 173–205). Springer, New York.

Ortmann S, Heldmaier G, Schmid J, Ganzhorn JU. 1997. Spontaneous daily torpor in Malagasy mouse lemurs. *Naturwissenschaften* 84:28–34.

Payne RS. 1971. Acoustic location of prey by barn owls (*Tyto alba*). *Journal of Experimental Biology* 54:535–573.

Plesner Jensen S, Honess P. 1995. The influence of moonlight on vegetation height preference and trappability of small mammals. *Mammalia* 59:35–42.

Price MV, Waser NM, Bass TA. 1984. Effects of moonlight on microhabitat use by desert rodents. *Journal of Mammalogy* 65:353–356.

Prugh LR, Brashares J. 2010. Basking in the moonlight? Effect of illumination on capture success of the endangered giant kangaroo rat. *Journal of Mammalogy* 91:1205–1212.

Prugh LR, Golden CD. 2014. Does moonlight increase predation risk? Meta-analysis reveals divergent responses of nocturnal mammals to lunar cycles. *Journal of Animal Ecology* 83:504–514.

Radespiel U, Sarikaya Z, Zimmermann E. 2001. Sociogenetic structure in a free-living nocturnal primate population: sex-specific differences in the grey mouse lemur (*Microcebus murinus*). *Behavioral Ecology and Sociobiology* 50:493–502.

Raxworthy C. 2003. Boidae, boas. In SM Goodman, JP Benstead (eds.), *The Natural History of Madagascar* (pp. 993–997). University of Chicago Press, Chicago.

Rode-Margano EJ, Nekaris KAI. 2014. Impact of climate and moonlight on a venomous mammal, the Javan slow loris (*Nycticebus javanicus* Geoffroy, 1812). *Contributions to Zoology* 83:217–225.

Schmid J. 2000. Daily torpor in the gray mouse lemur (*Microcebus murinus*) in Madagascar. *Oecologia* 123:175–183.

Schmid J. 2001. Daily torpor in free-ranging gray mouse lemurs (*Microcebus murinus*) in Madagascar. *Folia Primatologica* 22:1021–1031.

Schwab D, Ganzhorn JU. 2004. Distribution, population structure and habitat use of *Microcebus berthae* compared to those of other sympatric cheirogaleids. *Folia Primatologica* 25: 307–330.

Starr C, Mekaris KAI, Leung L. 2012. Hiding from the moonlight: luminosity and temperature affect activity of Asian nocturnal primates in a highly seasonal forest. *PloS ONE* 7:e36396.

Stokes MK, Slade NA, Blair SM. 2001. Influences of weather and moonlight on activity patterns of small mammals: a biogeographical perspective. *Canadian Journal of Zoology* 79:966–972.

Sutherland DR, Predavec M. 1999. The effects of moonlight on microhabitat use by *Antechinus agilis* (Marsupialia: Dasyuridae). *Australian Journal of Zoology* 47:1–17.

Tetreault N, Hakeem A, Allman JM. 2004. The distribution and size of ganglion cells in *Cheirogaleus medius* and *Tarsius syrichta*: implications for the evolution of sensory systems in primates. In CF Ross, RF Kay (eds.), *Anthropoid Origins: New Visions* (pp. 463–475). Kluwer, New York.

Upham NS, Hafner JC. 2013. Do nocturnal rodents in the Great Basin Desert avoid moonlight? *Journal of Mammalogy* 94:59–72.

Vermeij JG. 1982. Unsuccessful predation and evolution. *The American Naturalist* 120:701–720.

Vickery WL, Bider JR. 1981. The influence of weather on rodent activity. *Journal of Mammalogy* 62:140–145.

Vickery WL, Rivest D. 1991. The influence of weather on habitat use by small mammals. *Ecography* 15:205–211.

Wright PC. 1989. The nocturnal primate niche in the New World. *Journal of Human Evolution* 18:635–658.

Wright PC. 1992. Primate ecology, rainforest conservation, and economic development: building a national park in Madagascar. *Evolutionary Anthropology* 1:25–33.

Wright PC, Andriamihaja B. 2002. Making a rain forest park work in Madagascar: Ranomafana National Park and its long-term research commitment. In J Terborgh, C VanSchaik, L Davenport, M Rao (eds.), *Making Parks Work: Strategies for Preserving Tropical Nature* (pp. 112–136). Island Press, Washington, DC.