Impact of climate and moonlight on a venomous mammal, the Javan slow loris (Nycticebus javanicus Geoffroy, 1812)

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Abstract

Predation pressure, food availability, and activity may be affected by level of moonlight and climatic conditions. While many nocturnal mammals reduce activity at high lunar illumination to avoid predators (lunarphobia), most visually-oriented nocturnal primates and birds increase activity in bright nights (lunarphilia) to improve foraging efficiency. Similarly, weather conditions may influence activity level and foraging ability. We examined the response of Javan slow lorises (Nycticebus javanicus Geoffroy, 1812) to moonlight and temperature. We radio-tracked 12 animals in West Java, Indonesia, over 1.5 years, resulting in over 600 hours direct observations. We collected behavioural and environmental data including lunar illumination, number of human observers, and climatic factors, and 185 camera trap nights on potential predators. Nycticebus javanicus reduced active behaviours in bright nights. Although this might be interpreted as a predator avoidance strategy, animals remained active when more observers were present. We did not find the same effect of lunar illumination on two potential predators. We detected an interactive effect of minimum temperature and moonlight, e.g., in bright nights slow lorises only reduce activity when it is cold. Slow lorises also were more active in higher humidity and when it was cloudy, whereas potential predators were equally active across conditions. As slow lorises are well-adapted to avoid/defend predators by crypsis, mimicry and the possession of venom, we argue that lunarphobia may be due to prey availability. In bright nights that are cold, the combined effects of high luminosity and low temperature favour reduced activity and even torpor. We conclude that Javan slow lorises are lunarphobic – just as the majority of mammals.

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Introduction

To secure maintenance, survival and reproduction, animals adapt their behaviour to various factors, such as climate, availability of resources, competition, predation, luminosity, habitat fragmentation, and anthropogenic disturbance (Kappeler and Erkert, 2003; Beier 2006; Donati and Borgognini-Tarli, 2006). According to optimal foraging theory, animal behaviour can be seen as a trade-off between the risk of being preyed upon and the fitness gained from foraging (Charnov, 1976). Perceived predation risk assessed through indirect cues that correlate with the probability of encountering a predator may shape an animal’s behaviour (Vasquez, 1994; Thorson et al., 1998; Orrock et al., 2004).

One of the indirect cues that animals use to assess predation risk is moonlight (Beier et al., 2006; Upham and Haffner, 2013). Most mammals decrease activity or change habitat choice with increasing lunar illumination (lunarphobia) (Price et al., 1984; Hecker et al., 1999; Horning and Trillmich, 1999; Nash, 2007; Pentrían et al., 2011; Saldaña-Vásquez and Munguía-Rosas 2013; Prugh and Golden, 2014) to be more concealed from predators. Some species increase their activity in brighter nights (lunarphilia) due to prey availability, higher foraging efficiency, or better visual detection of predators (Table 1; Horning and Trillmich, 1999; Packer et al., 2011; Prugh and Golden, 2014). Whether a species is lunarphobic or lunarphilic depends on the primary sensory system (e.g., visual acuity), phylogenetic relatedness, and habitat cover (Hecker et al., 1999; Michalski and Norris, 2011; Saldaña-Vásquez and Munguía-Rosas, 2013; Prugh and Golden, 2014). Primates, for instance, are highly visually oriented (Gursky, 2003; Bearder et al., 2006) and are mainly lunarphilic, as opposed to rodents, lagomorphs carnivores and bats, which are largely lunarphobic (Prugh and Golden, 2014). Additionally to lunarphobia and lunarphilia, some species are lunarneutral, although the methods

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Table 1. Reactions of some animal species towards moonlight, and adaptive explanations. PA = predator avoidance, FA = food availability, FE = foraging efficiency, PD = predator detection.

<table>
<thead>
<tr>
<th>Species</th>
<th>Scientific name</th>
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<td><strong>Predator avoidance</strong></td>
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<tr>
<td>Kangaroo rat</td>
<td>Dipodomys sp. Gray, 1841</td>
<td>Lunaphobic</td>
<td>PA</td>
<td>Upham and Haffner, 2013</td>
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<tr>
<td>Lesser bushbaby</td>
<td>Galago moholi Smith, 1836</td>
<td>Lunaphilic</td>
<td>PA</td>
<td>Bearden et al., 2001; Bearden et al., 2006</td>
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<tr>
<td><strong>Food availability</strong></td>
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<td>Galapagos fur seal</td>
<td>Arctocephalus galapagoensis, Heller, 1904</td>
<td>Lunaphobic</td>
<td>FA, PA</td>
<td>Trillmich and Mohren, 1981; Horning and Trillmich, 1999</td>
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<tr>
<td>Spectral tarsier</td>
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<td>Lunaphilic</td>
<td>FA, FE, PA</td>
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<tr>
<td><strong>Foraging efficiency</strong></td>
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<td>Freckled nightjar</td>
<td>Caprimulgus tristigma, Rueppell, 1840</td>
<td>Lunaphilic</td>
<td>FE</td>
<td>Ashdown and McKechnie, 2008</td>
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<tr>
<td>African lion</td>
<td>Panthera leo (Linnaeus, 1758)</td>
<td>Lunaphobic</td>
<td>FE</td>
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<td>Male tree frogs</td>
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<td>PD</td>
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</tr>
</tbody>
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chosen may have an influence whether a certain reaction is found (Nash, 2007; Penteriani et al., 2011). The trade-offs regarding the reaction towards moonlight may vary between species, and even local populations (Lang et al., 2005; Saldaña-Vásquez and Munguía-Rosas, 2013).

Weather condition is a second cue that may affect animal activity, causing variation in the detection of prey and predators, and influencing thermoregulation (Hanya, 2004). In general, low temperature causes animals – prey and predator species – to decrease activity to conserve energy. Low temperature especially affects the activity of poikilotherm species like amphibians or arthropods (Fitzgerald and Bider, 1974; Fadamiro and Wyatt, 1995) but also homeotherm species that may decrease activity, employ social and postural thermoregulation (Donati et al., 2011), or go into torpor or hibernation (Schmid, 2000; Daussmann et al., 2005; Schuelke and Ostner, 2007; Smit et al., 2011). Humidity and precipitation may affect animal activity. Strong rain or wind generally decrease insect availability and can impede the ability of predators to detect prey (Vickery and Bider, 1981; Thies et al., 2006). Some animals are more active in high humidity and precipitation due to food availability or physiological needs (amphibians: Fitzgerald and Bider, 1974; rodents: Orrock et al., 2004; insects: Fadamiro and Wyatt, 1995; arthropods: Skutel-sky, 1996), some decrease activity due to energetic constraints (primates: Donati and Borgognini-Tarli, 2006; bats: Voigt et al., 2011).

Asian lorises (Lorisinae) are characterized by a suite of morphological traits that makes them sensitive to predators, foraging and temperature. Both slow (the genus Nycticebus) and slender (the genus Loris) lorises are arboreal slow climbers (Crompton et al., 1993), and rely on crypsis to avoid predators. Nycticebus is venomous, a trait that has been attributed to predator defence (Alterman, 1995; Nekaris et al., 2013), which might also affect its activity. High susceptibility to predators suggests that lorises would more likely be lunaphobic. Data from the wild, however, do not follow a consistent pattern. Wild red slender loris *Loris tardigradus* (Linnaeus, 1758) tended to lower activity in bright nights, although this was not significantly different from dark night behaviour; they rested, groomed more and whistled more frequently during bright nights, but not significantly suggesting a certain reaction towards moon light (Bernede, 2009). Although in general grey slender lorises *Loris lydekkerianus* Cabrera, 1908 were lunarnutral, they were in some aspects lunaphilic (Bearden et al., 2001, 2006), whistling more in bright nights, and foraging more for energy-rich insects (Bearden et al., 2001). Infants of *L. lydekkerianus* however, sought more habitat cover in bright nights, possibly as predator avoid-
ance strategy, indicating lunarphobia for this age class (Bearder et al., 2001). In Cambodia, the pygmy loris (Nycticebus pygmaeus Bonhote, 1907) was lunarphobic, especially in cold nights (Starr et al., 2012). Rogers and Nekaris (2011) report that Bengal slow lorises (Nycticebus bengalensis Lacépède, 1800) in Cambodia become more active during the dark moon phase. During surveys of the Javan slow loris (Nycticebus javanicus Geoffroy, 1812) lunar neutrality was suggested in that moonlight had no impact on detectability of the species (Nekaris et al., 2014). Captive greater slow lorises (Nycticebus coucang Boddaert, 1785) reduced activity with higher illumination. Lorisines have low metabolic rates, good fur insulation, and possess extensive vascular retia mirabilia that help them to stay active for prolonged periods (Whittow et al., 1977; Mueller, 1979). Most notably, Nycticebus spp. enter torpor for hours or days in cold temperatures (Nekaris and Bearder, 2011). Starr et al. (2012) proposed that the combined risk of both predation and heat loss outweigh the benefits of being active, and that temperature should be considered in further discussions of loris activity.

The Javan slow loris (Nycticebus javanicus), endemic to Java, Indonesia (Nekaris and Bearder, 2011), weighs around 1 kg, is known to go into torpor, and occurs at least up to 1800 m above sea level (asl) (Nekaris et al., 2014; Nekaris and Rode-Margono, unpub. data). Indeed, much of the forest left on Java where slow lorises are found is at altitudes above 1000 m (Nekaris et al., 2014; Voskamp et al., 2014). We thus examined the effect of lunar illumination and temperature on activity of the Javan slow loris at a high altitude site replete with numerous potential predators. We also examined microhabitat use in the light of understanding predator perception.

Material and methods

We conducted our study on the foothills of the active volcano Papandayan in West Java. The site was located at altitudes ranging from 800-1800 m asl, ranging into Zones that are in Java classified as sub-montane (1200-1800 m asl) and Montane Zones (1600-2400 m asl); at altitudes above 1500 m asl, ground frost can occur (Nijman, 2013). The research site was located at 57°6′6″-7°7′0″ and E107°46′0″-107°46′5″ and consisted of a mo-saic-like landscape with forest and bamboo fragments (locally known as ‘talun’) and agricultural fields. Average temperature is relatively constant, but precipitation varies during the year, and daily minimum temperature ranges between 10.4°C and 20.7°C.

We captured 12 animals by hand, took morphometric measurements, fitted a radio collar (ca. 17 g, Biotrack, UK) and released the animal at the capture site. From April 2012 to June 2013, we followed animals in two shifts from 18:00 h to 0:00 h and 00:00 h to 6:00 h (Wiens and Zitzmann, 2003) using antenna (6 and 8 element flexible Yagi antenna, Biotrack, UK) and receiver (R1000, Communication Specialists, US). We used instantaneous focal animal sampling with 5-minute intervals for behaviour and habitat data collection (Altmann, 1974). We followed the ethogram of Moore (2012) and grouped resting and sleeping into the category “not active” and all other behaviours except “other” into “active”. We recorded the heights of the animal and used tree. Assuming that a higher position in the tree provides more concealment by the canopy, we used the relative height (height of the animal divided by height of the tree) of the animal’s used tree as an indication of safety. We recorded any sighting of potential nocturnal predators, including common palm civets (Paradoxurus hermaphroditus [Pallas, 1777]) and leopard cats (Prionailurus bengalensis [Kerr, 1792]). Additionally, we had one to four camera traps (Cuddeback Attack IR; Bushnell Trophy cam night vision) installed in 185 nights (304 individual camera trap nights). Cameras were installed about 50 cm above the ground in relatively dense forest or bamboo patches with undergrowth, located within home ranges of radio-tracked slow lorises. With a TFA Nexus weather station (TFA Dostmann, Germany) located at our basecamp, we collected data on temperature, humidity, rain and wind, with one data point every hour. We calculated minimum temperature of the night and rain over the last 24 hours. We estimated cloud cover in the field to the nearest 10%. Luminosity was recorded using the exact percentage of the moon illuminated when above the horizon, using the programme MOONDV version 1 (Thomas, 1998). When below the horizon an illumination of 0 was recorded.

Statistical analysis

To increase independence of the data we used only every 6th data point of our dataset, yielding single observations of the same individuals that were at least one hour apart. We excluded the first and last hour of the
night (18:00 to 19:00 and 05:00 to 06:00) to ensure that astronomical twilight is excluded from the data. Astronomical twilight is defined as the moon being 18° below the horizon (Erkert, 2003). Twilight effects on activity may result in peaks at dawn and dusk and an overrepresentation of certain behaviours usually performed in these periods (Bearder et al., 2001; 2006; Erkert and Cramer, 2006). We applied a logistic regression model due to the non-normal distribution of our data (c.f. Starr et al., 2012). We used the binary dependent variable “active” and “not active” (Field, 2009). The predictor variables were sex, number of observers, luminosity, minimum nightly temperature, average humidity per night, wind, cloud cover, rain per hour and relative height of slow loris. Humans can be seen as predators (Charles-Dominique, 1977), and although we did not witness hunting of slow lorises for the pet trade in our study area it was reported for neighbouring villages and is generally common in West Java (Nekaris et al., 2009). We then applied a similar model to the presence of potential predators with one night where camera traps operated or direct observations were conducted as sample unit. For these data we used illumination of the night (number of hours the moon was visible multiplied by moon phase), and we excluded cloud cover. Days without observations or camera traps were excluded. We included an index of effort into the model, consisting of the number of teams observing per night weighted by two to account for a higher viewing angle, plus the number of camera traps working that night. For both models, none of the predictor variables correlated significantly above $r^2 = 0.6$. We used the forced entry method as we had specific predictions about the model (Field, 2009). If the odds ratio of a factor is above 1 there is a positive relation between dependent and independent variable.

Results

We collected 7169 5-minute observation points of 12 radio-collared adult individuals, resulting in approximately 600 hours of direct observation and 1036 used data points. The activity budget of all animals per hour can be seen in Table 2. There was a significant relationship between activity and the different hours of the night ($\chi^2 = 22.708$, df = 9, $p<0.007$), with animals being less inactive than expected between 19:00 and 20:00.

The logistic regression model with slow loris activity as the outcome variable was highly significant ($\chi^2 (1) = 116.158$, df = 11, $p<0.001$; $R^2 = 0.148$ (Cox and Snell), 0.213 (Nagelkerke)), with lunar luminosity ($B = -3.926 \pm 1.863$, $p = 0.035$), humidity ($B = 0.039 \pm 0.018$, $p = 0.029$), clouds ($B = 0.727 \pm 0.308$, $p = 0.018$), relative height ($B = -3.957 \pm 0.492$, $p < 0.001$) and the interaction of minimum temperature and moon ($B = 0.234 \pm 0.113$, $p = 0.038$) having significant effects on whether slow lorises are active or inactive. While luminosity and relative height have negative effects on activity, humidity and cloud cover have positive effects. The interaction of minimum temperature and moonlight showed that temperature affected activity during bright nights, but not dark nights. Slow lorises are more active when it is warmer. In dark nights they are equally active in warm and cold nights.

Camera trapping revealed six independent photos of the leopard cat, ten of the Javan ferret badger (Melogale orientalis [Horsfield, 1821]), and 14 of the common palm civet. The logistic regression model with predator presence as the outcome variable was not significant ($\chi^2 (1) = 12.523$, df = 7, $p=0.085$).

Farmers reported to us that domestic dogs sometimes detected and cornered slow lorises. We have never observed any flight or freezing reaction of Javan slow lorises.
lorises towards common palm civets or leopard cats. In contrast, we have witnessed a sub-adult feeding unperturbed by an adult male common palm civet within 5 m distance.

**Discussion**

**Lunar illumination and predation risk**

Our model on slow loris activity revealed a negative effect of lunar illumination and relative height on activity, a positive effect of humidity and cloud cover, and an interaction effect of lunar illumination and temperature. Activity was not affected by the number of people observing the slow lorises, neither was an interaction effect with luminosity detected. The predator model was not significant, thus the detection of predators was not affected by moonlight or any climatic factors.

Most primate species increase their activity with increasing lunar illumination (Gursky, 2003; Kappeler and Erkert, 2003; Bearder et al., 2006; Donati and Borgognini-Tarli, 2006; Fernandez-Duque and Erkert, 2006). This can be explained by the high visual orientation in primates and higher effectiveness of foraging and detection of potential predators in bright nights (Gursky, 2003). Instead of hiding in the dark, some lunaphilic primate species additionally use mobbing and warning calls to deter predators and warn conspecifics (Gursky, 2006; Fichtel, 2007; Nash, 2007; Eberle and Kappeler, 2008). In contrast, Javan slow lorises in our study seemed to reduce their activity in brighter nights, as was found for pygmy lorises (Starr et al., 2012), Bengal slow lorises (Rogers and Nekaris, 2011) and greater slow lorises (Trent, 1977). We can confirm lunaphobia for Javan slow lorises. Slow lorises thus resemble more the behaviour of other lunaphobic mammals (Prugh and Golden, 2014). This was explained by Starr et al. (2012) with the animals’ anti-predator behaviour relying on crypsis and concealment, and may be enhanced by the relatively disturbed and open habitat at our study site.

Although lunaphobic, we did not find any evidence that activity of slow lorises could be negatively affected by human presence, neither was there any apparent relation with the behaviour of predators. Slow lorises did not engage in more active behaviour like foraging, feeding and travelling in higher and denser canopy, but in contrast are more active in lower heights. Confirmed predators of *Nycticebus* are orang-utans (Utami and van Hooff, 1997), snakes (Wiens and Zittmann, 1999), hawk-eagles (Hagey et al., 2003), and monitor lizards (Kenyon et al., 2014). Although all of these taxa may not be sympatric with Javan slow lorises, adaptations to such predators may still be responsible for their behavioural responses (Goodman et al., 1993). The African potto (*Perodicticus potto* [Mueller, 1766]) is comparable to Javan slow lorises in size and ecology and is predated upon by viverrids of relatively small size and by domestic dogs (*Canis lupus* Linnaeus, 1758) (Nash, 2007; Nekaris et al., 2007); pottos showed reactions to viverrids in predation experiments (Charles-Dominique, 1977). Despite presence of potential predators, slow lorises did not show any fear when encountering potential non-human predators. Similar oblivious reactions to potential predators occurred in red and grey slender lorises and in greater slow lorises (Wiens, 2002; Nekaris et al., 2007). Although hunting is the main threat to Javan slow lorises (Nekaris et al., 2009; 2013), the number of observers had no effect on slow loris activity. Lorises may not fear people because they do not perceive people as predators or they are habituated due to the presence of local farmers.

One alternative explanation to predation pressure is a potential higher availability of prey during either moonlit or dark nights. Lang et al. (2005) attributed high activity during dark moon phases of the lunaphobic Neotropical insectivorous bat *Lophostoma silvicolum* Tomes, 1863 to high prey availability of katydids. Foraging depth of Galapagos fur seals (*Arctocephalus galapagoensis* Heller, 1904) followed the moonlight-dependent horizontal migration of fish and squid (Horning and Trillmich 1999). The effect of insect abundance depends on the food preferences of the insectivorous predator. Although these data are not yet available for our field site, it is possible that the higher activity of slow lorises in dark nights follows the higher prey abundance; we are investigating this possibility with future studies.

We suggest that not predator avoidance but alternative factors like higher prey availability cause the slow loris to be more active in darker nights, perhaps due to the extreme morphological adaptations of lorises to avoid predators in the first place. Lorisines rely heavily on crypsis, moving slowly and freezing when feeling threatened (Nekaris et al., 2007). Their fur colour blends in with tree bark and makes animals difficult to detect (Nekaris et al., 2010). Slow lorises are among the few mammal species that are venomous (Alterman, 1995; Hagey et al., 2006; Ligabue-Braun et al., 2012; Nekaris et al., 2013). We are not aware of studies on other venomous mammals with a focus on the influence on...
moonlight on behaviour. Although uncommon in vertebrates (Pough, 1988), slow lorises may show Mullerian mimicry (Moore, 2012; Nekaris et al., 2013) with Indian cobras (*Naja naja* [Linnaeus, 1758]). Morphological and behavioural defences against predators can effectively reduce a prey’s perception of risk (Stankovich and Blumenstein, 2005), and the combinations of slow lorises’ adaptations might be effective enough to make them rather fearless animals when it comes to direct or indirect encounters with potential predators.

**Climatic factors**

Of the environmental factors, only humidity and cloudiness had a significant independent effect. Different effects of humidity on the activity of animals have been found (positive: Fitzgerald and Bider, 1974; Orrock et al., 2004; Skutelsky, 1996; negative: Kappeler and Erkert, 2003; Donati and Borgognini-Tarli, 2006). Slow lorises become more active with increasing humidity, possibly because of a higher availability of arthropod prey, which also become more active in higher humidity (Fadamiro and Wyatt, 1995). Swifts increase flight height in lower humidity, following flying insects that adapt their flying height to humidity (Shamoun-Baranes et al., 2006). Slow lorises include many flying insects like Coleoptera and Lepidoptera in their diet (Wiens et al., 2006; Starr and Nekaris, 2013). As slow lorises cannot leap or fly, they may be more actively foraging when humidity is high and insects fly low. Thus, we attributed the positive effect of higher humidity on activity to an adaptation to the activity of flying insect prey. Higher percentage of cloud cover contributes to the darkness that is favoured by Javan slow lorises. As the temperature at our study site can drop to about 10°C, it is likely that temperature would have affected the activity of Javan slow lorises. Although we could not find an independent effect of temperature, we detected an interaction effect of luminosity and temperature in Javan slow lorises, just like for pygmy lorises (Starr et al., 2012). Indeed, during these inactive bouts, Javan slow lorises, like pygmy lorises, might not move for hours at a time. Many small endotherm species show heterothermy (Heldmaier and Ruf, 1992; Heldmaier et al., 2004), including several nocturnal primates such as lemurs of the family Cheirogaleidae and lesser bushbabies (*Galago moholi* Smith, 1836) (Schmid, 2000; Smit et al., 2011; Dausmann et al., 2005; Schuelke and Ostner, 2007; Nowak et al., 2010). *Nycticebus* spp. are able to enter torpor (Whittow et al., 1977; Xiao et al., 2010). We have already found evidence for torpor in one animal at our study site (Rode-Morgano and Nekaris, unpub. data) and we are further investigating through physiological measurement if animals at our site regularly enter torpor during cold temperatures. Just as for reaction towards moon light, the insignificant model for potential predators did not indicate an effect of climate factors on their activity.

**Conclusion**

Nash (2007) rightfully stressed that crypsis and predation are not unitary phenomena but interact in complex ways. Most primate species are lunarphilic, but slow lorises seem to be the exception from that rule and decrease activity in bright moonlight (lunarphobia) like most other mammals. A higher activity when cloud cover is higher may contribute to this behaviour. Javan slow lorises seem to be indifferent to potential predators and do not shift their activities into more covered habitat. We suggest that lunarphobia in slow lorises is not due to an increased perceived predator risk, but due to other factors like lower availability of prey species in moonlit nights. Additionally, slow lorises may be well-adapted to avoid or defend against predators by crypsis, venom and mimicry, and thus, do not need to be afraid in the dark.

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