Reinhardt, K, Wirdateti, and Nekaris, K

Climate-mediated activity of the Javan slow loris, Nycticebus javanicus


doi: 10.3934/environsci.2016.2.249

This version is available: https://radar.brookes.ac.uk/radar/items/d260cb02-90ab-4e1e-a05b-4dfb12f0de1e/1/
Research article

Climate-mediated activity of the Javan Slow Loris, *Nycticebus javanicus*

Kathleen D Reinhardt $^{1,3}$, Wirdateti $^{1,2,3}$ and K.AI. Nekaris $^{1,3,*}$

$^1$ Little Fireface Project; Cisurupan, Garut, Java, Indonesia
$^2$ Research Centre for Biology-LIPI, Jakarta-Bogor, Cibinong, Indonesia
$^3$ Nocturnal Primate Research Group, Oxford Brookes University, Oxford, UK

* Corresponding: Email: anekaris@brookes.ac.uk; Tel: +44 (0)-186-548-3767.

Abstract: Joint impacts of anthropogenic disturbance and climate change are of pressing concern for modern conservationists. Climate change patterns have various diminishing effects on the biodiversity of an ecosystem, requiring an understanding of a species' ability to adapt. Agricultural practices are expanding at an altitudinal gradient on the Indonesian island of Java, forcing endemic species to range at increased elevation with lower temperatures, and in human-populated areas. One example is the Critically Endangered Javan slow loris (*Nycticebus javanicus*), which finds itself increasingly restricted to montane regions with extreme climate patterns and habitat disturbance. We observed wild *N. javanicus* in a highly fragmented, montane agroforest area to determine if climate variables and forest connectivity influence activity budget and behavior. Lorises ranged at different altitudes (1275 m above sea level (asl)—1570 m asl) and were observed for six months in Cipaganti, West Java. Using multinomial regression analyses, we found loris individuals were most likely to engage in increased foraging, feeding and travelling behavior than resting when relative humidity increases and in habitats with greater forest connectivity. Regression analyses found effects of relative humidity and forest connectivity to be the most significant predictors of *N. javanicus* foraging behavior ($P = 0.001$, $P = 0.030$). We suggest that future-climate shifts and increased anthropogenic disturbance will detrimentally influence wild populations of *N. javanicus*, requiring immediate plans for mitigation in conserving these already scarce wild populations. We also suggest the altering of reintroduction protocols in relation to climate and geographic region.

Keywords: Activity budget; climate influence; humidity; behavioral adaptation; agroforest, montane
1. Introduction

Climate change creates shifts in seasonality, rainfall, ambient temperature, disease dynamics, habitat structure, as well as anthropogenic activities [1], which can detrimentally influence wildlife mortality rates. Global climate warming forces agriculturalists to increase farming practices in elevation to maintain successful crop yields, thus forcing wildlife populations to either shift home ranges to higher elevations (with varying vegetation and phenology composition) or overlap with agricultural, human-populated land [2]. Such constraints restrict the behavioral patterns of non-human primates, influencing foraging, resting, group size and home ranges [3-5]. Influence of climate shifts on a species’ home range is additionally impeded by anthropogenic disturbance, limiting a population’s ability to shift range or disperse. This influence demands an understanding of interactive behaviors between primates and their ability to adapt between habitat type and climate pattern shifts.

Many studies on the influence of climate and climate change have focused on large-bodied terrestrial or arctic marine mammals, with fewer analyses on small, arboreal mammals [6,7]. Many primate field studies have focused on climate-mediated behavior in primary forest, but for those taxa that are threatened and occur in rapidly disappearing habitats, understanding their behavior and the potential influence of climate is even more important [8]. To address this gap, here we focus on a small arboreal primate, endemic to the Indonesian island of Java—the Javan slow loris (Nycticebus javanicus).

Multiple forest types once characterized Java, including 6500 flora species of which 4500 were native [9]. Now, less than 9% of home ranges remains, occurring on mountain peaks that are restricted to altitudes above 800 m asl [10]. Many of Java’s lowland species are already extinct (orang-utan Pongo spp.) or occur only in small forest remnants (Javan rhinoceros Rhinoceros sondaicus). In West Java, centuries of intensive agricultural practices have transformed a majority of rainforests into mosaic agroforest—an area where agricultural crops are predominantly grown along with trees and other non-agricultural vegetation [11]. Many of these trees are not native, with origins, for example, from South and Central America. Still, the nature of these mosaics allow a number of small-bodied nocturnal mammals to persist—including the Javan binturong (Arctictis binturong penicillatus), Javan ferret badger (Melogale orientalis), two species of civet (Paradoxurus hermaphroditus, Viverricula indica), colugo (Galeopterus variegatus), Java mouse-deer (Tragulus javanicus), the tailless fruit bat (Megaerops kusnotoi), and one primate species, the Javan slow loris (N. javanicus).

Due to intensive deforestation on Java combined with its heavy persistence in illegal wildlife trade, N. javanicus is listed as Critically Endangered on the IUCN Red List [12]. This species lives in uni-male, uni-female pairs in home ranges of approximately 4.5 ha, weighing between 850 and 1100 grams in body weight. As a nocturnal arboreal specialist, N. javanicus relies heavily on a diet of insects, gum and nectar [13]. The historic habitat of this species was primarily lowland forest, but now remaining populations of N. javanicus must adapt to high altitudes, cool temperatures and heavily fragmented forests.

Temperature is extremely important for slow loris ecology. Two species of slow loris, both Nycticebus pygmaeus and N. javanicus go into torpor in cold climates [13-16]. Starr et al. [17] found in a temperate lowland forest that temperature highly impacted the behavior of Nycticebus pygmaeus, the smallest of the slow loris species, with an average body mass of 423 +/- 6.17 g for males and
539 +/- 6.17 g for females [15]. Starr recommended future behavioral studies on *Nycticebus* to take climate variables into account. Rode-Margono et al. [15] found similar patterns among *N. javanicus* in Cipaganti, West Java, where temperatures in 2012 ranged from a minimum high of 20.7 °C and a minimum low of 10.4 °C, ranging between altitudes of 1350–1650 m asl. Compared to other primate species that enter torpor, the body mass of *N. javanicus* is unexpected to utilize torpor or hibernation, which may suggest this is an extreme response to environmental circumstances by the population in Cipaganti. In examining the effects of climate and moonlight on the behavior of *N. javanicus*, Rode-Margono and Nekaris [18] found differences in behavior based on minimum temperature and relative humidity, but did not take into account elevation or habitat disturbance. Additionally, climate data used in their models were recorded from a single weather station installed at 1345 m asl at the field station base camp, which omits the possibility of analyzing microclimate influence.

Here we collect and present more detailed data on the activity budget of *N. javanicus* in Cipaganti, West Java. We observed animals occupying various microclimate areas at different altitudes of 1275–1395 m asl (Habitat A), 1330–1479 m asl (Habitat B) and 1430–1570 m asl (Habitat C) for 6 months. We installed and examined vegetation plots within each habitat, while monitoring temperature, humidity and dewpoint with associated HOBO U23-001 climate station loggers. We predicted that temperatures in Habitat C would represent increasingly cooler average temperatures, as altitude increases. In relation to this, we hypothesized that slow lorises would present behavioral adjustments of climate-mediated activity budgets. In particular, we predicted slow lorises would increase resting time as a method of behavioral thermoregulation at higher altitudes to conserve energy, under the assumption that the minimum temperature would be more extreme than other loris home ranges.

2. Methodology

Java experiences climatic variation throughout the year and between regions, caused by air mass oscillations from the inter-tropical convergence zone [9]. This cycle further creates variation between lowland and montane temperatures, where temperature decreases at an average of 0.6 °C for every increased 100 m asl [10,19]. We conducted this study from February until August 2014 in Cipaganti, Cisurupan, Garut District, West Java (7°16′44.30″ S, 107°46′7.80″ E, 1200 m asl). Cipaganti is located on the mountain, Gunung Puntang, which is a part of the Java-Bali Montane Rain Forests ecoregion (Figure 1). The habitat around Cipaganti is characterized by traditional gardens mixed with an annual perennial rotating crop system—rows of crops, interspersed with rows of tall trees. Dominant trees in this system heavily utilized by lorises include string and sweet bamboo (*Gigantochloa apus, G. atter*), cajeput tree (*Malaleuca leucadendra*), fairy duster (*Calliandra calothyrsus*), green wattle (*Acacia decurrens*), avocado (*Persea americana*) and Indonesian mahogany (*Toona sureni*) [12]. With agriculture as the predominant occupation in Cipaganti, local crop types range from tea plantations, chayote, carrot, cabbage, tomato, and cassava and potato crops.
Figure 1. Map of field site, located in Cipaganti, Garut, West Java; Coordinates 7°16’44.30” S, 107°46’7.80” E, 1200 m ASL. Elevation is represented with a green gradient scale of value, and the village of Cipaganti labelled with an indicative ‘X’.

The area of Cipaganti is classified as only slightly seasonal, with a mean annual rainfall of 2000–3000 mm and an average of 1–3 dry months throughout the annual year, from June to August [20,21]. Both temperature and humidity vary more between day and night than between months of the annual year, while wind speed and sunshine are more annually seasonal [9]. To record microclimate data, we installed HOBO-U23 Climate Station loggers in three randomly selected vegetation plots within each study group’s home range. Loggers collected data on ambient temperature ($T_a$) in °C, percent of relative humidity ($RH_m$) and dewpoint measurements. Loggers were set at 15-minute intervals at the start of every hour (GMT+1 Time zone), to correspond with behavioral data collection methods (Figure 2).

We fitted individually identified slow lorises with 19 g Biotrack radio-collars and monitored them on a rotating basis. For this study, we focused on six adult lorises that formed three social groups of uni-male uni-female pairs. The home ranges of these individuals occurred between 1275–1570 m asl among three different microclimate areas (1275–1395 m asl; 1330–1480 m asl; 1430–1570 m asl). With the assistance of local field trackers, we located animals using Biotrack antenna and Sika receiver and observed them using red filter Clulite head torches from 17:00–5:00. Using instantaneous focal sampling at 15-minute intervals, we collected 220.5 hours of observations using a modified version of the Rode-Margono et al. [12] behavioral ethogram. Forest connectivity was measured on a scale of 0 to >5, with 0 being no branch connectivity for lorises to access for travel, and >5 being five or more branch routes for a loris to access. We conducted all research in adherence with RISTEK, as well as ethical guidelines provided by the Association for the Study of Animal Behaviour; our research received approval from the Oxford Brookes University Animal Ethics Sub-committee.
Figure 2. Activity budgets of three study groups of *N. javanicus*, ranging at different altitude and habitat. Activity budgets are represented in percentages of time from February through August 2014. Each study group represented varying home range altitudes of 1275–1395 m asl (Habitat A), 1330–1479 m asl (Habitat B) and 1430–1570 m asl (Habitat C).

We collected both behavior and climate data at 15-minute intervals, to increase independence of variables. All focal point samples without corresponding climate data were omitted, yielding a sample size of *n* = 887. We created a model using Multinomial Logistic Regression analyses to determine predictability of climate factors, altitude, and habitat disturbance on the activity of *N. javanicus* individuals. *T*<sub>a</sub>, RH%, altitude and forest connectivity were used as independent variables to determine the predictability of the dependent variable, behavior (resting, foraging, feeding and travelling) where ‘resting’ was used as the reference category, among the three study groups.

We used a Runs test to confirm independence of focal data points. To determine if there was a time-lag in *T*<sub>a</sub> influence on behavior, we used a Friedman ANOVA to compare behavior with ambient temperatures: a.) at the focal point of behavior, b.) 15-minutes prior to behavior and c.) 30-minutes prior to behavior. *T*<sub>a</sub> at the time of behavior was found to have the most significant influence on loris behavior (*P* = 0.020), and was thus used as the temperature covariate for the regression model. Spearman rank-correlation tests were run to test the correlation of regression covariates. All residuals were tested, using Shapiro-Wilk Test of Normality (*P* ≥ 0.05). We performed all statistical analyses using SPSS V21.0, with *P* value set at ≤0.05.

3. Results

Activity budgets varied between the three study groups (*r* = −0.112, *n* = 668, *P* = 0.004) in all four behaviors of focus. Time spent resting differed between the three habitat areas (14% at Habitat A; 16% at Habitat B; 4% at Habitat C). Slow lorises ranging in Habitat C spent more time traveling than other lorises (18% at Habitat A, 16% at Habitat B, 21% at Habitat C), as well as the highest percentage of time spent foraging (11% at Habitat A, 10% at Habitat B, 26% at Habitat C) and feeding (6% at Habitat A, 10% at Habitat B, 14% at Habitat C).
Study group habitats varied in $T_a$ ($r = -0.082, n = 708, P = 0.028$). Never exceeding 18.2 °C, Habitat C displayed a constant lower $T_{MEAN}$ between the three habitats from February through August 2014, while Habitat B displayed the lowest $T_{MIN}$ during the months of June and July, reaching as low as 12 °C. Habitat A displayed the least variation and distance between $T_{MIN}$ and $T_{MAX}$ through the entirety of this study (Figure 3).

![Temperature variation graph]

Figure 3. Temperature variation in °C between habitats A, B and C during the months of February 2014 through July 2014. For each habitat, we indicate temperature factors of $T_{MAX}$; $T_{MEAN}$; $T_{MIN}$.

Multinomial regression analyses found $T_a$, RH%, altitude and habitat disturbance to be fitting covariates in the model for predicting individual loris behavior ($\chi^2 = 7.178, df = 8, P = 0.000$) where resting behavior is used as the reference category. RH% was the only covariate found to be significant in predicting all behavioral categories ($\chi^2 = 1.113, df = 10, P = 0.000$). As RH% increases, lorises are more likely to engage in an increased amount of time spent travelling ($P = 0.005$), foraging ($P = 0.003$) and feeding ($P = 0.005$) as opposed to the reference category, resting. Effects of increased RH% and forest connectivity were found to be most significant ($P = 0.001$, $P = 0.030$) in predicting foraging behavior (Table 1). While altitude was found insignificant as a predictor in individual loris behavior, time spent foraging varied significantly between each study group, where each social pair had equal sample sizes ($r = 0.171, n = 191, p = 0.018$).
Table 1. Influence of climate and habitat on behavior of *N. javanicus* in Cipaganti, Java (between the months of February and August of 2014): determined using multinomial logistic regression analyses with ‘resting’ behavior as the reference category, displaying model coefficients for each behavioral category.

<table>
<thead>
<tr>
<th>Behavior</th>
<th>Factors</th>
<th>B</th>
<th>SE</th>
<th>Exp(B)</th>
<th>P</th>
</tr>
</thead>
<tbody>
<tr>
<td>Travel</td>
<td>Connectivity</td>
<td>−1.002</td>
<td>1.071</td>
<td>0.367</td>
<td>0.349</td>
</tr>
<tr>
<td></td>
<td>Altitude&lt;sub&gt;(m)&lt;/sub&gt;</td>
<td>0.000</td>
<td>0.010</td>
<td>1.000</td>
<td>0.987</td>
</tr>
<tr>
<td></td>
<td>&lt;i&gt;T&lt;/i&gt;&lt;sub&gt;a&lt;/sub&gt;</td>
<td>0.409</td>
<td>0.416</td>
<td>1.505</td>
<td>0.326</td>
</tr>
<tr>
<td></td>
<td>&lt;i&gt;RH&lt;/i&gt;%</td>
<td>0.356</td>
<td>0.125</td>
<td>1.427</td>
<td>0.005 *</td>
</tr>
<tr>
<td>Forage</td>
<td>Connectivity</td>
<td>2.202</td>
<td>0.197</td>
<td>0.817</td>
<td>0.0001 **</td>
</tr>
<tr>
<td></td>
<td>Altitude&lt;sub&gt;(m)&lt;/sub&gt;</td>
<td>−0.003</td>
<td>0.010</td>
<td>0.997</td>
<td>0.772</td>
</tr>
<tr>
<td></td>
<td>&lt;i&gt;T&lt;/i&gt;&lt;sub&gt;a&lt;/sub&gt;</td>
<td>0.327</td>
<td>0.421</td>
<td>0.387</td>
<td>0.437</td>
</tr>
<tr>
<td></td>
<td>&lt;i&gt;RH&lt;/i&gt;%</td>
<td>0.372</td>
<td>0.125</td>
<td>1.451</td>
<td>0.003 *</td>
</tr>
<tr>
<td>Feed</td>
<td>Connectivity</td>
<td>−0.321</td>
<td>0.245</td>
<td>0.725</td>
<td>0.161</td>
</tr>
<tr>
<td></td>
<td>Altitude&lt;sub&gt;(m)&lt;/sub&gt;</td>
<td>−0.003</td>
<td>0.012</td>
<td>0.997</td>
<td>0.778</td>
</tr>
<tr>
<td></td>
<td>&lt;i&gt;T&lt;/i&gt;&lt;sub&gt;a&lt;/sub&gt;</td>
<td>0.409</td>
<td>0.416</td>
<td>1.000</td>
<td>0.999</td>
</tr>
<tr>
<td></td>
<td>&lt;i&gt;RH&lt;/i&gt;%</td>
<td>0.356</td>
<td>0.125</td>
<td>1.427</td>
<td>0.005 *</td>
</tr>
</tbody>
</table>

Bold P values represent statistical significance, with * indicating significance <0.05, and ** indicating significance <0.001. Covariate Factors: <i>T</i><sub>a</sub>, ambient temperature; <i>RH</i>%, percent relative humidity; Altitude, elevation measured in meters.

4. Discussion

Our aims were to determine the behavioral responses and activity budget adjustments of *N. javanicus* between three study groups in the montane agroforest area of Cipaganti in West Java. Whilst focal animals demonstrate a variation in activity budget between altitude and climate, results differ from those expected. Individuals ranging at higher altitude (Habitat C—where <i>T</i><sub>MEAN</sub> was consistently lower than Habitats A and B) were observed to spend more time both foraging and traveling, with the least amount of time observed resting. Though mutually exclusive in the behavioral ethogram, increased time spent traveling may be attribute to increased foraging, as a need to acquire appropriate nutritional intake to cope with lower temperature extremes and resource availability during the dry period. These results are similar to patterns observed in studies on haplorrhine species ranging at high altitude including baboons (*Papio cynocephalus anubis, P. c. hamadryas, P. c. papio, P. c. ursinus*) and snub-nosed monkeys (*Rhinopithecus bieti*). Research on multiple populations of *Papio spp.* found foraging and feeding to be climate-mediated, as temperature influenced ecological and vegetation conditions which then influenced food availability [22]. Similarly, *R. bieti* increases foraging as a coping strategy in temperate forests with extreme climates and phenological seasonality [23].

Current climate change trends are resulting in the uncoupling of temperature and humidity—two climate factors that were previously associated in direct correlation with one another [24]. This may result in unprecedented behavioral variations, with precipitation being one of the more influential climate factors on mammalian activity patterns. Increased <i>RH</i>% and forest connectivity suggest lorises are more likely to spend more time engaged in foraging, feeding and
traveling behavior, rather than resting. This response to RH% may be associated with climate influence on arthropods. Increased humidity has been observed to increase the activity of arthropods—a significant prey (30%) in the loris diet [25,26], which may attribute to the significant relationship displayed between foraging, forest connectivity and humidity in the regression parameter estimates [27]. This could suggest a need for lorises to increase time spent foraging in high altitude habitats where insects are indeed more active, in response to higher humidity levels. Additionally, insects are more abundant along edge environments, increasing foraging activity in more disturbed area. Overall insignificance found on the influence of $T_{\text{MEAN}}$ in this region may be a result of the limited time scale in which this study was done, as well as the small altitude scale between study groups.

Lower $T_{\text{MIN}}$ in Habitat B (1415 m) during the months of June and July may be a result of wind chill with slope direction, as the plot was located on a South slope and may thus represent a unique microclimate area. Previous research in this area conducted from 2012 through 2013 found temperatures to range daily from 20.7 °C to as low as 10.4 °C—suggesting temperatures may be lower in months of the year outside this study [18]. The majority of the timescale in which this study took place was during the dry season in Cipaganti. Previous research has found many species to increase foraging activity substantially during the dry season, where resources are fewer for folivore and frugivore species [28], but little research on seasonal variation has been done for exudate resources. All El Niño events since 1970 have caused Java to experience harsher dry seasons and more droughts, having a negative impact on harvest yields, water shortage and more frequent forest fires [9]. All droughts since the event have been associated with El Niño, and similar events in the future may further restrict N. javanicus.

Climatic factors have a substantial influence on the seasonality and growth of plant foods, thus affecting temporal availability of resources. Cool temperatures slow down phenology development, inflicting shifts in floral production stages [29]. While decelerated phenology production is nutritionally beneficial for folivorous species, it largely affects the foraging patterns of nectar and gum feeding species. Slow lorises predominantly feed on exudates, insects, and floral nectars [12,30]. Researchers of a population of reintroduced N. javanicus on Gunung Salak in West Java observed lorises to consume 89.97% of their diet through nectar of a legume inflorescence, Calliandra calothrysus [31]. In our study area, all three study groups’ microclimate areas contain nectar (C. calothrysus) and gum-producing species, which were used by lorises regularly during this study. Nectar provides both water and amino acids in small quantities between flowers, requiring an increase in foraging activity to consume adequate nutrients. Climate change driven behavioral responses and adaptations are often idiosyncratic, thus potentially detrimental to co-dependent relationships between species. We have already observed N. javanicus to transfer pollen non-destructively between plant individuals [32]. Despite an increase in foraging by these study groups, if lower temperatures persist and indeed slow down phenology development and floral reproduction, this could in turn influence pollination success of C. calothrysus as well as decrease food availability for N. javanicus.

Further research is recommended with additional measurements on slope, geographic orientation as well as weather factors such as rainfall, wind speed and strength in relation to microclimate, especially during the months of September through January. During these months, wind speed drastically increases and rainfall is more consistent [9]. Pearson correlation analyses found forest connectivity and wind to be positively correlated between the three study groups, which
might suggest wind could additionally be influential on foraging and travel behavior. Wind direction, speed and flow can influence ambient temperatures at different microclimate area and forest edge. If forest loss and fragmentation should continue as a result of climate change and increased anthropogenic activities, two-thirds of the diet of *N. javanicus* could be influenced by wind variation, as wind speed influences insect abundance and the speed at which they travel [33,34]. Furthermore, if insects are pollinators of *C. calothrysus*, this could be detrimental for two of the three major food types lorises consume: insects and nectar.

Time budgeting adjustments allow animals to manage energetics for surviving in demanding climates where resources are scarce [35]. Resource availability also influences activity budgets, as energy expenditure depends greatly on nutrient intake and accessibility. Small-bodied nocturnal primates have been observed to respond to such constraints by use of behavioral and physiological thermoregulation, to maintain core body temperature and energy expenditure [36-39]. Such behaviors include adjustments of inactivity and even the use of hibernation or torpor—a physiological process of lowering basal metabolic rates. Torpor use suggests a trade-off survival method between energetically demanding behaviors (such as foraging and travel), nutritional intake and thermoregulation. Thermoregulation and torpor use have been observed in wild lemurs and galagos [35,40], but until now, only captive data have been published on this rare behavior in slow lorises [14-16]. As part of an on-going study in the area, we have not only observed Javan slow lorises to enter extended periods of inactivity in a huddling posture during extreme cold (8 °C) temperature, but have also recorded thermal torpor [41]. This points towards a vital influence of climate on behavior within this geographic region.

5. Conclusion

We suggest continued research and conservation on the endemic species, *N. javanicus*, in the context of future climate change. Populations ranging in the Cipaganti area are more likely influenced by relative humidity and forest connectivity between habitats. Should current climate patterns in this montane region persist, temporal effects will slow down phenology development, depleting resource availability for nectar and exudate feeding animals. Global warming increases sea levels and temperatures, forcing agriculturalists to utilize submontane and montane regions increasingly for more successful crop yields. Thus, continuing climate trends could create further habitat loss and fragmentation in the home ranges of *N. javanicus*. Future climate projections are estimated to display an increase in ambient temperatures by 2–6 °C by 2090, as a result of greenhouse effect and human activity [9]. This temperature increase would further heighten the intensities and alteration of both wind and rainfall patterns, resulting in limited resource availability, affecting behavior, habitat use and mortality rate of *N. javanicus*.

These results also have important implications for captive slow loris conservation. Heavily impacted by illegal wildlife trade throughout their range, confiscated slow lorises of unknown geographic origin (including forest type and altitude) are being reintroduced in high numbers [42]. The majority of these animals may originate from lowland forests are being released in high altitude forest area with low success rates [29]. An understanding of how wild lorises deal with local climate variations will be vital to regulate these reintroductions. Continuing research on the impact of climate on lorises would provide vital information for wild and captive population management, as well as reintroduction protocol. In lieu of these studies’ findings and climate change projections,
understanding the limitations of this seemingly adaptable species to climate fluctuations will be key to future conservation planning.

Acknowledgements

We thank Indonesia RISTEK and the regional Perhutani and BKSDA for authorizing the study. Funding was provided by Amersfoort Zoo, Augsburg Zoo, Brevard Zoo, Cleveland Zoo and Zoo Society, Columbus Zoo, Conservation International Primate Action Fund and Margot Marsh Biodiversity Fund, Cotswold Wildlife Park, Disney Worldwide Conservation Fund, Henry Doorly Zoo, International Primate Protection League, Mohamed bin al Zayed Species Conservation Fund (152511813), Memphis Zoo, National Geographic (GEFNE101-13), People’s Trust for Endangered Species, the Royal Geographic Society with IBG, Shaldon Wildlife Trust, Sophie Danforth Conservation Biology Fund and ZGAP. We thank our field team Y. Nazmi, A. Nunur, D. Rustandi, D. Spaan and D. Ahmad. Finally, we thank members of the Nocturnal Primate Research Group and Oxford Brookes University Primate Forum for useful comments, especially S. Cheyne, G. Donati, K. Hockings, M. McLennan, M. Sigaud, E. Racevska and V. Nijman. We thank the editor and two anonymous reviewers for their detailed and helpful comments.

Conflict of interest

All authors declare no conflicts of interest in this paper.

References


