

Research Article

The Influence of Sex and Weather on the Activity Budget of Javan Slow Lorises (*Nycticebus javanicus*) in Garut Regency, West Java

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ABSTRACT

The Javan slow loris (*Nycticebus javanicus*) is a nocturnal primate endemic to Java. Previous studies on slow loris activity are limited to general daily activity, and there is a lack of research on the potential sex differences in slow loris activity. This study aims to analyze differences in the daily activity of the Javan slow loris based on sex. From August to December 2018, the daily activity of six wild Javan slow lorises was recorded using behavioral observations with instantaneous point sampling at 5-minute intervals. Differences in male and female slow loris activity were analyzed using the Generalized Linear Mixed Model (GLMM). We set sex and weather as fixed factors and individuals as random effects. The results of this study showed that females spent more time feeding and less time resting than males. In addition, the Javan slow loris behavior was affected by temperature and humidity like other slow loris species.

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INTRODUCTION

Daily activity budgets are key behavioral indicators of the survival strategies that species adopt to maximize individual fitness and longevity, and may also reveal the core requirements for a species' existence within a habitat (Repi et al. 2019). Daily activity budgets vary widely among primate species and are dictated by various factors, including social structure, nutritional requirements and ecological factors such as habitat type, food resource availability, and season (Korstjens et al. 2010; McFarland et al. 2014; Strier 2017).

Daily activity budgets are further influenced by morphological and reproductive differences between the sexes; leading to differences in nutritional requirements (Key & Ross 1999; Lodberg-Holm et al. 2021). It is generally agreed that the females of a species bear the greatest direct costs of reproduction through the energy consumption required for gestation and lactation, while males bear indirect costs of reproduction through consuming energy by

maintaining territories and guarding mates against rivals (Key & Ross 1999; Sussman et al. 2005; Thompson & Georgiev 2014). Differences in the strategies employed to efficiently exploit resources to meet varying nutritional needs between the sexes may lead to variations in activity budgets (Anirudh et al. 2020).

The Javan slow loris (*Nycticebus javanicus*) is a small nocturnal primate endemic to Java (Lehtinen 2013). The species is under threat due to habitat loss and wildlife trafficking in Southeast Asia and is classified as Critically Endangered by the IUCN Red List (Nekaris et al. 2015) and listed as Appendix 1 on CITES (Nekaris et al. 2008). Javan slow lorises are socially monogamous primates that live in family units consisting of a mated pair and several offspring (Barrett et al. 2021). Unlike many other socially monogamous primates, recent research has shown that adult slow loris males are actively involved in juvenile development and act as “social fathers” to offspring within their family unit; engaging in play behavior with juveniles to strengthen social bonds and to provide motor training for young individuals (Fernandez-Duque et al. 2009; Barrett et al. 2021).

The Javan slow loris has a geographic distribution in West, Central, and East Java (Nekaris et al. 2014; Voskamp et al. 2014; Wirdateti et al. 2019). Their habitat in West Java includes primary forest, secondary forest, and bamboo forest (Pambudi 2008). Javan slow lorises are also found outside of protected areas in traditional plantation gardens and forest gardens in Sumedang, Ciamis, and Tasikmalaya, West Java (Winarti 2003; Winarti 2011)

Previous studies on the daily activity budget on Javan slow lorises in plantation areas have found that the Javan slow loris spends 10-26% of its active time foraging (Reinhardt et al. 2016; Romdhoni 2021), with 5-15% of the total activity budget attributed to feeding (Reinhardt et al. 2016; Romdhoni 2021). Resting, including sleeping, constitutes 4-16% of their activity budget, while 14-39% of the daily activity budget is attributed to traveling (Rode-Margono et al. 2014; Reinhardt et al. 2016; Romdhoni 2021). Ecological factors, including habitat connectivity, food resource availability, rainfall, temperature, and humidity have also been shown to significantly affect slow loris behavior (Rode-Margono et al. 2014; Reinhardt et al. 2016; Cabana et al. 2017; Barrett et al. 2021).

Previous studies on the daily activity of slow lorises have been limited to general daily activity and studies into the sex-based differences in the daily activity of Javan slow lorises are lacking. A detailed understanding of the activity budget of threatened species such as the Javan slow loris is critical to their conservation efforts. Knowledge of how the activity budget of the Javan slow loris differs between the sexes may allow for more specialized management plans both in-situ and ex-situ. Therefore, this study aims to identify differences in adult Javan slow loris activity budgets based on sex while also considering the effects of temperature and humidity.

MATERIALS AND METHODS

Study Area

This research was conducted at the Little Fireface Project (LFP) field site from August to December 2018. The research was conducted in traditional plantation gardens, referred to as *talun*, in the village of Cipaganti, Garut, West Java, Indonesia (Figure 1).

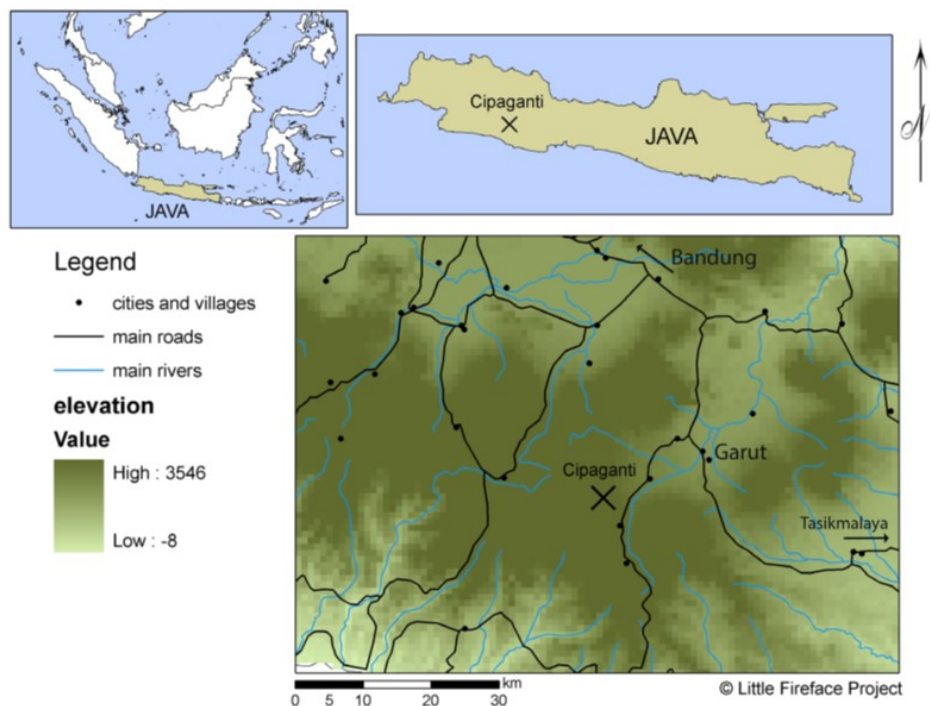


Figure 1. Location of the field site (Rode-Margono et al. 2014).

Behavioral Observations

We collected data on six adults Javan slow lorises (three males and three females) fitted with VHF radio-collars (BioTrack, UK). We followed one individual per night, with a total duration of 12 hours per observation. We did not follow multiple lorises simultaneously because each individual has their own home range. Due to limited human resources we focused on one individual per night. The behavior of slow lorises was collected using an instant point sampling technique with 5-minute intervals (Altmann 1974). If the Javan slow loris performed a rarely observed behavior between the 5-minute intervals, we collected data on an ad libitum basis (Altmann 1974; Rode-Margono et al. 2014). We recorded the behavior data using a detailed behavioral ethogram adapted from Rode-Margono et al. (2014) (Appendix 1). We collected the weather data (temperature and humidity) via a HOBO weather station.

Data Analysis

We used a Generalized Linear Mixed Model (GLMM) to see differences in activity budget. We set weather (temperature and humidity) and sex as fixed factors and individuals as random effects. We used IBM SPSS Statistic v 26. We considered a p-value of 0.05 as the threshold for significance.

RESULTS AND DISCUSSION

Results

Sex based differences in activity budget

The research was conducted on six individuals for a total of 378.33 hours of observation over 35 days. The total instances of active observation were 1107 times and the total time of active observation was 92.67 hours.

We found a significant difference between male and female slow lorises in feeding ($p < 0.001$) and resting ($p = 0.021$) behavior (Table 1). Females spent more time feeding (8.32%) than males (2.93%) and less time resting (3.25%) than males (7.17%). The percentage of other behaviors did not change between male and female slow lorises (Figure 2).

Environmental factors affecting activity budget

With an increase in temperature, slow lorises spent significantly more time feeding ($p < 0.001$) and sleeping ($p < 0.001$) and significantly less time doing the following behaviors: alert ($p < 0.001$), forage ($p = 0.008$), social ($p < 0.001$), and travel ($p < 0.001$) (Table 1). Humidity also had a significant influence on the time spent alert, feeding, foraging, resting, sleeping, and socializing (Table 1).

Discussion

Javan slow loris daily activity based on sex

Our study found that across eight main behaviors observed in Javan slow lorises, two key behaviors, feeding and resting, differed significantly in proportion of total activity budget between the sexes. Our data indicates that female Javan slow lorises attributed significantly more of their active time to feeding than males. In contrast, males rested significantly more than females within their daily activity budget (Figure 2). These findings are in direct contrast to studies on other monomorphic primate species, including other *Nycticebus* species. Research on the feeding time of captive greater slow lorises (*N. coucang*) and eastern lesser bamboo lemurs (*Hapalemur griseus*) revealed no significant difference between the sexes (Duncan 1982; Grassi 2002). How-

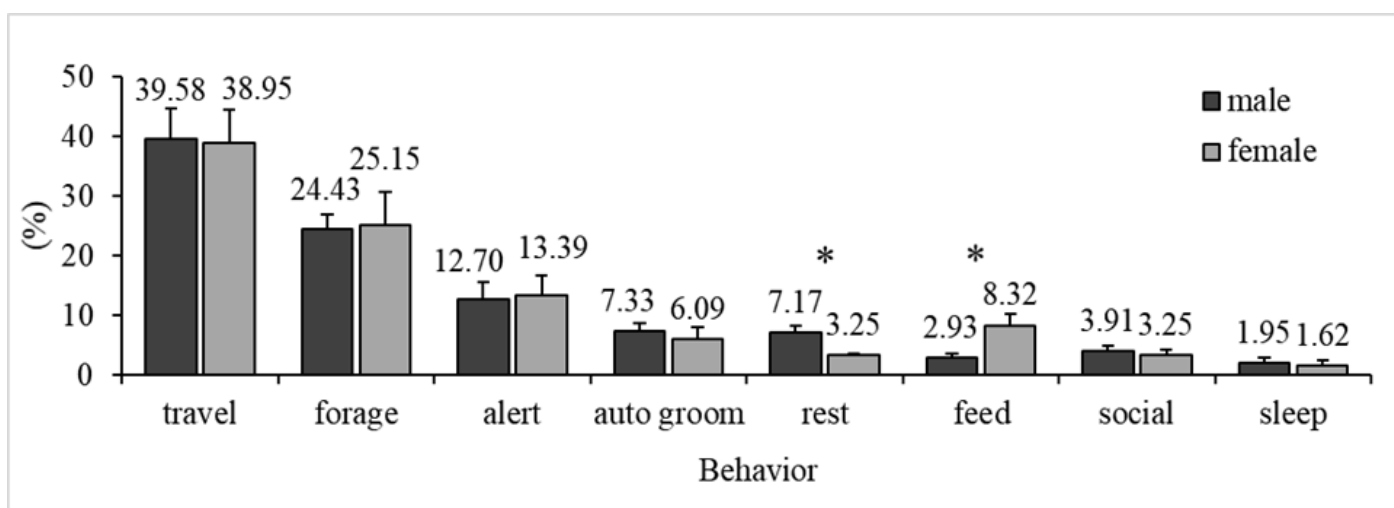


Figure 2. Javan slow loris behavior percentage based on sex (3 females, 3 males). *Significantly different ($p < 0.05$).

Table 1. Results of the generalized linear mixed model explaining the effect of sex, temperature, and air humidity on the behavior of six Javan slow lorises in Cipaganti, West Java.

Behavior	Factor	Coefficient	Std. Error	t-value	Sig.
Alert	Sex	-0.039	0.506	-0.078	0.938
	Temperature	-0.131	0.009	-15.435	0.000*
	Humidity	-0.008	0.002	-3.574	0.001*
Feed	Sex	1.432	0.412	3.473	0.001*
	Temperature	0.125	0.010	12.327	0.000*
	Humidity	0.100	0.003	32.872	0.000*
Forage	Sex	0.040	0.294	0.136	0.892
	Temperature	-0.017	0.006	-2.768	0.008*
	Humidity	0.020	0.002	12.473	0.000*
Groom	Sex	-0.414	0.438	-0.945	0.350
	Temperature	-0.015	0.011	-1.400	0.169
	Humidity	0.002	0.003	0.790	0.434
Rest	Sex	-1.114	0.464	-2.401	0.021*
	Temperature	0.016	0.012	1.361	0.181
	Humidity	-0.029	0.003	-9.436	0.000*
Sleep	Sex	0.093	3.011	0.031	0.975
	Temperature	1.048	0.037	28.558	0.000*
	Humidity	0.053	0.009	5.976	0.000*
Social	Sex	-0.839	1.274	-0.659	0.514
	Temperature	-0.290	0.022	-13.327	0.000*
	Humidity	0.015	0.007	2.179	0.035*
Travel	Sex	-0.217	0.313	-0.694	0.491
	Temperature	-0.108	0.005	-21.448	0.000*
	Humidity	-0.002	0.001	-1.339	0.188

*Significantly different ($p < 0.05$)

ever, direct comparisons between the activity budgets of captive individuals and wild individuals are complicated by the fact that individuals in captivity do not face the same challenges as wild individuals in terms of food availability and predation risk and environments vary widely (Melfi & Feistner 2002). Regarding research on wild individuals, Wiens (2002) found no significant differences in the daily time budget of resting, feeding or social behavior between male and female greater slow lorises; however the inclusion of sexually immature individuals in the data analysis of this study may obscure potential differences in reproduction-related changes to the activity budget between adult male and female slow lorises.

As a monogamous species, the Javan slow loris lacks sexual dimorphism, and males and females are roughly the same size and weight (~905g) (Barrett et al. 2021). Monomorphic species are generally expected to have similar energy expenditure outside of reproduction costs (Key & Ross 1999; Cabana et al. 2017). However, female nutritional requirements are closely linked to reproduction; during gestation and lactation, females may adjust their activity budget to compensate for the increased energy requirements of reproduction (Ganzhorn et al. 2004).

In other monomorphic primates such as ring-tailed lemurs (*Lemur catta*), females have been shown to become more selective in nutrient intake in periods of lactation (Rasamimanana & Rafidinarivo 1993; O'Mara & Hickey 2014) which may lead to changes to daily activity. Research on feeding time in male and female sifakas (*Propithecus verreauxi*) also showed a significant difference at the end of the lactation period, in addition to differences in diet (Koch et al. 2017). In contrast to our study, Anirudh et al. (2020) found significant differences in feeding and foraging behavior between male and female adult Philippine slow lorises (*N. menagensis*), as males were observed feeding significantly more while females spent significantly more time foraging. They also observed that feeding activity for male individuals was well distributed throughout the active period, whereas for females, most of the feeding behavior occurred at the beginning of the active period. These findings suggest that males and females may adopt different foraging strategies to maximize individual requirements, however as the authors note, the study was conducted on individuals released from captivity; therefore, observed behavior may differ from their wild counterparts (Anirudh et al. 2020). Female Javan slow lorises have a gestation period of 6 months, a relatively long period considering their small size (Poindexter & Nekaris 2017) and may result in significant changes to nutritional requirements during reproduction. Two of the three females observed in this study were known to have been in a period of gestation, and subsequently lactation, during the period of data collection. Their higher energy requirements during this time likely explains our feeding behavior findings.

An increase in the proportion of time spent on one activity within an activity budget causes a decrease in the proportion of time spent on one or more other activities. As the other behaviors analyzed in this study were not significantly different between the sexes, this suggests that the increased feeding behavior exhibited by the focal female individuals directly resulted in less time spent resting. Conversely, as males have lower nutritional requirements than females, they may be able to balance energy expenditure by increasing period of resting rather than increasing energy intake (Reinhardt et al. 2016)

Javan slow loris daily activity in relation to environmental factors

In line with previous studies on the effects of environmental factors on Javan slow loris activity, this study found that temperature and humidity had significant impact on several behaviors. Temperature had a significant positive relationship with sleeping and feeding behavior, and a significant negative relationship with foraging, traveling, social, and alert behavior. Humidity had a significant positive influence on sleeping, foraging, feeding, and social behaviors and a significant negative influence on resting and alert behavior. Environmental factors may directly affect slow loris behavior through changes in energy requirements and indirectly through changes to the habitat in response to fluctuations in climatic conditions (Reinhardt et al. 2016). The slow

lorises in this study live in an agricultural area between 1100-1500m asl, covered with cultivated fields, abandoned fields, tree plantations, and bamboo patches. Each field is often bordered by trees, creating a connected canopy for the lorises (Rode-Margono et al. 2014).

Slow lorises are specialized exudativores that also feed on insects, nectar, and small vertebrates and rarely eat fruits (Wiradateti et al. 2005; Nekaris & Bearder 2007). According to Cabana et al. (2017), the Javan slow loris eats exudates (38-60%) predominantly and insects (12-27%) with flower nectar consumed seasonally and fruit consumed rarely. They consumed exudates from *Accacia decurrens* and nectar of *Calliandra calothyrsus* (Rode-Margono et al. 2014; Cabana et al. 2017; Romdhoni 2017). Male slow lorises consume more exudates and nectar, while female slow lorises consume more arthropods (Romdhoni 2017). While exudates, the staple food source of Javan slow lorises, are available year-round, it is of low nutritional value and therefore slow lorises must supplement this diet with other food sources (Cabana et al. 2017). Other key slow loris food sources such as insects, nectar, and flowers are seasonally available and this may affect slow loris feeding and foraging behaviors (Cabana et al. 2017).

Increased humidity may affect the activity of arthropods (Reinhardt et al. 2016). Insects comprise approximately 10-18% of the Javan slow loris's diet, including flying insects such as Lepidoptera and Coleoptera, and insect consumption varies between seasons (Wiens et al. 2006; Starr & Nekaris 2013; Cabana et al. 2017). In higher humidity, insects have been shown to fly lower (Shamoun-Baranes et al. 2006). Slow lorises cannot leap, so they may take advantage of lower flying insects during periods of increased humidity by selectively feeding more on insects. This study did not analyze food source selection and therefore cannot draw further conclusions on potential changes to feeding behavior because of environmental factors.

Rode-Margono & Nekaris (2014) and Reinhardt et al. (2016) did not find a correlation between temperature and Javan slow loris activity. We found, however, that Javan slow lorises decreased feeding and sleeping at lower temperature. We also found that travel and forage time increased at lower temperature, suggesting a possible need to travel farther searching for food to compensate for the lower food availability in the colder period (Campera et al. 2021). Nekaris et al. (2021), found a higher use of canopy bridges during hotter periods, suggesting a positive relationship between travelling and temperature. Our study might be temporally limited, and other patterns might emerge if a larger data collection period is considered.

CONCLUSION

Significant differences in the activity of male and female slow lorises were found in feeding and resting behavior. Male slow lorises fed more and rested less, while female slow lorises ate more and rested less. The Javan slow loris behavior is affected by environmental factors (temperature and humidity).

AUTHORS CONTRIBUTION

K.A.I.N. directed the long-term field project, conceptualised the project, and acquired the funding. H.R. wrote the original draft manuscript and conducted the field work. H.B. supervised field research activities. H.R. conducted the statistical analysis. D.P., E.I, K.H., M.C., and K.A.I.N. reviewed, revised, and proofread the manuscript.

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CONFLICT OF INTEREST

The authors declare no conflict of interest. The funders had no role in the design of the study; in the collection, analyses, or interpretation of data; in the writing of the manuscript, or in the decision to publish the results.

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APPENDIX

Table A. Ethogram of Javan slow loris adapted from Rode-Margono et al. (2014).

No	Behavior	Description
1	Alert	Remain stationary like in “rest” but active observation of environment or observer.
2	Feed	Actual consumption of a food item.
3	Forage	Stationary or movement associated with looking for food (often including visual and olfactory searching).
4	Auto groom	Lick or use tooth comb on own fur.
5	Rest	Remain stationary, often with body hunched and eyes are open.
6	Sleep	Remain stationary in huddled position with head between the knees, or eyes are visible but closed.
7	Social	All interactions with conspecifics, including aggression, allogrooming, play, and other social behaviors.
8	Travel	Continuous, directed movement from one location to another.
