

## Article

# Influence of Moon Luminosity, Seasonality, Sex and Weather Conditions on the Activity Levels of the Nocturnal Javan Slow Loris

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**Abstract:** The activity patterns of mammals depend on environmental changes (e.g., moon luminosity, food availability, weather) and endogenous rhythms. Behavioral observations are traditionally used to estimate the activity patterns of animals, but low visibility and the cryptic nature of some species entail that, in certain conditions, the animal is visible only for around 60% of the time. Recent advances in technology allow automatic data collection on the activity levels of animals. We used five years of data collected via accelerometers to understand how moon luminosity, seasonality, sex, and weather conditions influence the activity levels of the nocturnal and cryptic Javan slow loris. We collected 9589 h on six females and 7354 h on six males. Via Generalized Additive Mixed Models, we found that lorises are lunarphobic; they reduce activity levels during cold nights, they have higher activity levels when the relative humidity is close to 100%, and they have high peaks of activity between December and February and between June and August. The activity levels are thus influenced by avoidance of predators, food availability, consumption of insects and nectar, physiological, and behavioral adaptations to cold temperatures and energy requirements during reproductive stages. We highlight the importance of using bio-loggers for cryptic animals as with behavioral observations only, and the observer might underestimate active behaviors and overestimate inactivity.

**Keywords:** Indonesia; accelerometer; bio-logger; *Nycticebus javanicus*; primate; Zeitgeber; masking factors; temperature; predator avoidance; food availability



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## 1. Introduction

The activity patterns of mammals are regulated by changes in the environment and endogenous clocks [1,2]. Mammal activities follow fixed rhythms that are circannual and circadian but are also influenced by predictable environmental factors (i.e., Zeitgebers) and less predictable factors (i.e., masking factors) that can take precedence over the main rhythms [3,4]. The main example of Zeitgeber is the photoperiodic variation that synchronize activity patterns of most of mammal species [5,6]. The effect of photoperiodic variations and day–night length variations are more evident in species far from the Equator with high seasonal variations in daylight and climate [6,7]. Masking factors are dependent on regional conditions and are taxon-specific [5]. Examples of masking factors are nocturnal luminosity (that is influenced not only by moon phases but also by weather conditions), predation risk, anthropogenic disturbance (including noise and light pollution), and food availability [8–12]. Masking factors can also have a direct inhibitory or excitatory effect on several physiological and behavioral variables [3,13,14].

Moon luminosity is a major masking factor influencing the activity of mammals as it is directly linked to increased predation risk, but also to a higher visibility of food or prey [15,16]. Prey species thus often reduce their activity levels during bright nights (i.e.,

lunarphobia), although they can also adapt the strategy to increase their activity levels during bright nights to increase their potential to spot predators and have the additional advantage of maximizing their foraging efficiency (i.e., lunarphilia) [17,18]. Predators are thus usually lunarphilic if they are at the high end of the food chain [19], although there are cases when predators can adapt to their prey and entrain their activity pattern to match that of their favored prey [20]. The choice between lunarphilia and lunarphobia is not always straightforward and it depends on a balance between costs (i.e., increased predation risk) and benefits (i.e., increased detection of predators and food) [16]. This results in high variability, even within the same species (e.g., in several species of ungulates; reviewed by Gordigiani et al. [21]).

Seasonality can influence activity patterns in several ways. Day length variation is the main Zeitgeber as discussed above, but its effect can be masked by other seasonal variations in food availability and weather conditions [7,10,21,22]. To save energy, many mammal species reduce their activity levels during cold and dry periods, when food availability is also low [23]. Low temperatures can reduce activity of mammals that need to save energy by behavioral (e.g., thermoregulation) and/or physiological adaptations (e.g., torpor and hibernation) [24]. In the tropics, such behavioral and physiological adaptations are also present during prolonged dry periods that usually correspond to the colder months [25]. High relative humidity can further influence the activity patterns of some mammals as it is associated with a higher availability of insects [26]. Heavy rains, however, reduce the activity levels as they decrease visibility [27]. Activity patterns can also differ between sexes, with females that can have either lower or higher energy intakes/costs than males during lactations and gestations [28]. The choice of either maximizing energy intake or minimizing energy expenditure depends on species and environmental conditions [29,30]. There are, however, cases when the activity patterns of females do not differ from those of males, even during periods of high energy needs (e.g., [31]).

The Javan slow loris *Nycticebus javanicus* is a critically endangered species and is also a venomous primate [32,33]. They are small bodied (~905 g), nocturnal, and live in small family groups consisting of an adult male, an adult female, and one to four offspring [33,34]. A previous study based on behavioral observations over one year highlighted a possible negative influence of the moon phase on this species, mainly related to the possible availability of preys during dark nights rather than the potential risk of predation [26]. The activity levels were also positively affected by the relative humidity, possibly because prey (i.e., insects) were more abundant during wet nights [26]. Detectability of prey rather than avoidance of predators thus seems to be the main factor influencing the activity levels of Javan slow lorises. The presence of venom was also previously linked to the possibility of defending themselves from predators or to capturing prey, but more recently was confirmed to be used in intraspecific competition [32]. Data collected via behavioral observation, however, are subject to bias on cryptic animals as animals may be out of view for 30–40% of their time, and active behaviors such as feeding might be underestimated [35]. Advances in technology over the last 20 years allowed the development of bio-loggers devices with the capacity to automatically record animal activities [36]. Accelerometers have proven very efficient at recording the activity levels of several species, with the ability to discern between active and inactive behaviors close to 100% [35,37].

Here we aim at assessing the influence of moon luminosity, seasonality (i.e., Julian date), sex, and weather condition (i.e., temperature and humidity) on the activity levels of Javan slow lorises collected via accelerometers over five years. Based on previous preliminary observations [26], we expect Javan slow lorises to be lunarphobic, as the availability of some key prey species might be higher during dark nights. The main reason to be lunarphobic, however, is predator avoidance, and nocturnal predators of adult lorises (e.g., Javan leopard *Panthera pardus melas*) are present at the study site but mainly in a nearby forest [38]. Furthermore, Javan slow lorises live in family groups and similar primates were found to be lunarphobic, as they can reduce predatory risk by increasing vigilance and have a higher foraging efficiency [37,39]. Thus, Javan slow lorises might not show lunarphobia

as the preliminary observations suggested, but rather a lunarphilia or neutral response to moon luminosity. Seasonality is also expected to influence the activity levels of Javan slow lorises, with a potential reduction of activity during dry periods (i.e., May–October) when resources are scarce, and they need to save energy. Javan slow lorises, in fact, were also found to reduce the number of crossings of wildlife bridges during the dry period to save energy [40]. The consumption of flowers, however, is higher during the dry period [41], and this might entail higher activity levels as the consumption of flowers needs longer feeding time to satisfy the energetic needs compared to other food items [42]. Sex is expected to have a significant influence of the activity levels of Javan slow lorises as females can experience periods of high energy requirements. Births in Javan slow lorises are aseasonal, and gestation and lactation both last approximately six months [43]. It is also possible for female slow lorises to have periods of overlap in pregnancy and lactation, which may increase their energetic costs. We predict humidity to have a positive influence on the activity patterns, as high humidity corresponds to periods of high availability of fruit and flying insects [26]. We also predict low temperatures to reduce the activity levels of Javan slow lorises, as this species occasionally enters torpor during cold and dry months [44].

## 2. Materials and Methods

### 2.1. Study Site and Subjects

For this study, we collected data on the activity levels of 12 adult Javan slow lorises (six females and six males) between June 2014 and October 2019. The Javan slow lorises at the study site are part of a population of more than 80 wild individuals routinely monitored since 2012 [32]. These individuals inhabit an agroforestry environment and can have a broad variation in home range size (2–50 ha), occasionally moving to a nearby forest [45]. Slow lorises are collared with VHF collars (Biotrack TW3, Wareham, United Kingdom) secured around their necks for individual identification and monitoring. The placement of collars around the neck is efficient for recording activity of slow lorises [34]. The 12 individuals included in this study were further equipped with accelerometer devices (Actiwatch Mini: CamNtech Ltd., Cambridge, UK) to the VHF radio collars. Activity levels are based on activity scores from accelerometer data. These devices were previously used to study the sleep patterns on the same individuals that showed a strictly nocturnal pattern of activity [34]. As explained in Reinhardt et al. [34], five additional individuals were equipped with accelerometers, but these devices provided unreliable data and were omitted from further analyses. A detailed description of the captures and of the routine checks on these devices is provided in Reinhardt et al. [34].

### 2.2. Data Collection and Processing

We programmed the accelerometers to store activity scores at 1-min epochs using the MotionWare software (CamNtech Ltd., Cambridge, UK). The same software was used to extract raw data on the activity scores [34,46]. Before the analysis, we inspected the raw data for potential recording errors and removed the data that were clearly skewed [34,46]. This can happen, for example, after a prolonged period of exposure to intense rainfall. These recording errors are evident from the inspection as they do not follow the regular patterns and/or values are much higher than the usual values relative to periods of high activity. We collected climate data including ambient temperature (°C) and relative humidity using a Hobo U30 weather station [47]. These data were collected every 15 min for the whole time the activity loggers were used. We also collected data on the nocturnal luminosity each night through Moon v2.0 software. The nocturnal luminosity index provided by this software considers moon phase and sunrise, sunset, moonrise, and moonset times (see Eppley et al. [48] for a detailed description).

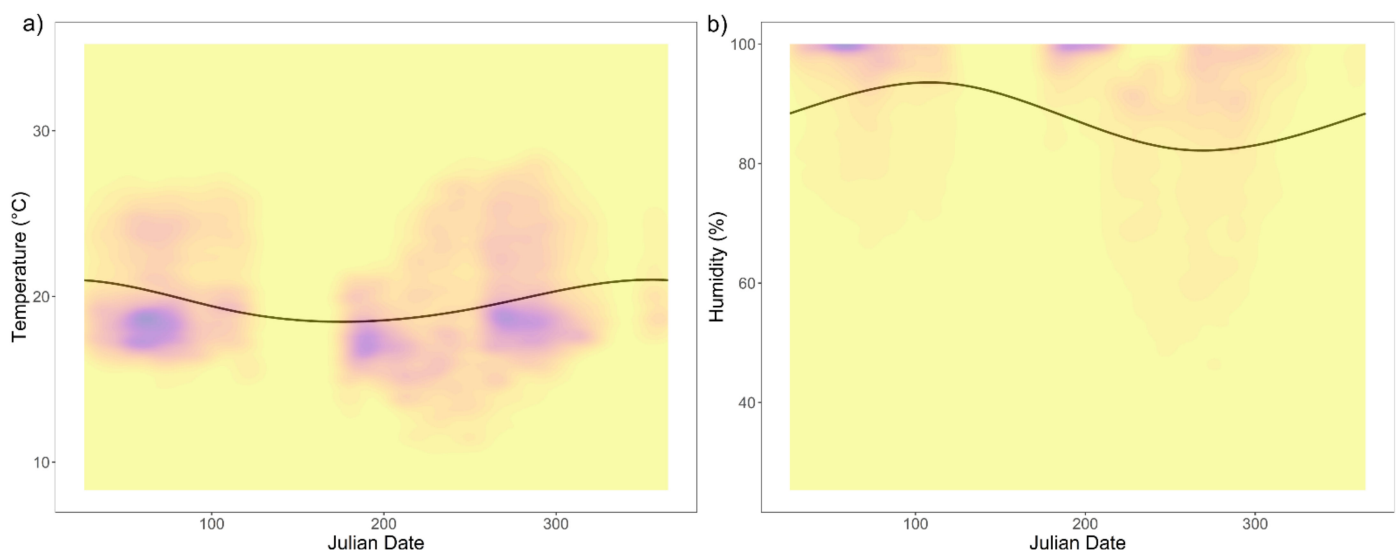
### 2.3. Data Analysis

We carried out statistical analysis using R v4.1.0. We used a Generalized Additive Mixed Model (GAMM) with the activity score as the dependent variable, moon luminosity,

relative humidity, seasonality (Julian date), and temperature as independent variables. We fitted the dependent variable to a Tweedie distribution with the time of the day as control variable (it is already known that they are strictly nocturnal, and they synchronize their activity in relation to sunset and sunrise; [34]) and the individuals as random effects. We used a fully restricted maximum likelihood method for model selection via bam command in the package ‘mgcv’ [49]. For Julian date and time of the day, we manually selected cyclic cubic regression splines to take into account the circularity of the variable [50]. We tested for concurvity and detected no issue (mean overall concurvity: 0.37; maximum pairwise concurvity: 0.55 between temperature and humidity). We used the bam command as the gamm command is not suitable for large datasets (>100,000 rows), while bam provides a fast and efficient way of performing additive models with very large datasets without relying on methods of subsampling [51]. We used GAMM as they provide a flexible approach because they do not assume a linear or other parametric form of relationship a priori and can be used to reveal and estimate nonlinear effects of the covariate on the dependent variable [50]. We considered significant values when the smooth term  $\pm 95\%$  confidence interval was higher or lower than the reference value (i.e., not crossing the reference line).

### 3. Results

The accelerometers collected a total of 9589 h on females (range: 375–3029 h) and 7354 h on males (range: 546–1962 h), corresponding to a total of 1,016,567 activity score records. The mean ambient temperature during data collection was 19.7 °C (range: 8.4–35.2 °C), and the mean relative humidity was 86.9% (range: 25.4–100.0%) (Figure 1). The nocturnal luminosity index ranged between 0.00 and 0.49 (mean: 0.18).



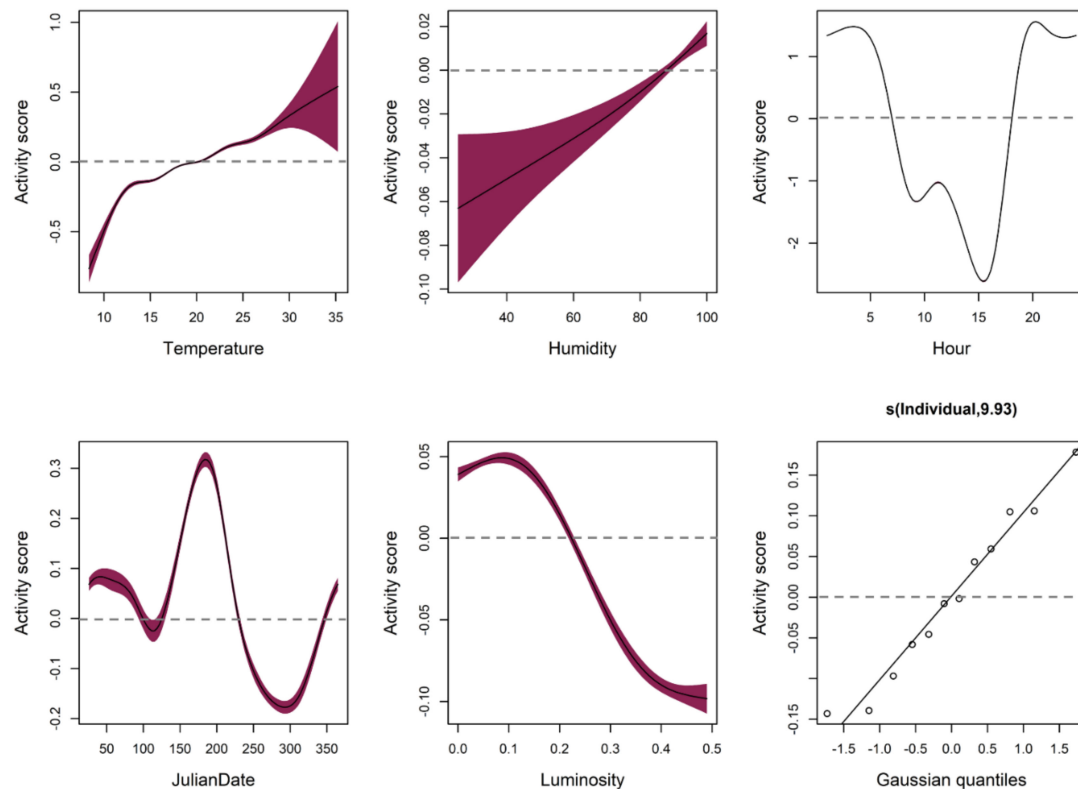
**Figure 1.** Heatmap showing the weather conditions, (a) temperature and (b) humidity, in relation to seasonality (Julian date) during the automatic data collection via accelerometers deployed on 12 Javan slow lorises (six females and six males) between June 2014 and October 2019. The black line indicates the mean value.

The activity levels of Javan slow loris were influenced by all the predictors (Table 1; Figure 2) (mean: 123.8; range: 0–8000 counts of activity). Males had higher activity scores than females (Table A1). Javan slow lorises were strictly nocturnal and increased the activity level with an increase in humidity following an almost linear trend. The activity of Javan slow loris dropped at low temperatures (<12 °C) and was higher than the reference value at temperatures between 20 °C and 30 °C. The activity levels reached two high peaks between December and February and between June and August, and a low peak between September and November. The activity levels of Javan slow lorises were higher at low luminosity and were lower at high luminosity.

**Table 1.** Results of Generalized Additive Mixed Models to explain the influence of moon luminosity, seasonality (Julian date), temperature (°C), relative humidity, time of the day, and individuals (random effect) on the activity levels of Javan slow lorises *Nycticebus javanicus* in Cipaganti, West Java. Data were collected via accelerometers deployed on 12 Javan slow lorises (six females and six males) between June 2014 and October 2019.

Response Variable	Predictor	Estimate $\pm$ Std. Error	t-Value	p	Smooth Term		p
					Edf	F	
Activity level	Intercept	3.99 $\pm$ 0.04	90.8 *	<0.001			
	Sex <sup>a</sup>	0.18 $\pm$ 0.06	2.9 *	0.004			
	s(hour)				8.0	51075.6 *	<0.001
	s(humidity)				1.6	19.8 *	<0.001
	s(individuals)				9.9	503.3 *	<0.001
	s(julian date)				7.9	38975.0 *	<0.001
	s(luminosity)				3.0	603.1 *	<0.001
	s(temperature)				8.4	155.9 *	<0.001

<sup>a</sup> reference category: males; \*  $p < 0.01$ .



**Figure 2.** Smooth terms estimated via Generalized Additive Models to explain the influence of moon luminosity, seasonality (Julian date), temperature (°C), relative humidity, time of the day, and individuals (random effect) on the activity levels of Javan slow lorises *Nycticebus javanicus* in Cipaganti, West Java. Data were collected via accelerometers deployed on 12 Javan slow lorises (six females and six males) between June 2014 and October 2019.

#### 4. Discussion

Here we showed the influence of environmental variables (moon luminosity, seasonality, temperature, and humidity) and sex on the activity levels of the nocturnal Javan slow loris. As predicted based on previous preliminary observations [26], Javan slow lorises showed lunarphobia, thus reducing the activity in bright nights and increasing the activity in dark nights. Lunarphobia is linked both to the presence of Javan leopard, which can



forage in the agroforestry system, although it mainly ranges in the forest [38], and to the presence of some insect prey that are more active on dark nights [26]. Javan slow loris is thus more affected by the increased predation risk (predation risk hypothesis [16]) than by the increased foraging efficiency and detection of predators (visual acuity hypothesis [16]). Lunarphobia is a common strategy to reduce predation risk in other small and medium-sized nocturnal mammals [16–18,37].

The predictions on seasonality were only partially met as we found two high peaks, one between December and February (as predicted) and one between June and August (not predicted). The peak during the dry period was not predicted as resources are scarce and Javan slow loris is expected to reduce energy expenditures [40]. Additionally, the activity patterns should follow photoperiodic variations, thus in periods when day length is shorter (i.e., austral winter), activity levels are also expected to be reduced [37]. The peak in the dry season is mainly linked to an increase in consumption of the nectar of *Calliandra calothyrsus*, which is one of the main food items of Javan slow lorises [41]. This higher consumption of nectar might entail longer activity levels to forage, as confirmed by the positive correlation between the presence of *Calliandra calothyrsus* and the daily distances travelled [52].

The activity levels of Javan slow lorises dropped during cold nights, as predicted based on the known ability of this species to go into torpor [44]. This physiological adaptation is relatively common in nocturnal tropical primates, known to be present in bushbabies from Africa, lorises from Asia, and dwarf and mouse lemurs from Madagascar [25]. Apart from primates, heterothermy (i.e., torpor and hibernation) were found in more than 140 species from other mammalian orders in tropical or subtropical areas: Afrosoricida, Carnivora, Chiroptera, Dasyuromorphia, Didelpimorphia, Diprodontia, Eulipotyphla, Macroscelidea, Microbiotheria, Monotremata, Rodentia, and Xenarthra [24,53]. Behavioral thermoregulation can also be used by primates and other mammals during cold and dry periods, with huddling and other resting postures regularly used to save energy [23,54]. Extreme temperatures, however, reduce the activity levels of mammals [55], also evident from the high variability in activity levels in Javan slow loris at around 35 °C. Humidity also influenced the activity levels of Javan slow lorises, with peaks of activity when relative humidity was around 100%. This was predicted as high humidity corresponds to periods of high availability of fruit and flying insects [26].

Female Javan slow lorises had a lower activity level than male slow lorises, and this was expected since females experience high energy requirements during gestation, lactation, and overlap periods of lactation and gestation, when they might need to save energy. The low activity levels can also be due to the fact that female lorises park their infants and stay in proximity to their infants during the first months of life to return to visit the infant during foraging periods [56]. We did not include reproductive periods in the model as births in Javan slow loris are aseasonal, but reproductive state may have played an important role in shaping activity levels since females were either on gestation or lactation periods during the data collection [29,57]. Behavioral observations indicate that females tend to have a higher consumption of crude proteins, fruits, gum, and flowers during gestation and lactation than males [41], and they tend to have higher feeding time than males [58]. This would indicate that they would increase their energy intake instead of saving energy during periods of low food availability, but males have usually larger home ranges than females [40,45]. The activity levels might have thus been shaped by sex differences in the feeding and spatial ecology of the species, although these topics need further research.

Finally, we advocate the use of bio-logging devices such as accelerometers to collect long term data, especially on cryptic animals. Behavioral observations are invaluable tools to provide detailed information on the behavioral ecology of animals, but they might be biased, and activity levels might be underestimated or overestimated [36]. For example, we found that Javan slow loris increases its activity level during rain (relative humidity of 100%), but for an observer it might be difficult to collect data when raining (observations often stops when it is rainy—unless it is light rain—as the substrate is slippery and there is a risk of injuries). Activity levels and specific behaviors (e.g., feeding) might thus be

underestimated via behavioral observations, while inactivity might be overestimated. This adds up to the fact that, during behavioral observations, around 30–40% of the time Javan slow lorises were not visible because they are difficult to follow or because they are inside areas where they are difficult to spot (e.g., dense bamboo patches) [35].

## 5. Conclusions

We investigated the activity levels of Javan slow loris, collected over five years via accelerometers, and how they were affected by moon luminosity, seasonality, sex, and weather conditions. We found that Javan slow lorises were lunarphobic, thus reducing the activity during bright nights to reduce predation risk. Javan slow lorises had peaks of activity during the wet and hot period, when resources are abundant, and in the middle of the dry period, when they mainly feed on nectar, and they need to travel longer daily distances to gain energy. Javan slow lorises reduced activity levels during cold nights when this species is also known to enter torpor, and increased activity levels when relative humidity is around 100%, probably related to an increase in food availability. Female Javan slow lorises had lower activity levels than males, probably because gestation and lactation are particularly challenging, and females needed to save energy. We highlight the importance of using bio-loggers in addition to behavioral observations, as the latter method might underestimate active behaviors and overestimate inactivity.

**Author Contributions:** Conceptualization, M.C. and K.A.I.N.; methodology, M.C.; software, M.C.; validation, M.C., A.N.S. and K.A.I.N.; formal analysis, M.C.; investigation, M.C. and M.B.; resources, K.A.I.N.; data curation, M.C., M.B., A.N.S. and K.A.I.N.; writing—original draft preparation, M.C.; writing—review and editing, M.B., A.N.S. and K.A.I.N.; visualization, M.C.; supervision, K.A.I.N.; project administration, K.A.I.N.; funding acquisition, K.A.I.N. All authors have read and agreed to the published version of the manuscript.

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**Informed Consent Statement:** Not applicable.

**Data Availability Statement:** Data can be made available by the corresponding author by request.

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## Appendix A

**Table A1.** Activity scores (means and 95% CI) based on accelerometers deployed on 12 Javan slow lorises (six females and six males) between June 2014 and October 2019. The categories considered are based on the output of Generalized Additive Mixed Models (Table 1; Figure 2).

Variable	Category	N	Mean Score	95% CI
Sex	Female	575,394	121.4	120.9–121.8
	Male	441,172	127.0	126.4–127.5
Hour	18:00–6:00	507,438	227.7	227.1–228.2
	6:00–18:00	507,438	19.6	19.4–19.9
Humidity	>90%	555,272	162.8	162.3–163.3
	≤90%	461,294	76.9	76.4–77.3
Julian date	330–100	323,459	128.7	128.0–129.4
	150–220	161,432	156.3	155.3–157.4
	101–149 and 221–329	531,675	110.9	110.4–111.4
Luminosity	≤0.2	618,479	129.5	129.0–130.0
	>0.2	398,087	114.9	114.4–115.5

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