



**The effects of moonlight on the nocturnal movements and
behaviour of the Phillipine slow loris (*Nycticebus
menagensis*)**

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Abstract

The Philippine slow loris (*Nycticebus menagensis*) is a grossly understudied nocturnal primate species originating from South-East Asia. *Nycticebus* spp. is arboreal, cryptic and nocturnal by nature, creating logistical difficulties for researchers studying these populations in their natural habitat. *N. menagensis* is currently described as Vulnerable on the IUCN Red List and present within Appendix 1 of CITES, predominantly due to the recent decrease in population size. Population threats such as habitat fragmentation from anthropogenic disturbances such as logging as well as the existence of the wildlife trade in South-East Asia have placed the species under severe threat, with population numbers decreasing. This study investigated whether moon luminosity has an effect on the behaviour and nocturnal movements of six individuals in the area surrounding Danau Girang Field Centre (DGFC), Sabah, Malaysian Borneo between August 2015 and April 2016. Slow lorises were tracked using radio telemetry locating sleeping sites, and followed in six hour night shifts with behavioural observations being recorded and GPS location points marked. Illumination was found to have no significant effect on both the total distance travelled by individuals during nocturnal shifts and the average height occupied by lorises throughout these periods. Rainfall was also found to not have a significant effect on travel distance and height, however it was found to have a significant effect on the movement behaviour of lorises ($p < 0.05$). Slow lorises show lunar neutrality as illumination did not appear to have a significant effect on nocturnal movements and behaviours in terms of distances travelled and canopy height. It is hoped that this knowledge can help to broaden the knowledge for members of the genus *Nycticebus*, and their nocturnal behaviour patterns relating to climatic and environmental conditions. Nocturnal movement pattern is also a factor that can be understood more comprehensively to try and provide insight into the how the species survived in fragmented habitats.

Keywords: *Nycticebus menagensis*; nocturnal primate; moon luminosity; nocturnal behaviour; prosimian; quadrupedal movement

Research Highlights

1. *N. menagensis* exhibit lunar neutral behaviour in response to changing levels of moon luminosity. There were no significant effects found between bright or dim nights and the movements and behaviour of *N. menagensis*.
2. Changes in climatic conditions such as rainfall can have a significant effect on the movement patterns of *N. menagensis*.

Introduction

Research into nocturnal movement patterns of primates in South East Asia is an emerging field, typically due to their cryptic and arboreal nature within a dense rainforest habitat. Moon luminosity is an important aspect to consider when looking at the environmental variables affecting nocturnal primate activity and behaviour, particularly with regard to the cost-benefit trade off that occurs between predation and foraging needs. Little research has so far been conducted on the effects of lunar phase and moon brightness on behaviour and movement of primate species, potentially due to their nocturnal nature and their presence in dense difficult study areas (Nekaris & Bearder, 2007). The majority of research into moon brightness and circadian rhythms in nocturnal primate species has predominantly been conducted on laboratory specimens or individuals in captivity (Fernandez-Duque, 2003). Previous research has shown variation in behavioural responses to altering light levels, with many studies focusing on families such as Tarsiidae (*Tarsius spp.*), Galagidae (*Galago spp.*) and Lemuridae (*Eulemer spp.*) showing an increase in activity during periods of high moon illumination (Bearder *et al*, 2006). However, from the narrow collection of research conducted on Lorisidae (*Loris spp.*) results have concluded that changes in lunar phase have no effect on the activity levels of these species (Bearder, 2001). Studies into other mammal species have shown variation in predator-prey interactions. Clarke

(1983) showed that deermice (*Peromyscus maniculatus*) tended to increase nocturnal activity during periods of dim light to increase the probability of finding a mate and foraging, despite the increased risk of predation. A study into moon brightness on woolly opossums (*Caluromys philander*) saw a difference in antipredation mechanisms between sexes during periods of differing light intensity (Julien-Laferriere, 1997). Females tended to have a constant level of activity, while during periods of absent or low moonlight, activity levels in males were increased. This was also found in the African species of galago (*Galago moholi*) with a significant positive correlation between moonlight intensity and length of distance travelled for male individuals (Bearder, 2001). Furthermore, research into owl monkey (*Aotus* spp) nocturnal activity found that over an annual period, individuals were more active during full moon nights in comparison with new moon nights (Fernandez-Duque *et al*, 2010). Bearder (2003) has stated that the diversity of nocturnal primates is so far understudied and is emerging slowly, with emphasis placed on the need for further research into strepsirrhine species due to the increasing threats of habitat degradation.

Slow lorises (*Nycticebus spp.*) are nocturnal prosimians and are a member of the suborder Lorisoidea (Nekaris & Bearder, 2007). They are found throughout South-east Asia, including in Brunei, Indonesia and Malaysia (Nekaris & Bearder, 2007). Within the island of Borneo, four sub species of *Nycticebus spp.* are found – *N. bancanus*, *N. menagensis*, *N. borneanus* and *N. kayan* (Munds *et al*, 2013). *N. menagensis* - which is found in the island of Borneo, as well as islands to the northeast and southeast of Borneo and the Philippines (Munds *et al*, 2013) - is a cryptic, arboreal and nocturnal primate species. Due to growing habitat threat and a decreasing population size all species of *Nycticebus spp.* are described in Appendix 1 of CITES (CITES, 2016), and *N. menagensis* is also categorised as Vulnerable in the IUCN Red List (IUCN, 2016). Slow lorises are quadrupedal and do not have the ability to leap between areas of the canopy; they require canopy continuity to move through the forest habitat with ease (Munds *et al*, 2013). More research into the environmental needs of this species with regards to their movement and behaviour can highlight the importance of the maintenance of unfragmented

habitat. Slow lorises are also the only venomous primate species - Hagey *et al* (2006) found that they possess a brachial exudate, which combines with saliva to form a venomous compound used to deter predators and avoid predation (Hagey *et al*, 2006). Lorises use this adaptation by lifting their arms above their heads and licking the brachial glands to combine the saliva and the brachial toxin (Nekaris, 2014). Mothers have also been observed covering infants in the venom before leaving them during the night to forage (Nekaris *et al*, 2013). The possession of monochromatic vision (Starr *et al*, 2012), affects the way they are able to see and perceive predators and the ability to forage in dim conditions. Nocturnal primates are known to possess excellent visual acuity in order to assist detection of predators, prey location and movement through the environment (Bearder *et al*, 2006).

In terms of nocturnal activity in relation to moon illumination various explanations have been proposed regarding how nocturnal primates react to changes in lunar phase. Previous research of Lorinae has suggested that they possess vital adaptations such as crypsis and mimicry to minimise predation risk (Nekaris *et al*, 2007). There is generally thought to be a cost-benefit trade off regarding how lorises and other nocturnal mammals behave during periods of bright or dim lunar phase. Predator avoidance and prey capture or foraging are both crucial survival strategies that can be heavily influenced by changing light conditions. Optimal foraging theory explains how animal behaviour relates to the trade off between predation risk and the fitness that can be gained from foraging (Charnov, 1976). If a species or individual tends to increase their activity during periods of bright light it is referred to as lunarphilia due to the ability to increase prey detection and foraging efficiency (Rode-Morgano & Nekaris, 2014). Research has shown that primate species tend to be lunarphilic (Rode-Morgano & Nekaris, 2014), opposing the behaviour of lunarphobic species of rodents and bats which tend to decrease their activity during periods of bright light (Prugh & Golden, 2014). Pygmy lorises tended to reduce their activity during bright nights in order to minimise the risk of predation and reduce heat loss (Starr *et al*, 2012). It was also found that there was a difference in activity levels according to seasonality, during the dry season pygmy lorises were found to be lunar

phobic, whereas during the colder wet season they exhibited lunar neutrality (Starr *et al*, 2012). Woolly opossums tended to also increase their nocturnal activity when the moon was absent or low, however this response was only found in males (Julien-Laferriere, 1997). Nekaris *et al* (2014) found no evidence for lunar phobia or lunar philia in the Javan slow loris (*N. javanicus*). On the contrary, it has been suggested that nocturnal primates may be safer during periods of increased moonlight as their excellent visual acuity leads to the increased probability of seeing a predator before they are able to attack (Nash, 1986). Temperature is also a co-existing environmental variable that can have an effect on nocturnal movements and behaviour (Starr *et al*, 2012). Research into how both moonlight and temperature have an effect on the behaviour of pygmy lorises reported that as temperatures decreased, individuals would reduce their activity despite changes in luminance, while increasing activity during bright nights when temperatures were higher and vegetation and canopy cover were denser (Starr *et al*, 2012). It has been suggested that a non-existence of lunar phobia in some nocturnal mammal species may be due to a lack of correlation between moon luminosity and risk of predation as a result of their excellent visual capabilities (Gursky, 2003). From the limited range of research into the effects of lunar phase on nocturnal activity, Prugh & Golden (2014) used factors associated with luminosity responses to quantify the relationship. Predation risk, visual acuity and habitat mediated predation risk were all used to hypothesise the effects of moonlight on activity to find a quantified measure of the net effects of moonlight (Prugh & Golden, 2014).

This study aims to understand how changes in moon luminosity and different lunar phases affect the activity of *N. menagensis* throughout the night. Furthermore, it aims to look at how observed behaviours change according to moon brightness, particularly looking at how feeding and movement alters in these conditions. Previous research into how moon brightness affects activity levels is not extensive and therefore environmental variables such as cloud cover, have not been investigated as co-variables. The importance of these factors will be investigated in this study due to the potential effect these may have on nocturnal activity levels. This study was also concerned with whether

distance travelled and height of activity were variables that tended to change according with altering light conditions, by calculating how far lorises were travelling during the night and the height within the canopy that they were spending the majority of their time. This can provide insight into this understudied yet threatened species and help raise awareness of the importance of behaviour to have implications for further research and broaden the knowledge of slow loris species throughout a range of different habitat ranges.

Materials and Methods

The Lower Kinabatangan Wildlife Sanctuary (LKWS) covers an area of 27 000 ha of degraded and disturbed forest along the Kinabatangan River (Ancrenaz *et al*, 2004), protected by the State Government of Sabah. This study was carried out in Lot 6 of the LKWS at Danau Girang Field Centre (DGFC) (5°24' 48" N, 118°02' 16" E) between August 2015 and April 2016 (Fig 1). The area has a warm, wet and humid climate with a dry season usually lasting between March through to November and the wet season beginning in November and lasting until March, with a typical yearly precipitation of 3000mm (Ancrenaz *et al*, 2004). Rainfall occurs consistently throughout the year and due to the narrow variation in temperature (typically between 21-34 C) distinct seasons are not defined. The vegetation surrounding DGFC primarily consists of semi-inundated swamp and mixed riparian forest (Munds *et al*, 2013).

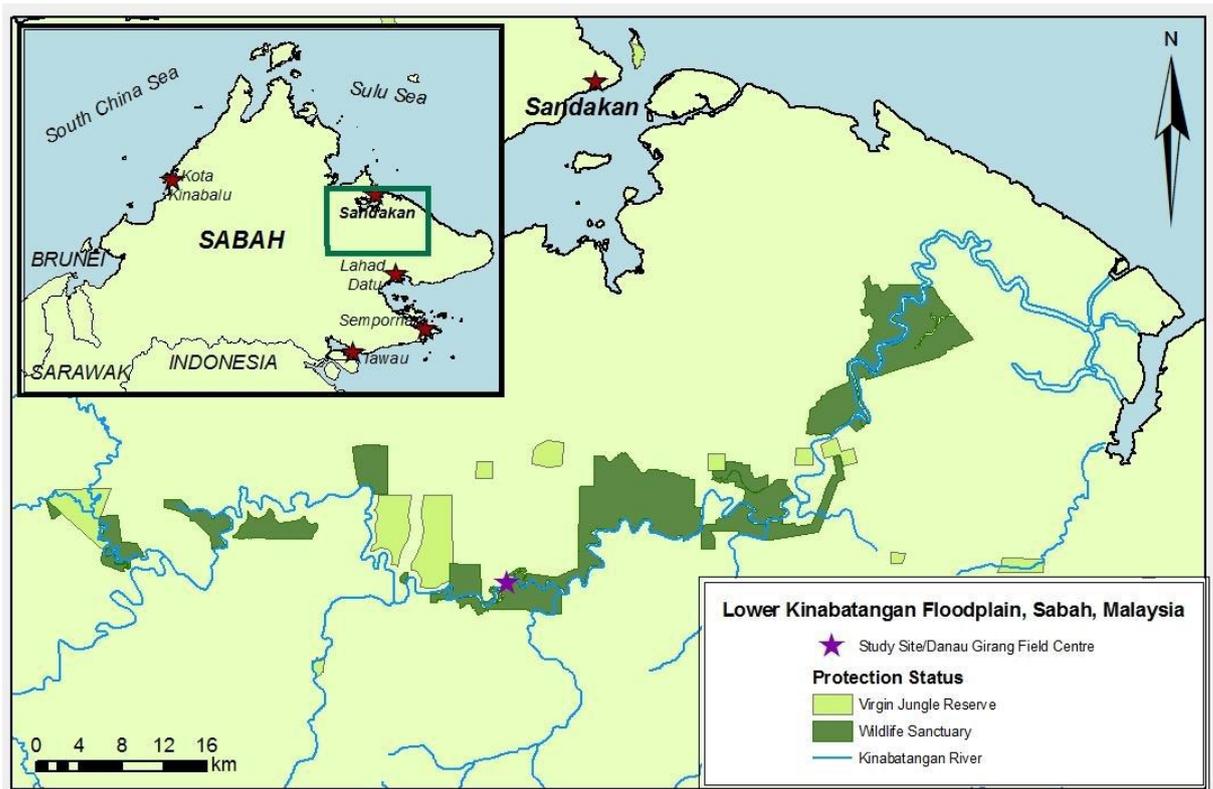


Figure 1. Map of the Lower Kinabatangan Wildlife Sanctuary, Sabah, Malaysia. The purple star indicates where Danau Girang Field Centre is situated (image courtesy of Danica Stark).

Collaring

Slow lorises were located using their reflective eye-shine, which is related to an intraocular biological reflector system that increases retinal sensitivity during dim illumination - the tapetum lucidum (Ollivier *et al*, 2004). When a slow loris was found, it was followed until it reached a height low enough for a research assistant to catch as safely as possible, with minimum stress caused to the slow loris. Thick gloves were worn to prevent bite injuries and the ethical guidelines for the 'handling and trapping of animals' was followed. All laws of Malaysian Borneo within Sabah were also adhered to at all times. The animal was either taken back to the field centre lab to be collared or collared at the capture site. The animal was fitted with a small BioTrack VHF radio-collar (BioTrack, UK), and red-filter light was used throughout the process to minimise stress to the individual. A selection of morphological measurements

was taken and recorded and an ear notch was cut for later identification purposes. When the process was complete, the animal was taken back to the tree at which it was caught and released.

VHF Tracking

This study is part of a long-term project that has been on-going since June 2011, and therefore will incorporate the behavioural and tracking data of all lorises tracked since the start of the project:– 3 adult females, 1 adult male and 2 juveniles.

Individual	Shift type	Follow dates
Boss		25/09/2013-21/03/2016
Bulu	3 hour (18:00-21:00, 21:00-00:00, 00:00-03:00, 03:00-06:00)	30/06/2014-06/12/2014
Dahi	6 hour (18:00-00:00/00:00-06:00)	01/04/2015-17/07/2015
Cowo	6 hour (18:00-00:00/00:00-06:00)	28/03/2015-15/05/2015
Gadis	6 hour (18:00-00:00/00:00-06:00)	30/01/2016-Present
Gebu	6 hour (18:00-00:00/00:00-06:00)	16/02/2016-Present

Table 2. The length of nocturnal shift observations (Including the start and end times) and the start and end dates of the period each Philippine slow loris (*Nycticebus menagensis*) was followed for at DGFC.

Animals were located by the signal emitted from each collar using a VHF antenna (RA-23K VHF Antenna, Telonics, BioTrack,UK) and receiver (R100 Telonics, BioTrack, UK).

Each collar emits a signal at a specific frequency that can be picked up by the receiver and tracked using the antenna. The signal becomes progressively

louder with increased proximity and responds to the directional bearing of the antenna (indicating in which direction the collar should be found).

The lorises were located during the day to identify the sleeping sites selected. Sleeping sites were found on a daily basis and trees were marked as a GPS location (GPS map 62, GARMIN, Hampshire, UK) using an identification code (e.g. LS 001, LS 002 etc.). Sleeping sites were identified to an individual tree by using a method of triangulation, a common method in wildlife tracking used to find point locations of individuals (Haskell & Ballard, 2007). Biodegradable flagging tape was attached to the tree for future recognition with a tag displaying the tree's identification code. If the loris had returned to a previously used sleeping tree, the tree identification code was recorded.

Tracking also took place throughout the night to record the animal's behaviour and movements. Data were collected in either 3 hour (18:00-21:00, 21:00-00:00, 00:00-03:00, 03:00-06:00) or 6 hour (18:00-00:00, 00:00-06:00) periods depending on the year of data collection, as shift length was increased to 6 hours in 2015 in order to increase data volume and the validity of continuous behavioural observations. Data were collected on consecutive nights where possible to try and eliminate environmental variables that may cause changes in behaviour over different nights. GPS location and behavioural observations were recorded at 15 minute intervals. General behaviour was recorded in several categories – moving, resting, grooming, feeding, vigilant or out of view. Subcategories were then recorded depending on the general behaviour seen e.g. moving was split into low, medium or high canopy levels. Other data that was collected included weather, presence of a conspecific, height, etc. Slow lorises were spotted with white light due to their reflective eye shine, when following the individual red light filters were applied to head torches to cause as little disturbance as possible and eliminate the possibility of torch-shyness (Nekaris *et al*, 2008).

Statistical Analysis

All statistical analyses were carried out using the statistical software R (version 3.2.2, R Core Development Team 2016). Significance was accepted at a level of 0.05. Point and polygon maps were created using QGIS 2.14.3 (QGIS Development Team, 2016). GPS co-ordinate locations were recorded every 15 minutes during night observations, these were inputted into QGIS and nocturnal home ranges calculated for each individual.

The `adehabitatHR` package was used in the R statistical program to calculate home range variables such as total distance travelled and step length. The `lme` package was also downloaded and used in the R statistical program to enable the use of linear mixed effects models. Mixed effects linear models were used to examine the significance of environmental variables rainfall, moon luminosity and cloud cover on the behaviour and movement observation data at a significance level of 0.05. Mixed effects models were used to ensure that multiple data entries per individual were accounted for.

Luminosity proportions were found using timeanddate.com according to the date each shift was conducted. Rainfall data (mm) was taken from the records collected between 2012 and 2016 and cloud cover taken from observational records.

Results

The average distance travelled by each slow loris throughout a whole night shift was 1113.365m. During the early shift (1800-0000) the average movement distance was 595.968m (± 34.557 m), and in the late shift (0000-0600) 538.550m (± 32.746 m). Figure 2 shows the distribution and overlap of nocturnal movement ranges between the sample of individuals used in the study. There was no significant difference in the distances travelled in the early shift compared to the late shift ($p > 0.05$).

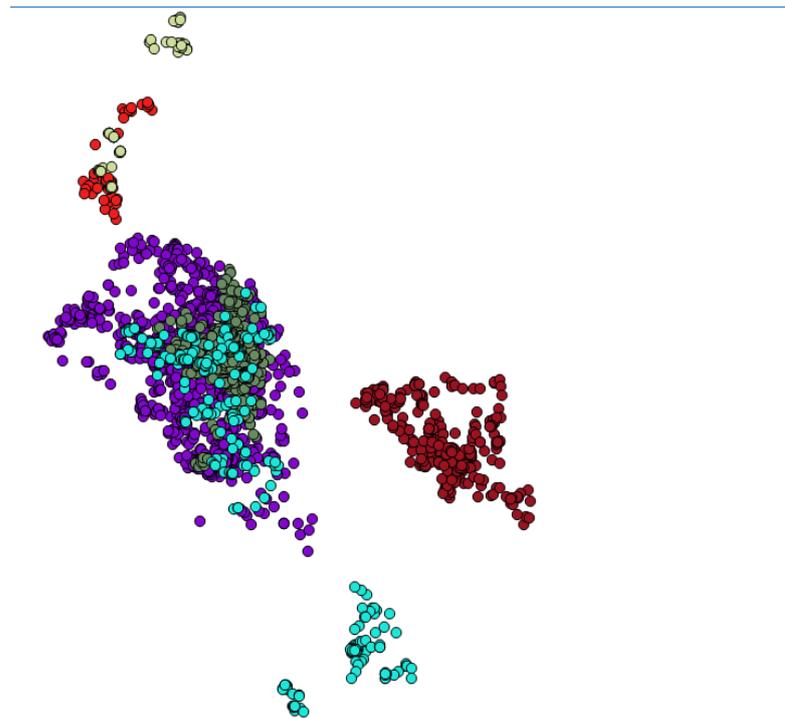


Figure 2. Point map created in QGIS of the spatial distribution of the Philippine slow loris (*Nycticebus menagensis*) in Malaysian Borneo. GPS coordinates of the individual's location were recorded every 15 minutes and plotted with a different colour for each individual.

Figure 3 shows the alterations in moon luminosity values throughout the dates in which individuals were tracked and followed. When compared with figure 3 it is possible to visualise the changes in average height occupied by individuals during these periods. Although average height was found to be insignificant when tested in a mixed effects model ($p > 0.05$) it is possible to ascertain from Figure 4 that some pattern may be present involving luminosity and height as a large amount of fluctuation occurs. It is possible that this may be due to the presence of environmental variables such as seasonality, rainfall, cloud cover and temperature and potential interactions.

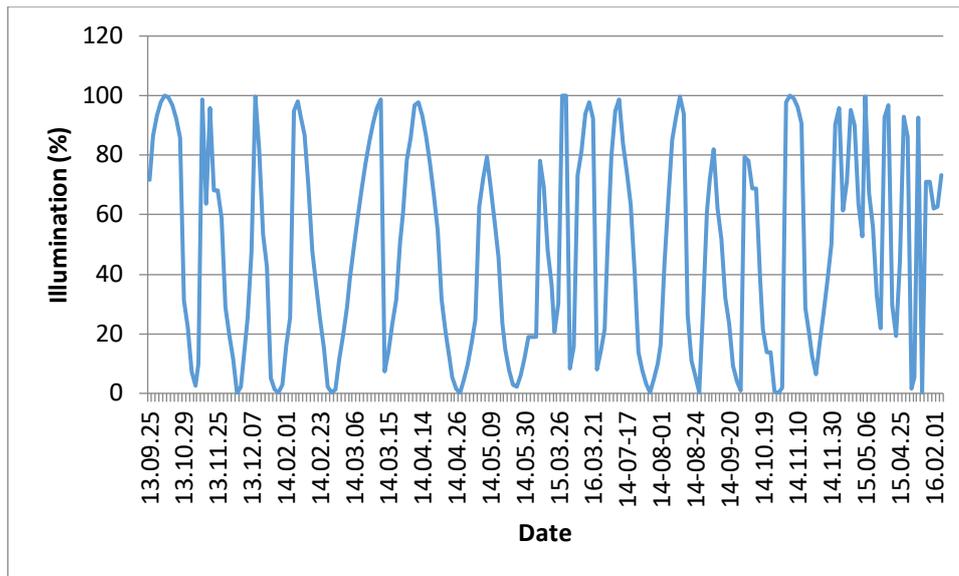


Figure 3. The percentage of moon luminosity throughout the time period in which following and tracking of the Philippine slow loris (*Nycticebus menagensis*) in Malaysian Borneo.

Illumination was found to have no significant effect on the total distance travelled, the amount of time spent moving and average height occupied by Philippine slow lorises when tested using the mixed effects model ($p > 0.05$). There was also no significant effect on the average height occupied by individuals when a log transformation was used on the data.

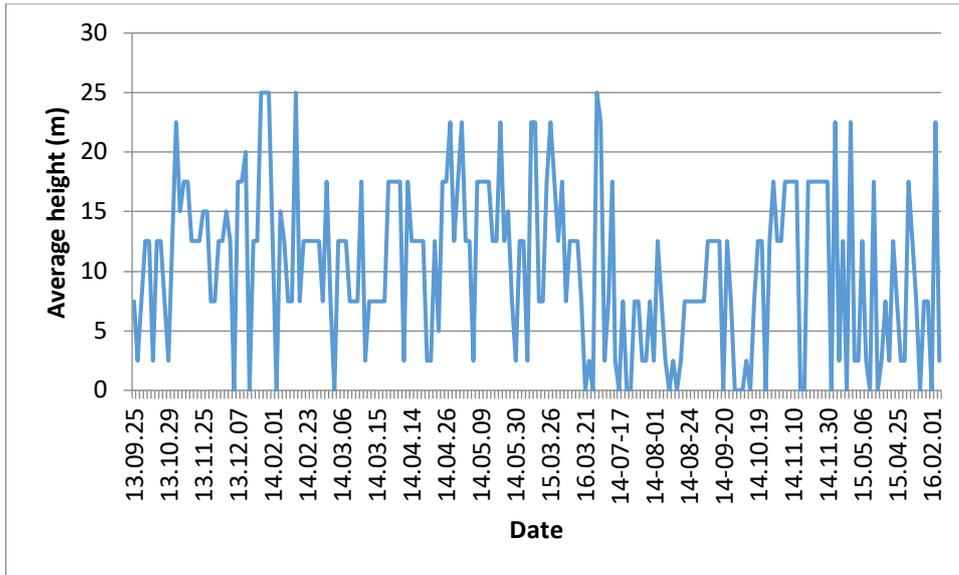


Figure 4. Variation in the average height occupied by the Philippine slow loris (*Nycticebus menagensis*) in Malaysian Borneo during the 6 hour tracking shifts following individuals at night, arranged chronologically by tracking date.

Moon category	Average height (m)					
	0-5	5-10	10-15	15-20	20-25	25+
1	8	13	22	11	4	3
2	4	6	9	4	1	1
3	2	3	6	5	1	
4	7	9	9	4	3	1
5	10	11	14	12	2	

Table 3. A count of the average height the Philippine slow loris (*Nycticebus menagensis*) would occupy at differing intensities of moon illumination. Illumination percentage was condensed into the following categories: 0-20% = 1, 21-40% = 2, 41-60% = 3, 61-80% = 4, 81-100% = 5.

Moon category was calculated according to illumination percentage – 0-20% = 1, 21-40% = 2, 41-60% = 3, 61-80% = 4, 81-100% = 5. The most common heights occupied when illumination categories were recorded as 1, 2, 3 and 5 was 10-15m. At an illumination category of 4 the most common heights were 5-10m and 10-15m. Individuals spent the least amount of time at heights of >20m.

Cloud cover was also estimated through observational data recorded in the field and tested against illumination to investigate if the presence of cloud obscured the illumination data and therefore skewed results, however cloud cover was found to be an insignificant environmental variable when tested against illumination and movement ($p>0.05$).

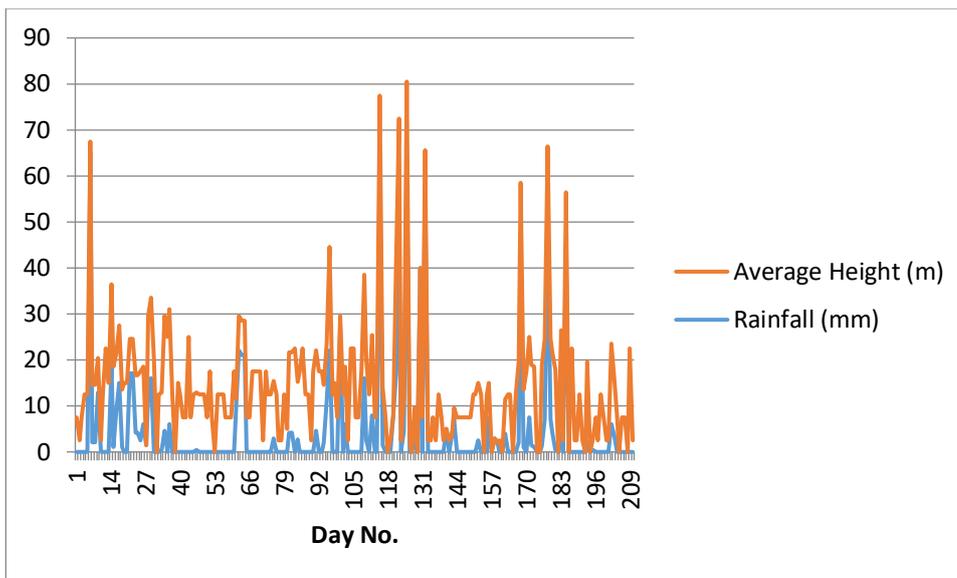


Figure 5. The effect of rainfall (mm) on the average height occupied by the Philippine slow loris (*Nycticebus menagensis*) in Malaysian Borneo.

No significant effect was found to exist between rainfall and total distance travelled during each shift ($p>0.05$). However, from the scatter plots created it is possible to visualise some potential correlational patterns. As seen in Figure 7 the pattern of the scatter graph line tends to show that up to a daily rainfall level of 25mm total distance doesn't seem to be affected. As rainfall level rises

above 25mm the total distance travelled tends to decrease steadily. The longest distance travelled was 930.5948m and was done during periods of low rainfall – the shortest distance of 32.769m was done during periods of high rainfall. However, when tested against movement (the proportion of time spent moving throughout each shift) using a mixed effects model rainfall was found to have a significant effect ($p < 0.05$) on the proportion of time spent moving during a nocturnal shift. This is seen in Figure 5 as the correlation follows the pattern of increasing rainfall leading to a decrease in the time spent moving.

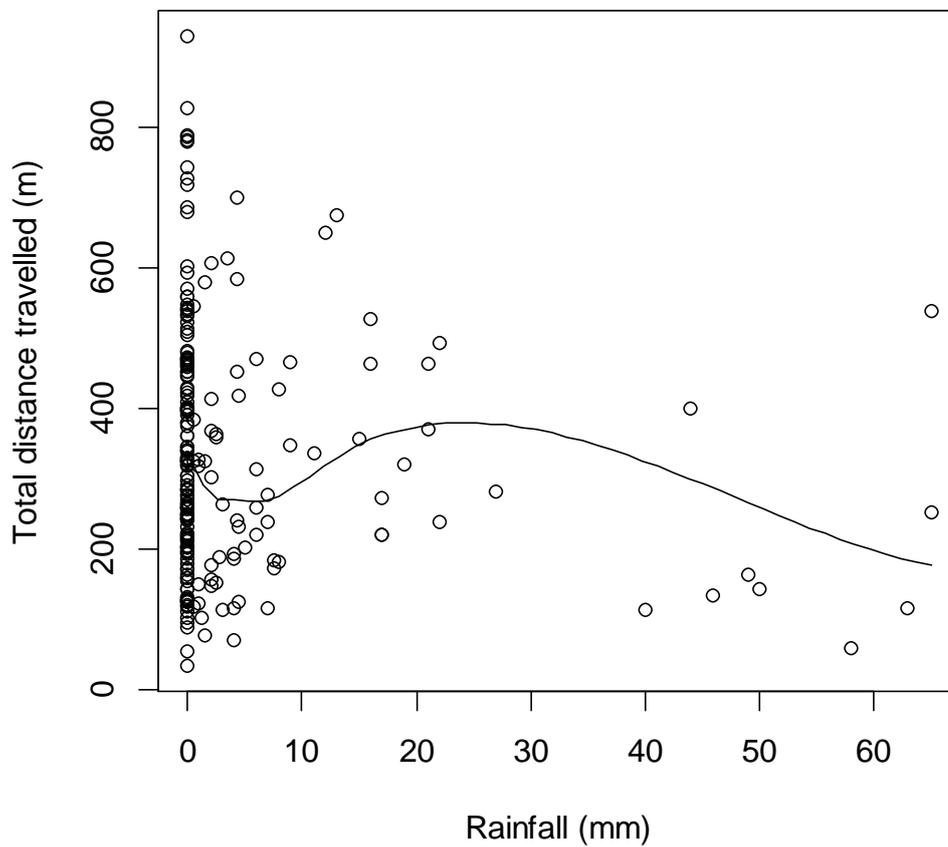


Figure 6. The effect of rainfall (mm) on the total distance travelled by a Philippine slow loris (*Nycticebus menagensis*) throughout a night shift in Malaysian Borneo.

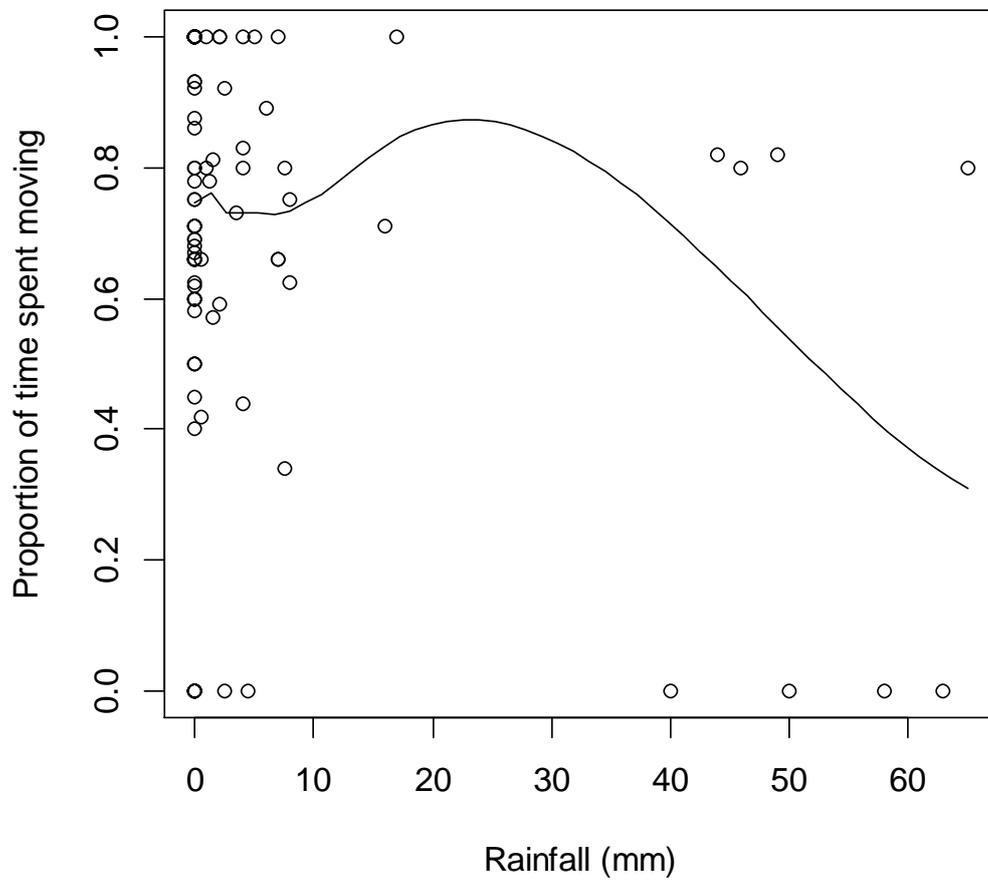


Figure 7. The significant effect rainfall has on the nocturnal movement budgets of the Philippine slow loris (*Nycticebus menagensis*).

Discussion

Illumination was shown to have no significant effect on the nocturnal movements or behaviour of slow lorises within Eastern Sabah, a result that concurs with research conducted by Bearder *et al* (2001). It was found that members of the family Lorisidae were found to exhibit no change in behaviour or activity in a comparison between full moon and new moon nights. It is possible that slow lorises are therefore exhibiting lunar neutrality as a survival strategy in itself – as both lunar philic and lunar phobic can provide negative impact on the survival success of the species. Previously, lunar responses have been attributed to antipredation strategies and the cost-benefit tradeoffs associated with foraging efficiency and predation risk. This study is consistent with these findings and supports the theory that there is great variation in the range of lunar responses exhibited by nocturnal primate species. As species within families such as Tarsiidae, Galagidae and Lemuridae have exhibited increases in activity according to altering levels of illumination (Bearder *et al*, 2006), it is important to understand the morphological and behavioural differences between these species and their relatives within the Lorisidae family. *N. menagensis* possesses extraordinary morphological adaptations to reduce the risk of predation as well as to increase the risk of survival if encountered by predators. Slow lorises face threat from predators on the ground (cats, civets), within the canopy (snakes) and from the skies (birds of prey) (Starr *et al*, 2012). *N. menagensis* can only be distinguished from other slow loris species genetically, or from fur markings on the head (Nekaris *et al*, 2008). They possess multiple morphological adaptations, including these fur and facial markings which aid a form of Mullerian mimicry as a method of predatory defence (Nekaris *et al*, 2013). *Nycticebus* spp. display remarkable morphological similarity to the spectacled cobra (*Naja naja*) with the facial markings resembling the eyespots and stripes of the cobra, increasing the likelihood that the slow loris will be mistaken for a more toxic model (Nekaris *et al*, 2013). Moreover, adaptations of postcranial anatomy allow them to remain completely still when they feel they are under threat from potential predators (Nekaris *et al*, 2013). These adaptations, together with the

evolution of slow loris venom (a brachial exudate that when combined with saliva becomes a toxic substance) and the toothcomb used to inject the secretions (Hagey *et al*, 2007) provide *N. menagensis* with an accomplished set of adaptations to maximise the success of survival when encountered by a predator. This may decrease the threat that brighter nights can pose with increased predator detection and the availability of defence mechanisms to aid the prevention of detection by predators, therefore decreasing the need to be lunar phobic.

Starr *et al* (2012) found that there may be an interaction between the lower temperatures experienced during brighter nights and the number of active behaviours observed. In the pygmy loris (*N. pygmaeus*) fewer active behaviours were observed during brighter nights when temperatures were lower, thought to be a method of minimising heat loss (Starr *et al*, 2012). This may act as a potential motive for nocturnal primates to exhibit lunar phobia due to the potential heat loss that can be caused by clear, bright nights. Therefore, it is metabolically wise to minimise heat loss in order to conserve energy and reduce the amount of time necessary to forage on clear nights when predation is more likely. This response may also apply to species of African nocturnal primates such as the Southern Lesser Galago (*Galago moholi*) with regards to their lunar philic behaviour. Bearder *et al* (2002) found that *G. moholi* increased their activity during brighter nights, a response that may be attributed to warmer temperatures. When temperatures are higher, the animal is at less risk of losing body heat and therefore will not have the need to conserve energy by restricting movement. Previous research has also shown temperature to have an effect on reducing the activity on even lunar philic loris species in spite of potentially helpful illumination levels (Fernandez-Duque, 2003). Foraging success also provides an alternative reason for lorises not exhibiting lunar philic behaviour – there may be potential higher prey availability during moonlit or dark nights (Rode-Morgano & Nekaris, 2014).

Rainfall was found to have a significant effect on the amount of time spent moving during nocturnal shifts by *N. menagensis*, with individuals spending

significantly more time moving during drier periods. Seasonality has previously been researched with regards to changes in luminosity and loris behaviour - Starr *et al* (2012) suggested that lorises may exhibit a lunar phobic response to moonlight as a result of seasonality and that individuals are more likely to increase their activity when temperatures are higher during the wet season due to the denser rainforest vegetation providing more efficient cover. Research has also found that slow lorises are known to become more active during periods of higher humidity (occurring predominantly during the wet season) due to a higher availability of arthropod prey (Rode-Morgano & Nekaris, 2014). This has been attributed to slow lorises conducting more active foraging when humidity is higher as insects are more likely to be flying a lower height (Rode-Morgano & Nekaris, 2014). However, this opposes the theory of lower temperatures decreasing the movement of slow lorises due to the need to conserve energy. The interaction of environmental and biological factors during nocturnal periods mean it is difficult for slow lorises to show a lunar philic or phobic response without a negative consequence occurring on energy conservation or potentially inferring an advantage for lunar neutrality amongst the species. Although the interaction between rainfall and height was found to be insignificant, as seen in Figure 5 increased rainfall tended to lead to a decrease in the average height occupied by *N. menagensis*. It is possible that this correlation could link with increased humidity and the increased presence of arthropod prey flying lower throughout the canopy, therefore increasing the foraging efficiency of the slow loris. Starr *et al* (2012) also agreed that a higher proportion of movement is more likely during the wet season, concurring that climatic changes are influential in the movements and behaviours of slow lorises, in spite of changes in moon luminosity. As slow lorises seem to favour the environmental conditions of the wet season, unfavourable conditions occur in the dry season when there is less rain to support tropical vegetation and invertebrates so prey availability will decrease and lorises may be forced to reduce their activity levels and conserve energy in response (Starr *et al*, 2012). Total distance travelled by individuals when tested against rainfall was also found to be insignificant, however as seen in Figure 6 the general trend shows a reduction in the distance travelled (m) with lower amounts of rainfall.

Although this may indicate lower activity levels, it may infer that due to increased foraging efficiency and a higher presence of arthropod prey lorises do not have to travel such long distances in order to find prey. Furthermore, Prugh & Golden (2014) found that although there are conditions in which nocturnal primates may exhibit a certain amount of lunar philia or phobia according to environmental circumstances, the net effect of illumination may increase predation risk.

The incredible visual acuity possessed by *N. menagensis* and other nocturnal primate species undoubtedly assists individuals in the capture of prey and increases foraging efficiency during bright nights (Gursky, 2003). Gursky (2003) also found that the benefits of foraging are dramatically increased during periods of high luminosity. This would indicate that these nocturnal mammal species would benefit from exhibiting lunar philia and increasing their activity levels rather than exhibiting lunar neutral behaviour. Therefore, it is interesting that *N. menagensis* do not take advantage of increasing light conditions and their visual acuity to maximise foraging efficiency and prey capture rates. It is important for future research to look further into the tradeoffs occurring between foraging and predation and the interactions this involves with co-variables such as moonlight and visual acuity.

It is also possible that lorises exhibit lunar neutrality due to the likelihood of being predated on by species that rely on other senses to predate. The only two confirmed predation events within the study have involved pythons (shall I include this?). Pythons are known to rely predominantly on heat and taste sensations to locate and kill prey, indicating that the presence or absence of light may not be as important for predation activity. This has been documented as Fredriksson (2005) states that reticulated pythons (*Python reticulatus*) possess infrared-sensitive labial pits in order to locate prey, an adaptation that can be used effectively in periods of darkness. They are also known to be less active during the day (Fredriksson, 2005), increasing the likelihood of predation occurring on nocturnal prey species such as *N. menagensis*. It is possible that due to the predation adaptations of *P. reticulatus* and the ability to detect prey in darkness climatic factors such as

temperature and rainfall may be more important in avoiding predation. Comparatively little research has been undertaken into the predation pressures on *N. menagensis* so this may be an implication for further research in order to understand their behaviour and movement patterns more comprehensively.

It is known that studying nocturnal primate species in the field is a difficult and time-consuming procedure in order to gain insightful and valid conclusions. Although this study was conducted over a relatively short period of time, it can provide useful and relevant information into how the species responds to environmental changes in terms of their movement patterns and behaviour. Research is scarce in the field of nocturnal primates exhibiting lunar neutrality, with the majority of published research focusing on the lunar philic or phobic nature of nocturnal primate species. insignificant effect of moonlight on movement increases the likelihood that slow lorises respond to high levels of illumination with lunar neutrality and although this may seem like a lack of a result, it is highly possible that they are responding like this as a survival and anti-predation strategy in itself. This study has shown how climatic factors such as rainfall and humidity can have a significant effect on the foraging efficiency and movements of slow lorises, providing an insight into the environments and habitats in which they are most likely to exhibit survival success and thriving populations. This study was limited due to a small sample size of six individuals and therefore a longer study with a larger sample size could provide a more accurate representation of the effects of climate and moonlight on populations as a whole. Research into how these variables affect lorises in different habitat locations with differing climates and vegetation is also crucial in determining how the external environment affects the behaviour and movement of loris species. It is hoped that by continuing to conduct efficient and focused research we will begin to broaden our knowledge on nocturnal primate behaviour in the future.

Conclusions

Although no effect of illumination was found in relation to behaviour and nocturnal movements, it raises the question of how lunar neutrality is used as a strategy to increase survival fitness in terms of foraging efficiency and predator avoidance. Further research should be conducted into climatic variables such as temperature and rainfall to determine the effects of these on behaviour and movement to be applied to populations as a whole. The broadening of knowledge on this species as well as other slow loris species can also be considered crucial in widening awareness of nocturnal primates and their needs to survive and thrive in captivity as well as in their natural habitat.

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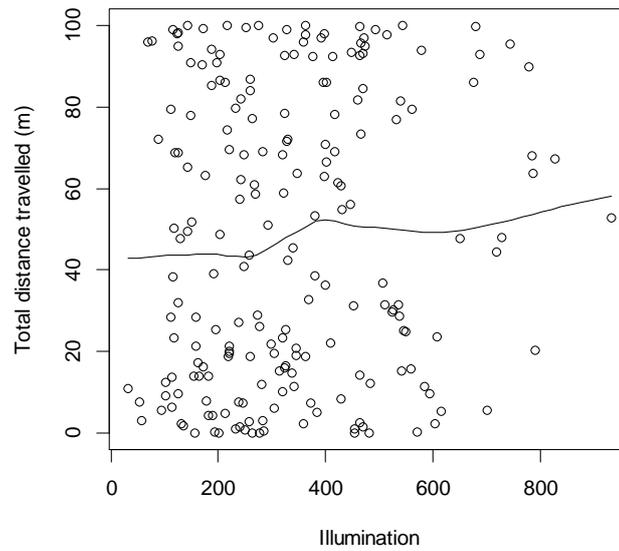
QGIS Development Team. 2016. QGIS Geographic Information System. Open Source Geospatial Foundation Project. URL <http://www.qgis.org/>

Appendices

Appendix 1

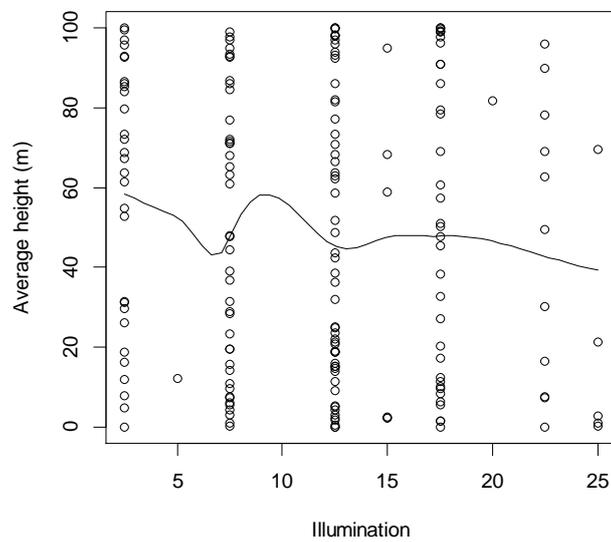
Shows interaction between illumination and total distance travelled through a scatter plot with attributed smooth line.

T value = 0.612055 p value = 0.5412



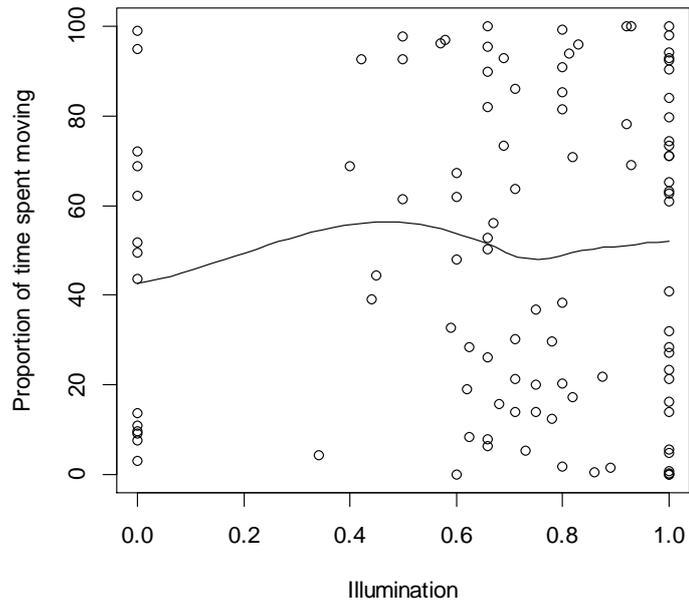
Shows interaction between illumination and average height occupied through scatter plot with attributed smooth line.

T value = -1.269004 p value = 0.2061



Shows interaction between illumination and proportion of time spent moving through scatter plot with attributed smooth line.

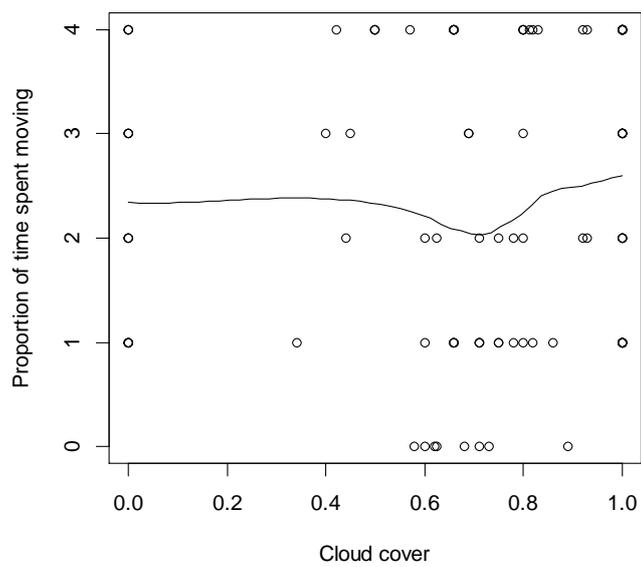
T value = 0.585698 p value = 0.5594



Appendix 2

Shows interaction between cloud cover and proportion of time spent moving through a scatter plot with attributed smooth line.

T value = 0.52417 p value = 0.6014



Appendix 3

Shows interaction between rainfall and total distance travelled through a scatter plot with attributed smooth line.

T value = -1.060413 p value = 0.2902

