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To Huddle or Not to Huddle: That is the Question. A Brief Study of the Basis for Huddling Behavior in Eulemur rubriventer

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A brief study of the basis for huddling behavior in *Eulemur rubriventer*

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ABSTRACT

Common behaviors observed in primates may have important biological and social foundations. This study looks at huddling behavior in several groups of *Eulemur rubriventer* in Ranomafana National Park, Madagascar, in order to compare the functions of huddling in relation to thermoregulation and social bonding. The proportions of time spent huddling as functions of rainfall and ambient temperature were used to explore the possibility of huddling as a means of thermoregulation. A positive relationship between loose huddling behavior and temperature was deemed significant. Data collected on proximity of individuals to each other (nearest neighbor) was able to establish a significant correlation between preferred partners in huddling compared with other activities. It is therefore unclear which function has greater influence on huddling behavior. However, behavioral adjustments in relation to changing conditions may be a very important attribute for the survival of primates and other species as the environment changes.

INTRODUCTION

The aim of this study was to investigate the causes of huddling behavior in *Eulemur rubriventer* (Red-bellied lemur). Two possibilities were analyzed: behavioral/social thermoregulation and social bonding. Huddling behavior has been studied in a variety of primates, as well as other mammals and birds (Gilbert *et al.* 2010; Gilbert *et al.* 2007; Ostner 2002). For purposes of this study, huddling is characterized as "an active and close aggregation of animals," as defined by Gilbert *et al*. (2010).

Thermoregulation

Social thermoregulation is an energy saving strategy for endothermic species. By increasing ambient temperature surrounding the group, each individual can lower its metabolic rate and achieve benefits in terms of survival, food and water needs, and reduced heat loss. This conserved energy can then be reallocated to other processes such as reproduction. The amount of energetic savings varies greatly between mammalian species from 8% up to 53%, as reported by Gilbert *et al. (*2010). Variables often involved in this include the size of individuals, group size, position within the huddle, and range of site specific temperature fluctuation.

Decreasing ambient temperature has been shown to increase occurrence of huddling in endothermic species such as emperor penguins (Gilbert *et al.* 2007). Social thermoregulation has been adopted by lemur species to deal with temperature-related stress. A study by Ostner (2002) on *Eulemur fulvus rufus* found that colder ambient temperatures decreased individual activity and increased participation in huddles. No studies have been done on this specific behavior in *Eulemur rubriventer*.

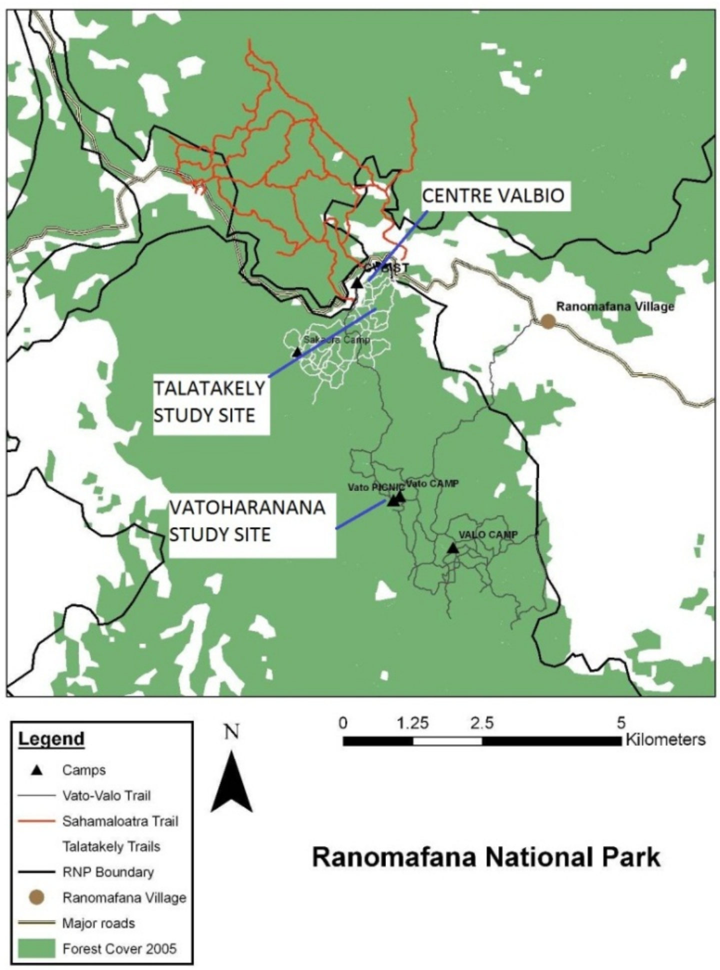
Sociality

There are likely social benefits from close group activities such as huddling, such as strengthening pair and familial bonds within a group. Grooming other individuals is an important life history characteristic of many primate species and may occur concurrently with huddling (Lewis 2010). In many frugivorous primate species, close social interactions are very important to maintain social structures (Muller and Soligo 2005). Shaffer (2012) found that huddling behavior can be almost entirely social in another primate, *Chriopotes sagulatus* (Northern Bearded Sakis); and resting was a wholly separate activity. Huddling occurred almost exclusively between males. This supports the possibility of strictly social causes of this behavior in certain species of primates.

STUDY SITE

Ranomafana National Park (RNP) is located in the eastern rainforest of Madagascar (between E 47°18' and E 47°37' longitude and between S 21°02' and S 22°25'in latitude) (MNP 2009). The 43,549 hectare park was created in 1991 and is managed by Madagascar National Parks (MNP). Located near the eastern entrance to the park is Le Centre Pour la Valorisation de la Biodiversité (Centre ValBio), an international research station that facilitates research within the park. To date, Ranomafana is home to 13 different species of lemurs, eight of which have been subjects of long-term studies in the park (Wright et al. 2012). Two research sites associated with Centre ValBio were used in this study: Talatakely and Vatoharanana (See Map 1). The Talatakely site is secondary disturbed forest due to selective logging between 1986 and 1989, as well as comparatively high tourist density. The Vatoharanana site is still considered undisturbed primary habitat despite the presence of numerous trails and some cattle grazing (Herrera *et al.* 2011).

Rainfall in Ranomafana ranges from approximately 1,600 to 4,017mm annually (Wright *et al*. 2011). The majority of this occurs during the cyclone season between December and March. These months also have the highest temperatures (30-32 °C). Average temperature in the dry season, which lasts from June through September, ranges from 4 to 12°C. Average rainfall for the study period was 20.86 mm. Average temperature was 22.7 °C.



Map 1: Ranomafana National Park showing the two sites of this study, Talatakely and Vatoharanana, as well as the study base, Centre ValBio.

SPECIES PROFILE

Eulemur rubriventer was first documented in 1850 by I. Geoffroy. Currently, their range encompasses the eastern rainforest of the Tsaratanana Massif down to the Pic d'Ivobe and the Manampatrana River (Irwin *et al.* 2005). It has been listed as "Vulnerable" on the IUCN Red List since 1990 (IUCN 2012). The population density of *E. rubriventer* in Ranomafana is most recently estimated at 8.63 individuals per km^2 for Talatakely and 13.45 individuals per km^2 for Vatoharanana (Herrera 2012 unpublished data).

This species has been documented as a cathemeral species; it is active periodically throughout a 24-hour cycle (Overdorff, 1988). It is mainly frugivorous, although it also feeds on flowers, nectar, leaves, fungi and occasionally invertebrates (Mittermeier *et al.* 2010). This lemur species forms pair-bonds, and therefore groups are relatively small, usually between 2 and 10 individuals. Groups are comprised of an adult female, adult male, and their offspring (Mittermeier *et al.* 2010). Like other lemur species, males and females do not vary significantly in size. Adults range between 78 cm and 93 cm in total length and weigh from 1.6 kg up to 2.4 kg (Mittermeier *et al.* 2010). However, males and females do exhibit dichromatic pelage. Both have a dark brown ventral side and a dark tail, but they differ in dorsal coloration. Males have a slightly redder brown dorsal side, and females have a light cream dorsal coloration. Males also display distinctive patches of white skin below the eyes and extending to the muzzle.

MATERIALS & METHODS

This study was designed to investigate two hypotheses concerning *E. rubriventer*. The first hypothesis was that huddling functions as a thermoregulatory behavior. The following predictions were established in order to test for support for this hypothesis:

1. The proportion of time an individual spends huddling will increase as ambient temperature decreases.
2. The proportion of time an individual spends huddling will increase with increasing rainfall.
3. The proportion of time an individual spends huddling will be lower for large individuals (i.e. adults) and higher for smaller individuals (i.e. juveniles).

The second hypothesis was that huddling is a social behavior that builds and strengthens bonds between individuals in a given group. The associated predictions are the following:

1. The proportion of time spent huddling does not change as a function of ambient temperatures.
2. The proportion of time spent huddling does not change as a function of differences in rainfall.
3. The proportion of time spent huddling does not differ between adults and juveniles.
4. A positive relationship exists between the proportion of time spent huddling with a particular nearest neighbor and the proportion of time spent with the same individual in other activities.

For this study, ten minute periods were chosen, during which a focal animal was followed continuously. The Instantaneous Focal-Animal Sampling method was used to make behavioral observations at 60 second intervals during each period (Altmann 1974). The focal animal was rotated after each period. If an individual in the focal order was absent for more than five minutes, the next animal became the focal. When the missing animal reappeared, it became the next focal in order to achieve equal observation time for each lemur.

The behavior categories for the instantaneous observations were traveling, feeding, resting, and out of sight (see Ethogram below). For feeding, the tree species was recorded as well as the part of the tree being consumed. This was categorized as fruit, flower/nectar, young leaves, or mature leaves. Resting included any behavior for which the animal was stationary at the time of observation. Self-grooming and grooming of other individuals was recorded under this category. Any huddling behavior was noted in additional detail including: which individuals were huddling, what order they were in if greater than two individuals and whether they were 'tight' or 'loose' (See Ethogram).

Ethogram:

- Travel: Any movement from one place to another at time of observation; excludes movement while foraging
- Feeding: Actively consuming or foraging for food-fruit, nectar, leaves etc.
- Resting: Any mostly stationary behavior. Includes but not limited to:
    - Grooming: cleaning of pelage- self or of others
    - Huddling: characterized as "an active and close aggregation of animals"(Gilbert *et al.* 2010)
        - Tight huddle: No spaces between individuals, often tails wrapped around each other
        - Loose huddle: Resting together, some spaces, tails uncurled, sometimes grooming selves or others
    - Alone: Resting alone; includes upright/open and balled/tight postures
- Out of Sight: unable to see focal animal due to travel, vegetation, conditions etc.

Other data collected for each ten minute period included: nearest individual(s) to the focal lemur, over story versus understory, canopy cover, and weather conditions. For nearest individual(s), the distance was recorded in ranges of 0 meters, ≤1 meter, ≤10 meters, ≥10 meters, and out of sight if no other lemurs were visible. Over-story is defined here as the highest level of tree canopy, and understory is anywhere from the ground up to that canopy. Canopy cover was evaluated as open, closed, or shade. Open is in full sun, closed indicates that no sunlight gets through, and shade falls in between the other two categories. Weather was categorized as sunny (0% ≤ sky < 50% clouds), partly cloudy (50% ≤ sky < 100% clouds), or cloudy (100% clouds). Presence of rain was also recorded, along with intensity. For the Talatakely site, temperature and rainfall data was collected by the Centre ValBio Weather Station at approximately 5:00 am each day. For the Vatoharanana field site, temperature was measured by a min/max thermometer placed in the shade. Rainfall was measured by a rain gauge mounted approximately 1 meter above the ground in an area with minimal canopy cover. Both were recorded daily at approximately 6:30 am and 7:00 pm.

In total, five distinct *E. rubriventer* groups were followed for two days each of data collection between November 8th, 2012 and November 24th, 2012 (See Table 1). Three groups were followed at the Vatoharanana site, including: Vato Group 3 (V3), Vato Group 7 (V7), and the newly discovered Vato Group 11 (V11). At the Talatakely site, Tala Group 4 (T4) and Tala Group 5 (T5) were studied. Group identification numbers were established by previous studies and have been retained for consistency and future comparison. Searching for groups began at approximately 7am for Vato and 8am for Tala. Once found (earliest time 7:45; latest time

12:30), groups were followed until either dark, or until lost out of sight. This averaged approximately 9 hours of group observation per day.

The lemur groups chosen for this study were semi-habituated by previous research studies and tourism in the park (Herrera *et al.*2011; Overdorff 1988; Tecot 2008; Wright *et al.* 2012). Following the example of the current *E. rubriventer* study being conducted by Rachel Jacobs no invasive measurements were taken during the study, nor were any animals captured or collared (Pers. Comm. November 2012). Therefore, Malagasy guides or research technicians were essential in finding the lemur groups on a daily basis. Some variation in data collected may be attributed to the difficulty of finding and following the study animals.

Thanks to previous and on-going study of the *E. rubriventer* groups in Ranomafana, most groups and individual lemurs can be identified based on a combination of distinctive features (Rachel Jacobs Pers. Comm. November 2012). This made following a focal individual viable for this study. Groups V3 and V11 had the same composition and similar markings, but identity was confirmed for each observation day by expert technicians from the Jacobs study. All other groups were easily distinguished by unique markings and group compositions.

Eulemur rubriventer Group	Individuals
Vato Group 3	Adult Male
	Adult Female
	Infant (not included in analyses)
Vato Group 7	Adult Male
	Adult Female
	Juvenile Female (2+ years)
	Juvenile Male (1 year)
Vato Group 11	Adult Male
	Adult Female
	Infant (not included in analyses)
Tala Group 4	Adult Male
	Adult Female
	Juvenile Female (1 year, twin)
	Juvenile Female (1 year, twin)
Tala Group 5	Adult Male
	Adult Female
	Juvenile Female (1 year)

Table 1: Individuals of *E. rubriventer* study groups. Each group was followed for two days.

RESULTS

Based on observation during this study, *Eulemur rubriventer* spent a majority of the day resting (combined average 56%). The remainder of the daytime is spent feeding or traveling between feeding and resting trees (See Figure 1). For each group, the average time spent huddling was 57.76% of the total proportion of time spent resting (min: 27.69%; max: 85.90%), and 29.29% of observed daily activity (See Figure 2).

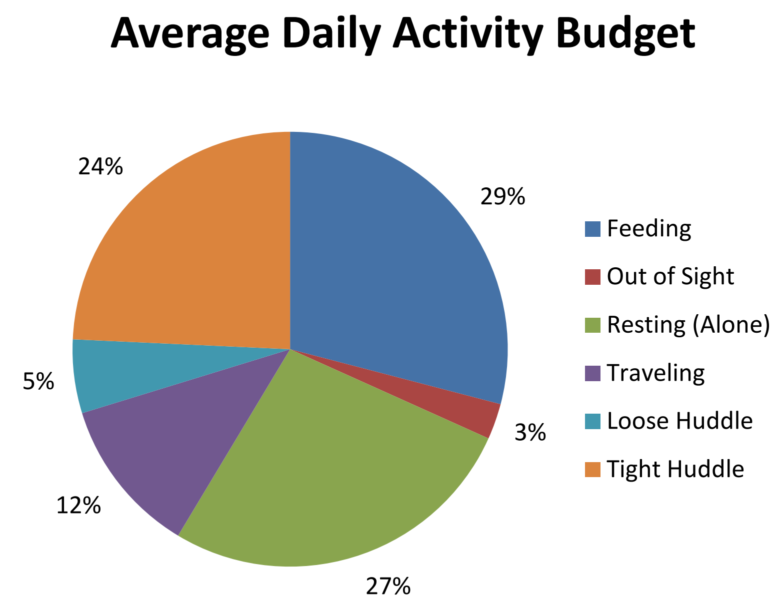


Figure 1: Proportion of time spent on each activity, averaged for all days of observation and all individuals.

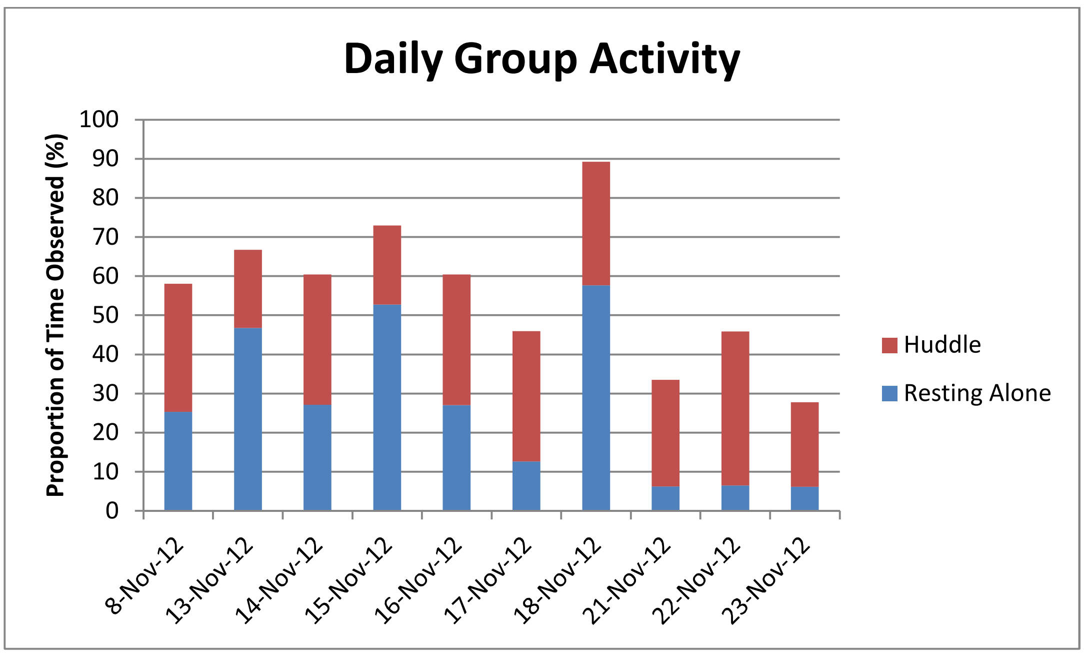


Figure 2: Bars show proportion of total time observed that members of each group (total of all individuals) spent resting each day. Red sections show the proportion of resting time spent huddling, loose and tight included. Blue sections show the proportion of resting time spent alone.

For analysis, the proportions of time spent in each activity were calculated for each individual and separated by day. This resulted in 30 total observations. Data was analyzed using SPSS Statistics 17. A p-value ≤0.05 is used here as the determination of significance.

Rainfall and temperature were compared for each day of behavioral data collection (Figure 3). A Spearman's rho test revealed that these variables are slightly but not significantly negatively correlated (r_s=-0.068, p=0.426). Average rainfall for the study period was 20.86 mm (min=0mm; max=150mm). Average temperature was 22.7 °C (min=18.5 °C; max=26 °C).

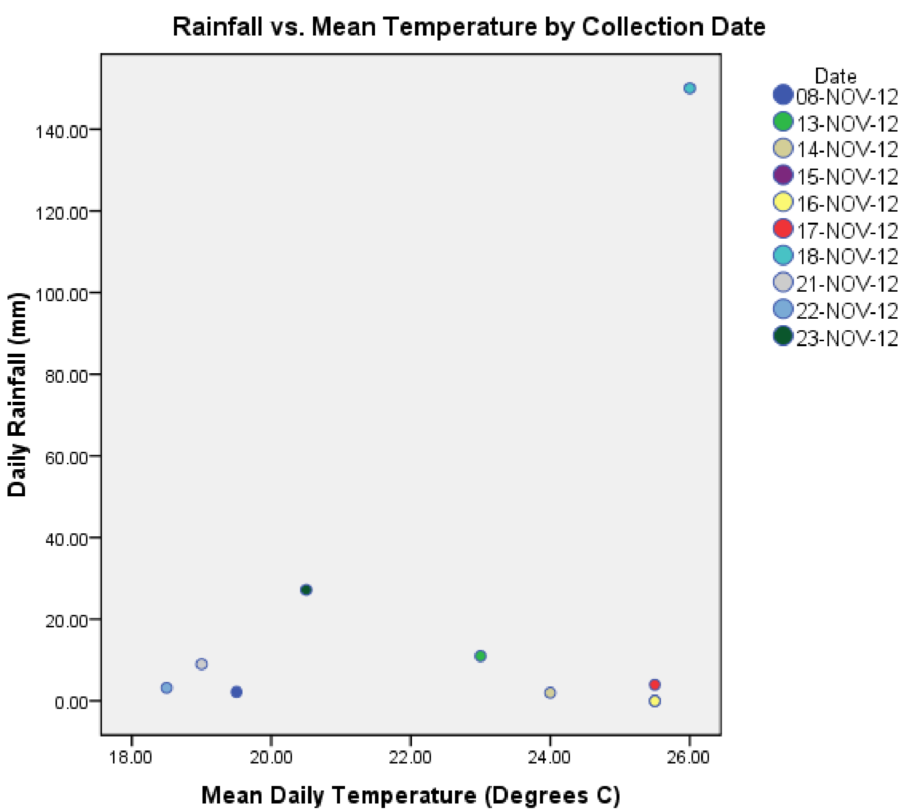


Figure 3: Comparison of rainfall and temperature data for observation days. Measurements on November 8th, 21st, 22nd, and 23rd were at the Talatakely site. The remaining dates, November 13th through the 18th were at the Vatoharanana site. Spearman's rho test results: r_s=-0.068, p=0.426, N=10.

Hypothesis 1: Thermoregulation

To test the first hypothesis that huddling functions as a way of regulating individual body temperature, a Spearman's rho test was used to check for correlation, including the magnitude and direction of correlation.

Temperature

First, the proportion of time spent huddling (both tight and loose huddle combined) was compared to the daily mean temperature for the site using a one-tailed Spearman's rho test (See Figure 4). This test found no significant correlation between these variables (p=0.331, N=30). The correlation coefficient in this particular test gave a slightly negative result (r_s=-0.083), which is the predicted trend.

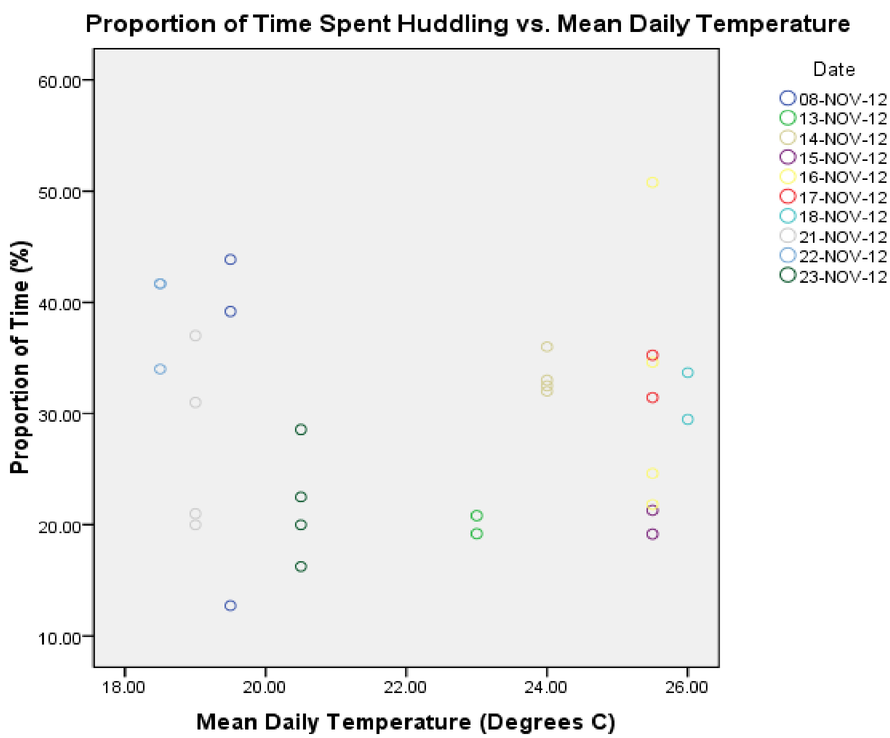


Figure 4: The proportion of time spent huddling compared here to the site specific ambient temperature (°C). No significant correlation was found (p=0.331, N=30, r_s=-0.083).

Rainfall

The same process was applied to compare proportion of time spent huddling and rainfall (See Figure 5). Again, no correlation of significance was established (p=0.092, N=30). The trend here was also slightly negative (r_s=-0.25), meaning the proportion of time spent huddling decreased with increasing rainfall.

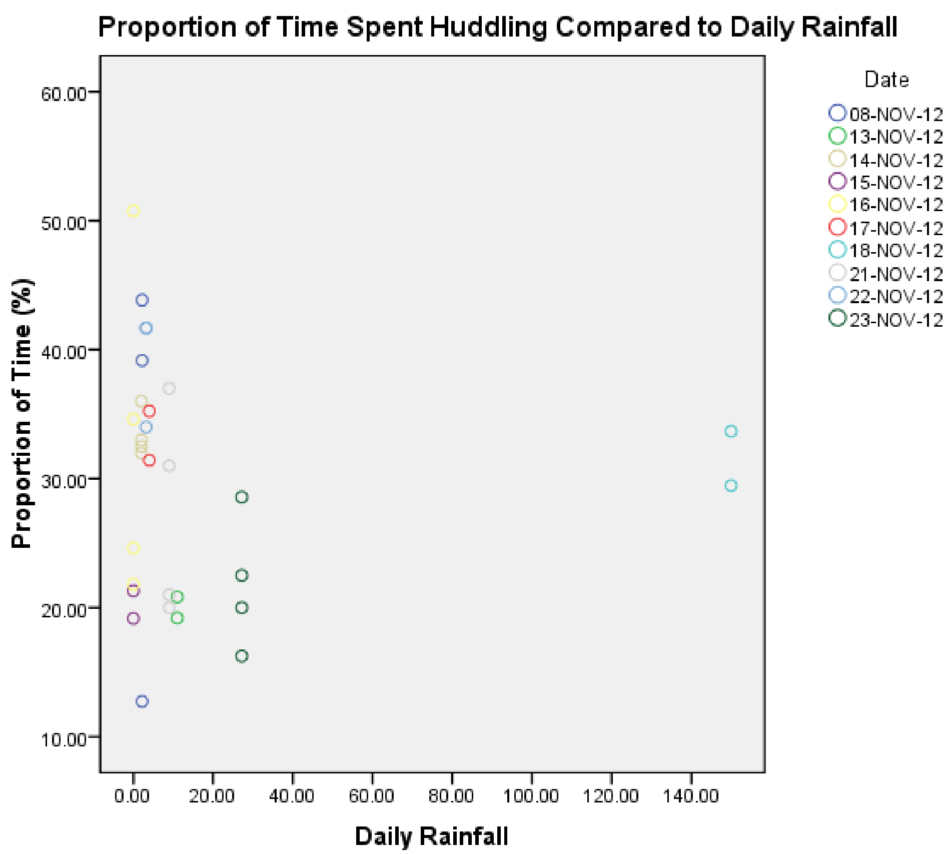


Figure 5: Proportion of time spent huddling compared to daily rainfall measurements. No significant correlation was determined (p=0.092, N=30, r_s=-0.25).

Body Mass

The third prediction was evaluated using a Mann-Whitney U test for two independent variables. This compared proportions of time spent huddling per individual, taking into account whether the individual was an adult or a juvenile (See Figure 6). This assumes that body mass of adults does not vary significantly between males and females. It also assumes that juveniles have smaller body size than adults. Each of the juveniles followed in this study were known to be less than two years of age (Rachel Jacobs Pers. Comm. November 2012) and were smaller than the adults observed. The test found no significant effect on behavior as a result of body size (U=92, p=0.746).

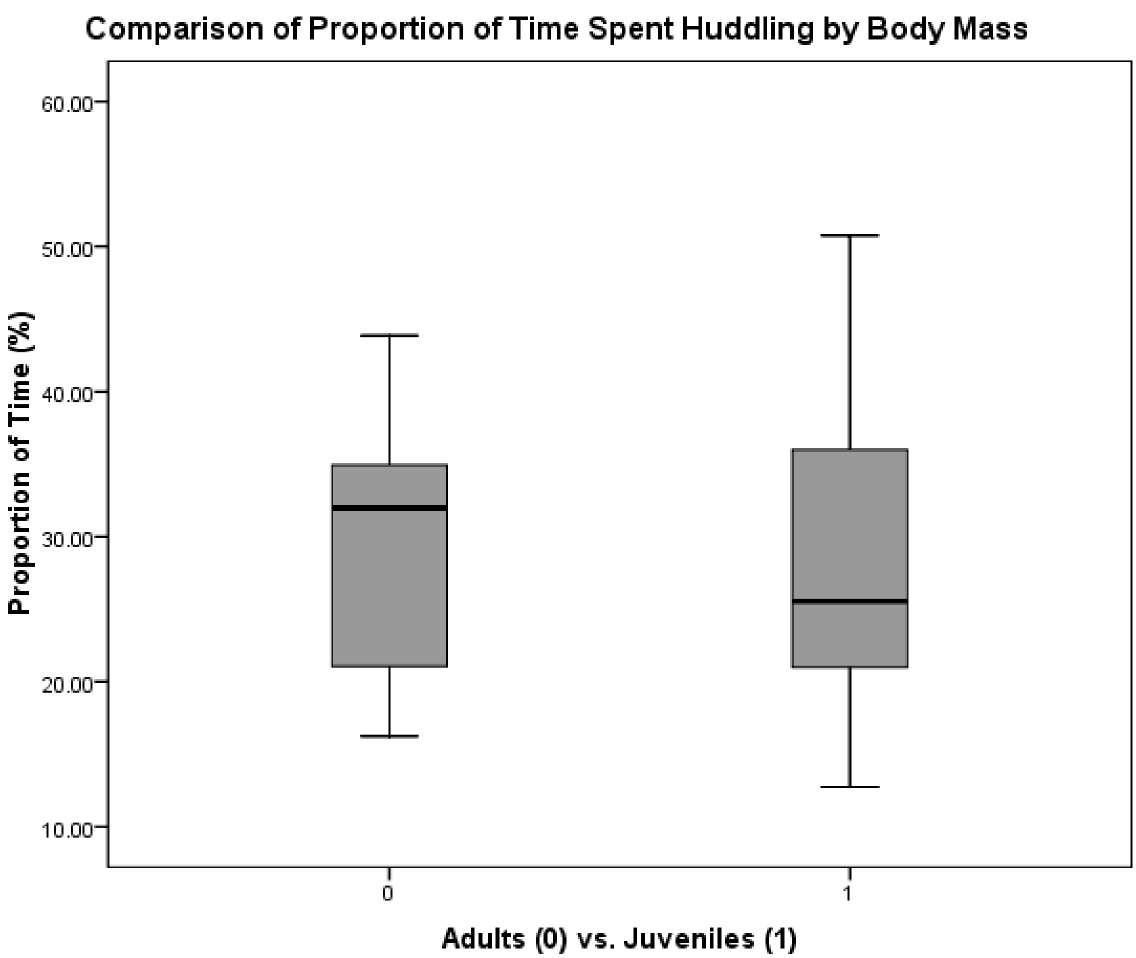


Figure 6: Proportion of time spent huddling compared for juveniles and adults (U=92, p=0.746, N=30)

Other Comparisons

Because two of the groups in Vato (V3 and V11) had infants, a Mann-Whitney U test was used to determine any effects of this group composition compared to groups without infants on the proportion of time spent huddling (See Figure 7). No significant effect was found (U=60, p=0.202).

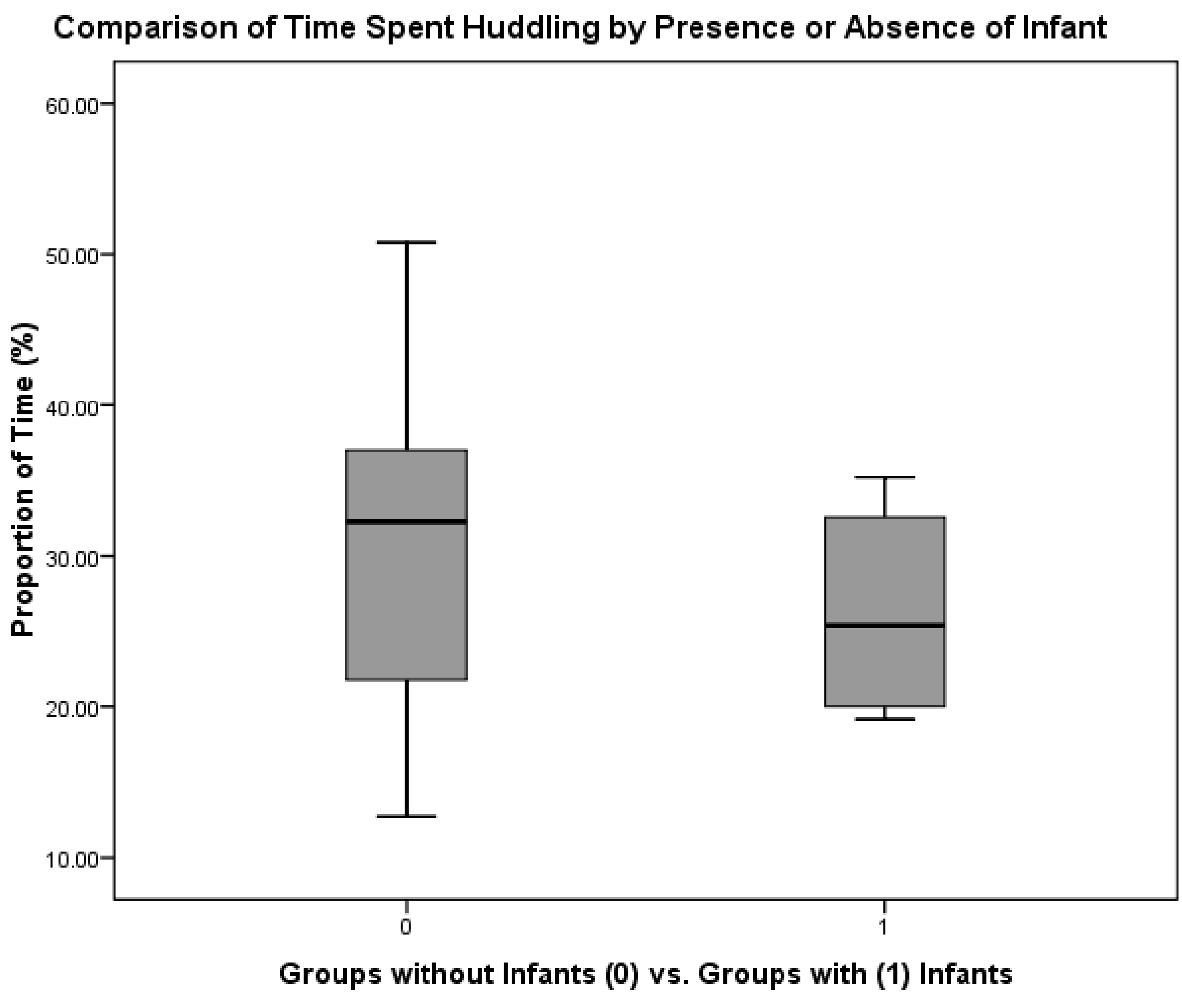


Figure 7: Proportion of time spent huddling compared for groups with (1) an infant (V3, V11), shown on the right, and groups without (0) an infant (V7, T4, T5), shown on the left, using Mann-Whitney U (U=60, p=0.202).

Tight vs. Loose

As another means of comparison, "huddling" was further divided into "tight" and "loose" (See Ethogram). The same analyses were done for temperature and rainfall in relation to each type of huddling. The results are summarized in Table 2, below. As previously stated, no correlations for general huddling were found to be significant. However, a significant correlation was established between loose huddling and ambient temperature. As temperature increased, so did loose huddling (r_s=0.319, p=0.043).

ACTIVITY	Temperature		Rainfall	
	Correlation Coefficient (r_s)	P-Value	Correlation Coefficient (r_s)	P-Value
Huddle-All	-0.083	0.331	-0.25	0.092
Tight Huddle	-0.236	0.105	0.179	0.171
Loose Huddle	0.319*	0.043*	-0.258	0.084

*Significance based on level p≤0.05

Table 2: Spearman's rho tests for correlation for total huddling as well as the "tight" and "loose" subcategories.

Hypothesis 2: Sociality

Support for predictions 1, 2, and 3 of the second hypothesis concerning huddling as a social behavior are also dependent on the same tests described above and resulting correlations.

For Prediction 4, the proportion of time spent in close proximity (usually less than 10m) with a particular individual (i.e. adult male with adult female, juvenile female with adult male) over all daily activities was compared to the proportion of time spent huddling with the same individual (See Figure 8). This relationship between nearest neighbors was found to be highly correlated (r_s=0.805) at a significance level p≤0.01, meaning individuals spent a high proportion of time with certain individuals as opposed to other members of the group. Groups V11 and V3 were excluded from calculations because they only had two adult individuals, and therefore were always nearest neighbors.

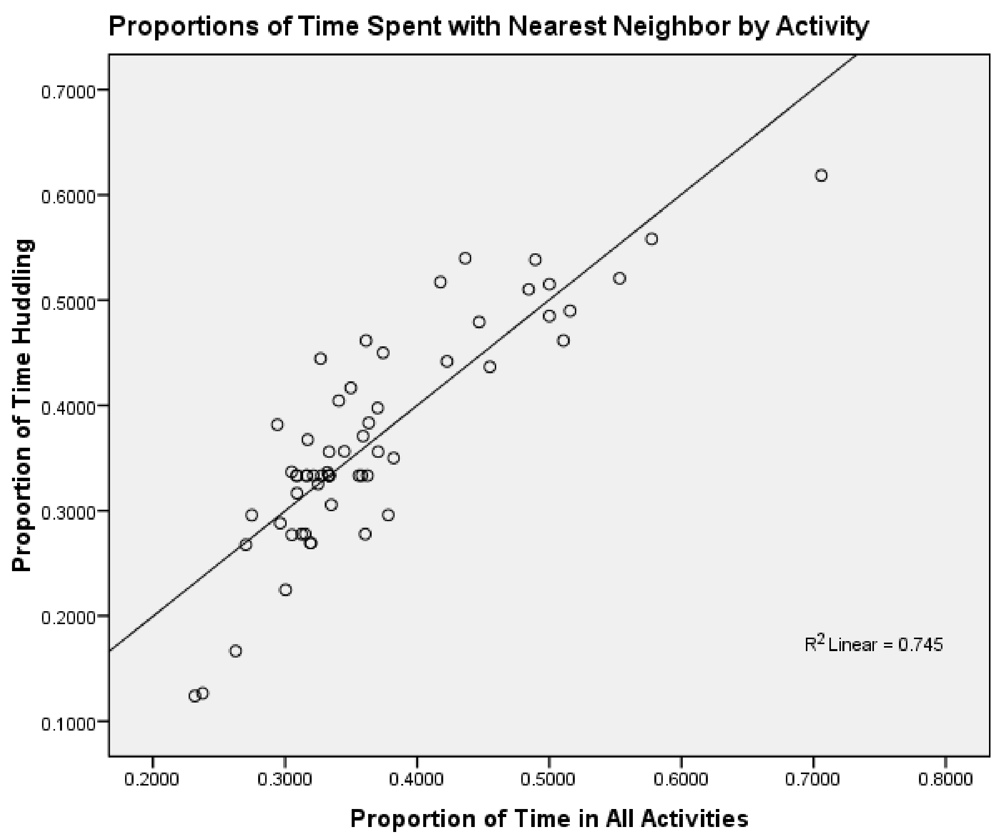


Figure 8: Correlation between pairs of individuals during huddling compared to during all daily activities (r_s=0.805, p≤0.01.) Line of Best Fit added to illustrate positive relationship (R^2=0.745).

For the combined proportions of time spent in loose and tight huddles, grooming coincided with huddling on an average of 6.06% of the time for all days of observation. Grooming occurred, on average, during 39.96% of observations for loose huddles of individuals. This behavior was rarely associated with tight huddling.

DISCUSSION

Few significant correlations were established based on the data collected during this study. It is possible that additional correlations exist between microclimatic conditions and huddling behavior in *E. rubriventer*, but the lack of any significant findings is likely due to the small sample size and short timeframe of this project.

E. rubriventer can be difficult to find, especially when morning conditions are rainy. This limits the amount of data able to be collected on days with large amounts of rainfall, which directly reduces the possibility of drawing correlations with rainfall and temperature. Two additional days were spent searching for groups T4 and T5 in Talatakely, but neither was found. Because the measurements were all taken during a three week period in November, there was not as much variation in temperature or rainfall as may occur on a more seasonal basis. This too diminishes the ability to see if a significant relationship exists between these factors annually.

For both hypotheses of this study, predictions 1, 2 and 3 could not be confirmed nor denied with statistical significance. For all huddling, the correlation coefficients for Spearman's test were slightly negative for both ambient temperature and rainfall (r_s=-0.083 and p=0.331, r_s=-0.25 and p=0.092, respectively). This is the predicted trend for temperature; as temperature increased, huddling declined. This supports huddling as a thermoregulatory behavior, but needs more investigation to establish a strong correlation. A negative correlation between rainfall and huddling, however, is the opposite of the predicted trend. The measurements for rainfall were for the whole 24-hour period, and therefore do not accurately reflect field conditions specific to the actual times of observation.

Body mass was not proven to be a factor in proportion of time spent huddling, as the proportion of time spent huddling did not significantly between juveniles and adults. Therefore no support was shown for the prediction that larger individuals, those able to produce more heat, would have less of a need to huddle than would smaller individuals. Groups with infants compared to groups without did not vary significantly in terms of the proportion of time spent huddling.

When tight and loose huddling were analyzed separately, loose huddling was determined to increase with increasing temperatures (r_s=-0.319, p=0.043). This may support huddling as a means of both social bonding and thermoregulation. Loose huddling is likely a social interaction because almost 40% of this type of huddling behavior was accompanied by partner grooming. Since the proportion of time spent in loose huddles increased with increasing temperature but tight huddling did not, individuals may gain warming benefits from huddling, and require less cooperative regulation as ambient temperature rises. Warmer weather means they associate less tightly with one another, but still remain in very close proximity in order to interact socially.

Testing of Prediction 4 for Hypothesis 2 showed that *E. rubriventer* does have preferred partners that are consistent between huddling and all other activities. Small group sizes may be a factor here, as there are not many partner options. This supports huddling as a social behavior; as a pair-bonded species, individuals may try to maintain strong relationships for the survival of the group.

CONCLUSIONS

As with many behaviors, huddling likely serves multiple purposes for *Eulemur rubriventer.* This study was unable to isolate one driver of this activity, but mixed results may indicate that huddling serves both thermoregulation and social bonding roles. There may be linkage to additional factors such as predator defense that should be investigated as well.

A longer term equivalent of this study is necessary to accurately determine the causes of huddling behavior in this species. Future work should span over an entire year to incorporate seasonal fluctuations. Although difficult to execute in the field, the results would also benefit from 24-hour observation of the groups since this species exhibits cathemeral activity. Rainfall and temperature data should be taken for shorter time intervals, as opposed to totals for 24-hour periods. Food availability and nutritional content could also be added to a study of this kind to provide more perspective on the energetics of huddling behavior.

Behavioral responses to changes in environment such as precipitation and temperature may be very important in a species' ability to adapt to greater climatic changes over time. In a study of behavior and hormonal responses to seasonality, Tecot (2008) found that *E. rubriventer* is able to adjust its energy usage and intake to compensate for changes in conditions. With further global climatic change imminent, as well as likely continued habitat degradation across Madagascar, it is critical to understand how lemur species, and especially *E. rubriventer,* may be able to evolve and survive. As lemurs are endemic to Madagascar, these unique primates need to be a high conservation priority, and further studies must help facilitate this as changes occur.

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