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Effect of Light Level on Feeding Behavior in a Lemur Species (Eulemur Rubriventer) With a Color Vision Polymorphism.

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ABSTRACT

Understanding the visual capabilities and correlated behavior of prosimians provides vital information regarding the evolution of color vision. Feeding behavior in particular is often modified based on color vision status in various primate taxa. The present study examined feeding behavior under various light conditions in *Eulemur rubriventer*, a lemur species with a color vision polymorphism in which only females can have trichromatic vision. Behavioral observations were conducted for a single *E. rubrventer* group over a 13 day study period in April 2012. Results found no significant difference in rates of frugivory or exploitation of green vs. non-green food between male and female *E. rubriventer*. However, female *E. rubriventer* were found to exploit non-green food at a higher average light level than males. Overall, results are suggestive of some behavioral modifications for dichromats based on light level.

INTRODUCTION

How do we see color in the world around us? If we are to answer this question we must look to our primate relatives, whose visual capabilities are living evidence of the capabilities of our human ancestors. The study of primate vision enables us to understand the evolution of color vision as a whole, but there are still many pieces missing in the puzzle. Much work remains, especially, in understanding prosimian color vision. The present study aims to improve knowledge of prosimian vision and correlated behavior by examining feeding behavior under various light conditions in *Eulemur rubriventer*, a lemur species with a color vision polymorphism.

Study Species: Eulemur rubriventer

Eulemur rubriventer, the red-bellied lemur, is a species of true lemur endemic to Madagascar. *E. rubriventer* are characterized by a dark reddish brown dorsal coat and a black tail. The species is sexually dichromatic; females have a cream colored ventral coat while males maintain the dark reddish brown color. Males can also be identified by large white spots underneath their eyes which are absent in females (Mittermeier, *et al.* 2010).

E. rubriventer group size ranges from 2-10 individuals and consists of a pair-bonded adult male and female and their offspring (Merenlender 1993; Irwin, *et al.* 2005). On average, females begin to reproduce at 5.5 years of age (Merenlender 1993), and one infant is born per group each year. Infant mortality is estimated as high as 50% (Mittermeier, *et al.* 2010). Offspring generally emigrate from their natal group at around 2 years of age but do not emigrate again once they have established a pair-bond (Overdorff 1991). *E. rubriventer* are territorial, usually occupying a home range between 12-15 ha in size, and exhibit high site fidelity (Overdorff and Tecot 2006; Mittermeier, *et al.* 2010). The small group size and strict social structure of *E. rubriventer* may leave them more vulnerable to environmental stress than lemur species with more flexible group structure (Hennessy *et al.* 1995).

E. rubriventer are currently classified as "vulnerable" on the IUCN red list (IUCN 2008). It is therefore imperative that measures are taken to better understand the species in support of conservation efforts.

Primate Color Vision

E. rubriventer display an opsin gene polymorphism in which some individuals in the population have dichromatic vision while others have trichromatic vision (Bradley, unpublished data). The color vision status of various primates has gained much recent attention due to its significance in understanding the evolution of vision. Humans and most Old World monkeys have trichromatic vision and therefore express genes for opsin photopigments that absorb short (S), medium (M), and long (L) wavelengths. The S opsin is specified by an autosomal gene while the M and L opsins are specified by adjacent genes located on the X-chromosome (Nathans, *et al.* 1986; Jacobs and Deegan II 1999).

New World monkeys and prosimians also have an autosomal S opsin gene, but have only one opsin gene locus on the X-chromosome which specifies an M/L opsin (Shyue, *et al.* 1995).

This suggests that the M and L opsin genes arose via a gene duplication event occurring after the evolutionary divergence of Old World and New World monkeys (Jacobs and Deegan II 1999). *E. rubriventer* have two alleles at the M/L opsin locus, one specifying an M opsin, and one specifying an L opsin (Bradley, unpublished data). Heterozygous females (~2/3 of all females) therefore express two different M/L opsins due to X chromosome inactivation and are trichromatic, whereas homozygous females and all males express only a single type of M/L opsin and are dichromatic (Jacobs 1998). These dichromatic individuals have difficulty discriminating between colors in the red/green range. A similar polymorphism is found in most New World monkeys as well as some prosimians (Shyue, *et al.* 1995; Tan and Li 1999; Jacobs, *et al.* 2002).

Feeding Behavior, Activity Patterns, and Luminosity

E. rubriventer are highly frugivorous but are also known to eat flowers, nectar, leaves, dirt, mushrooms, stems, and bark (Overdorff 1991). Color perception is an important aspect of efficient foraging. Smith, *et al.* (2003) found that trichromatic individuals in two different species of polymorphic tamarins identified ripe fruits against a green leaf background more quickly than dichromatic individuals from the same species, suggesting a selective advantage in foraging for trichromacy.

Although frugivorous primates are generally diurnal, *E. rubriventer* display a cathemeral activity pattern (Overdorff 1988) and therefore forage in a vast array of light levels. Since color perception is strongly influenced by lighting conditions (Endler 1993; Endler 1997), it is likely that primates forage under conditions most conducive to color discrimination in order to maximize foraging efficiency. More specifically, because color vision is best under higher lighting conditions (Schneider and von Campenhausen 1998), trichromats would tend to forage more in high luminosities. This has been supported by several studies such as Yamashita *et al.* (2005), which reported that females (assumed to be indicative of trichromatism on average when compared with males) of polymorphic primate species fed on non-green foods in conditions of higher luminosity than males of the same species. Interestingly, a study by Paramei, *et al.* (1998) suggested that low lighting may be the optimal condition for color discrimination in human dichromats and a study by Freitag and Pessoa (2012) provided evidence that dichromatic marmosets were better able to detect orange targets in medium lighting (as compared with high and low lighting).

Study Site: Ranomafana National Park

Ranomafana National Park (RNP) is a protected area located 65 km northeast of Fianarantsoa at 47°18'-37' E and 21°2'-25' S. RNP consists of 3 parcels of land totaling 43,500 hectares of surface area and comprised mainly of mid altitude rainforest (DuPuy and Moat 1995). Rainfall averages 1500-4000 mm per year, although this varies dramatically between the wet (mid-October - mid-April) and dry (mid-April - mid-October) seasons. From 2005-2011 the average rainfall in April, the month during which the present study was conducted, was 21.2

mm with a minimum temperature of 15.4° C and a maximum temperature of 22.4° C (Centre ValBio Station Records). The highly unpredictable rainfall of the site, and of Madagascar in general, results in highly variable availability of fruit from year to year and season to season (Overdorff 1993; Dewar and Richard 2007). Ranomafana is also subject to extreme weather such as yearly cyclones, which results in further disturbance of food availability and habitat (Jury 2003).

An incredible amount of biodiversity can be found at RNP. The park is inhabited by at least 12 lemur species and is home to the largest known population of *E. rubriventer* in the world (Wright 1992). Population density of *E. rubriventer* at RNP is estimated at 5.25 individuals per km^2 (Irwin, *et al.* 2005). The present study was conducted in the Talatakely parcel of RNP, a site which was exploited heavily for lumber prior to the establishment of the park in 1991 and is currently in the process of regenerating (Wright 1992). Talatakely has been previously described as ripe-fruit abundant during the month of April, notably due to high availability of ripe Chinese-guava, though food availability is highly variable from year to year (Tecot 2007). Talatakely is currently inhabited by 7 groups of *E. rubriventer* (Centre ValBio Station Records).

METHODS

Home Range Determination

The present study took place between April 6 and April 19, 2012 and focused on a single group of habituated *E. rubriventer*, Talatakely 5. To gain information on the home range of Talatakely 5, GPS coordinates were taken every 30 minutes using a Garmin eTrex Vista HCX (Garmin International) during observation periods. GPS coordinates were mapped using Google Earth (Google, Inc.) and the area of the home range was calculated using the Earth Point Polygon Area calculator (http://www.earthpoint.us/Shapes.aspx).

Behavioral Data Collection

Talatakely 5 is composed of four individuals: an adult male (Max), adult female (Fiona), juvenile male (Jasper), and baby female (Pookie). Individuals were easily distinguishable based on sexual dimorphism and age difference. Behavioral data was collected instantaneously every 60 seconds using 10-minute focal animal observations, rotating evenly through the group (Altmann 1974). Observation time totaled 2466 minutes; 617 for Max, 613 for Fiona, 618 for Jasper, and 618 for Pookie.

Data was collected for activity budgeting using broad behavioral categories: resting, social, feeding/foraging, or moving. Resting was defined as any behavior where the focal lemur remained in one place and was not participating in mutual grooming. Social was defined as any behavior where the focal animal was interacting with another. Feeding/foraging was defined as any behavior where the focal animal was actively eating or searching for food. Moving was defined as any behavior where the focal animal was moving unrelated to social interaction or feeding/foraging. Data was also collected for the height of the focal animal in the tree, and lighting conditions (see below). Feeding data was collected on plant species, part of plant eaten (fruit, leaves, etc.), and color of food each time the focal animal participated in feeding/foraging behavior.

Because the vision status of the *E. rubriventer* in Talatakely 5 is not currently known, the present study was undertaken based on the assumption that one or both of the females in the group may have trichromatic vision and that the behavior of the females may therefore be different on average than the behavior of the males.

Light Level Conditions

Broad lighting conditions were assessed for the focal animal every 60 seconds under the categories open, shade, and closed. Open was defined as the condition in which the focal animal was in complete sunlight. Shade was defined as the condition in which the focal animal was in partial sunlight, with some sunlight blocked by overhead branches. Closed was defined as the condition in which the focal animal was in complete shade with all sunlight blocked by overhead branches. Lighting conditions were also assessed in standard lux units (lx) every 15 minutes in both open and shade conditions as defined above using a Universal Enterprises Digital Light Meter DLM2 (Universal Enterprises, Inc.). If open conditions could not be found in which to take a light meter reading, the data point was left blank. When analyzing light condition data, the cutoff for high vs. low lighting was set at 1000 lx (~95th percentile of shade readings and the ~15th perentile of open readings) semi-arbitrarily based on breaks in the data. Finally, data collected on the height of the focal animal in the trees was used as a third parameter for estimating light levels, based on the assumption that greater height in the trees would signify higher light levels.

RESULTS

Home Range

The observed home range for Talatakely 5 during the study period covered approximately 13.91 ha as determined by GPS data **(Figure 1)**.

Activity Budget

A general activity budget was estimated in order to understand general behavior patterns of the group and to compare findings with previous studies for consistency. Talatakely 5 spent the majority of their time resting with smaller amounts of time devoted to feeding/foraging and moving and a very small amount of time budgeted for social activities **(Figure 2A)**. There was little variation of activity budget amongst individuals in Talatakely 5, although Pookie spent only 67.48% of her time resting - much less time than anyone else **(Figure A1)**. A comparison of activity budget by gender revealed that the males spent more time on average resting ($p<0.05$, $t=2.39$, $n=2466$) than the females but less time on average feeding/foraging ($p<0.05$, $t=2.93$, $n=2466$). No significant difference was found in general activity budgeting between males and females for socializing ($p>0.05$, $t=1.46$, $n=2466$) or moving ($p>0.05$, $t=1.57$, $n=2466$) **(Figure 2B). (Table A1)**.

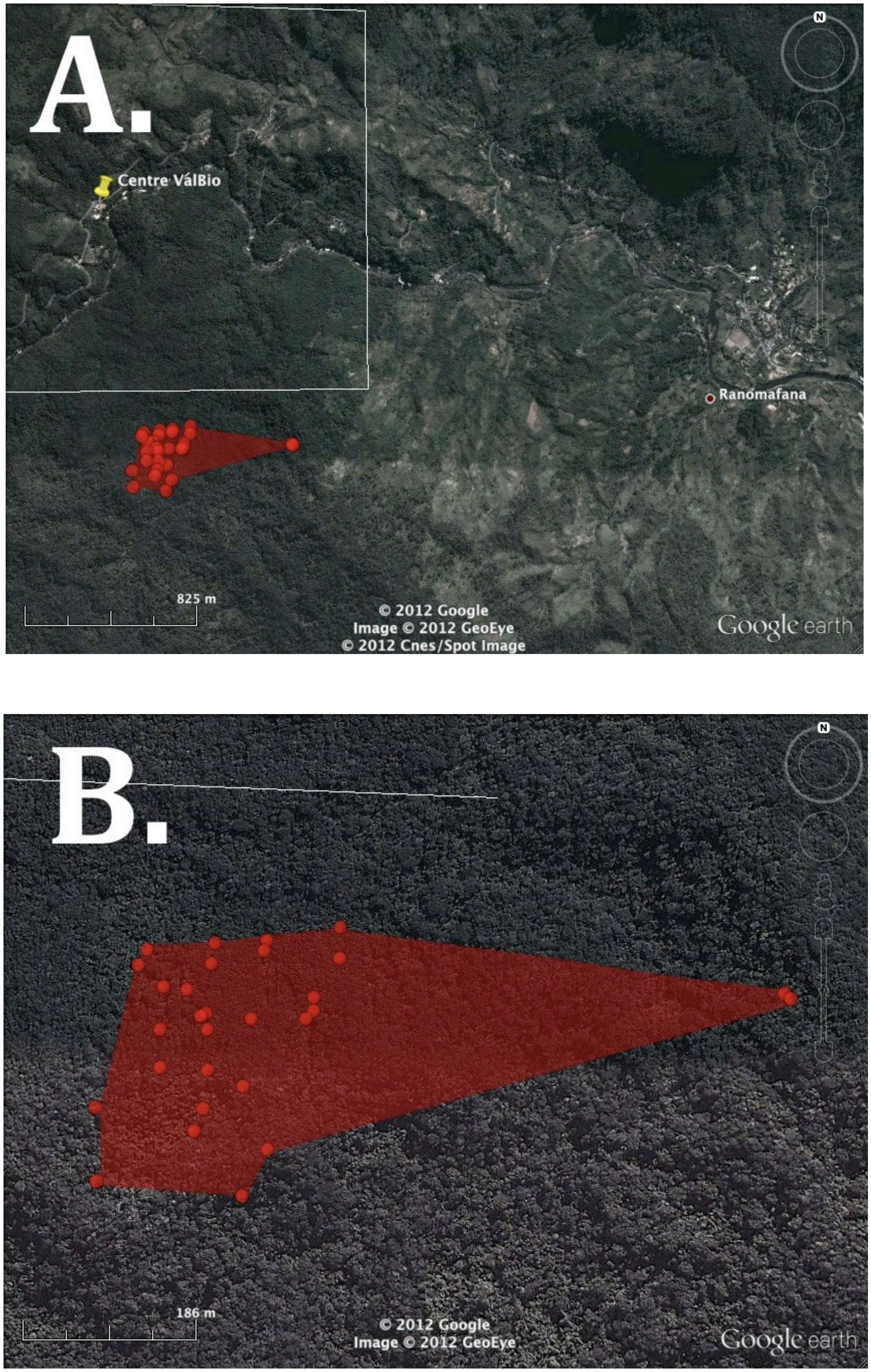
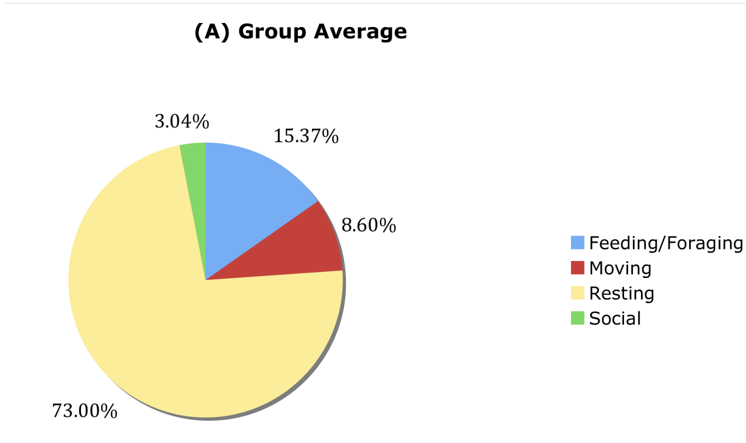


Figure 1. The observed home range of *E. rubriventer* group Talatakely 5 from April 6 - April 19, 2012 **(A)** in the surrounding area; **(B)** close-up. Red dots signify GPS data collection points. Area of the observed home range was calculated to be approximately 13.91 ha.



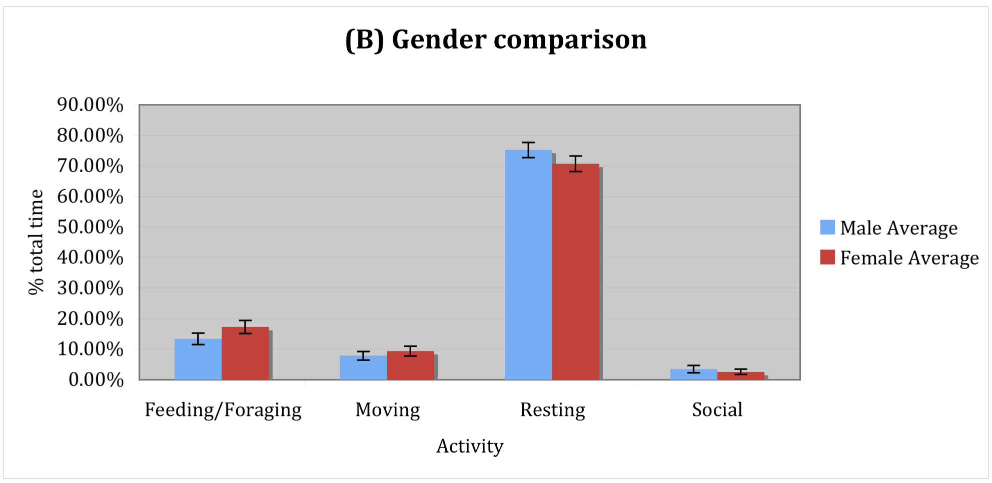


Figure 2. General activity budget for *E. rubriventer* group Talatakely 5 from April 6 - April 19, 2012. **(A)** Group average (n=2466); **(B)** Gender comparison (n=2466). Error bars = 95% CI.

The main objective of calculating activity budgets for Talatakely 5 in the present study was to determine whether some activities occurred more frequently at higher or lower light levels. This was done several ways to ensure that there were a variety of parameters by which the effect of light on behavior could be assessed, and to provide information on how different methods of light level data collection might ultimately affect data analysis.

First, activity budgets were calculated by gender with average light meter readings **(Figure 3A)**. Due to a small sample size, few of the results were significant. However, females were found to have spent a larger amount of time in higher lighting (mean = 1252.73 lx) overall than males (mean = 973.97 lx, $p<0.05$, $t=2.49$, $n=1917$). Activity budget was also calculated based on parameters of high and low lighting and open and shade/closed conditions **(Figure 3B-C)**. The group overall spent 15.28% of their time in high lighting and 84.74% of their time in low lighting ($n=1917$). Similarly, the group spent 16.75% of their time in open conditions and 83.25% of their time in shade/closed conditions ($n=2466$).

Gender comparison for low lighting and shade/closed conditions yielded similar results, but larger differences can be seen between activity budgets in high lighting and open conditions probably due to the smaller sample sizes. For example, females participated in feeding/foraging behavior more than males in high lighting conditions ($p>0.05$, $t=0.92$, $n=293$) but less than males in open conditions ($p>0.05$, $t=1.19$, $n=413$). Higher sample sizes for low lighting and shade/closed conditions yielded more convincing and consistent results.

In low lighting conditions, females spent significantly more time feeding/foraging than males ($p<0.05$, $t=2.62$, $n=1624$) and significantly less time resting than males ($p<0.05$, $t=2.34$, $n=1624$) **(Tables A2-A6)**. Despite small sample sizes, clear trends can be seen when higher lighting conditions are compared with lower lighting conditions. Across genders, feeding/foraging and moving occurred at a higher frequency in high lighting, while resting and socializing occurred at a higher frequency in low lighting.

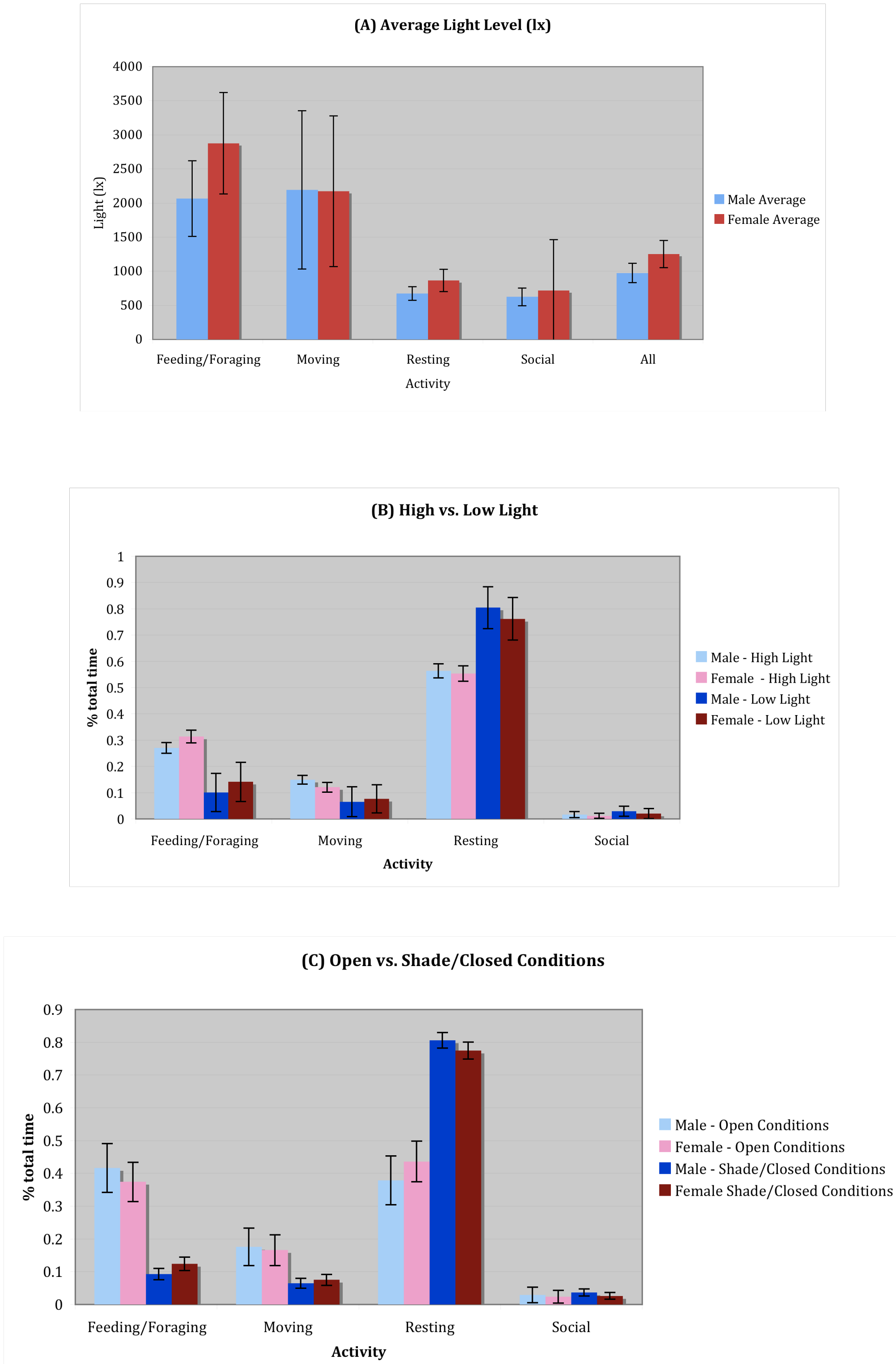


Figure 3. Activity budget comparisons for male and female from *E. rubriventer* group Talatakely 5 from April 6 - April 19, 2012. **(A)** With average light levels (lx); **(B)** High light (n=293) and low light (n=1624); **(C)** Open conditions (n=413) and shade/closed conditions (n=2053). All error bars = 95% CI.

Some of the differences in activity budget between gender in high vs. low lighting conditions can be attributed to differences in general activity budget. For example, in the general activity budget, females spent more time feeding/foraging than males. To account for this, percent change in time allotted for feeding/foraging in high or low conditions compared with general activity budget was calculated for males and females **(Table 1)**. This comparison shows that males budgeted 11.66% of their time for feeding/foraging overall, and 28.38% of their time for feeding/foraging in high light conditions, a 143.31% increase ($p<0.0005$, $n=1255$). Females budgeted 17.30% of their time for feeding/foraging overall, and 30.34% of their time for feeding/foraging in high light conditions, only a 75.37% increase ($p<0.0005$, $n=1375$). Therefore, although females spend more time feeding in high light than males, males increased their feeding/foraging budget in high light much more than females.

Table 1. Percent total time budgeted for feeding/foraging overall and in high and low light for males and females of *E. rubriventer* group Talatakely 5 from April 6-April 19, 2012. High and low light shown with percent change in percent time budget.

	Male	**Female**
Overall Feeding/ Foraging Time	11.66%	17.30%
High Light	28.38%	30.34%
% change from overall	143.31% (p<0.0005, n=1255)	75.37% (p<0.0005, n=1375)
Low Light	10.13%	13.96%
% change from overall	-13.13% (p=0.14, n=1236)	-19.31% (p<0.05, n=2025)

Height of the focal animal in the trees was used as a third parameter by which to test for a possible effect of lighting on activity budget. Males and females participated in all behaviors besides feeding/foraging at significantly different average heights **(Figure 4) (Table A7)**.

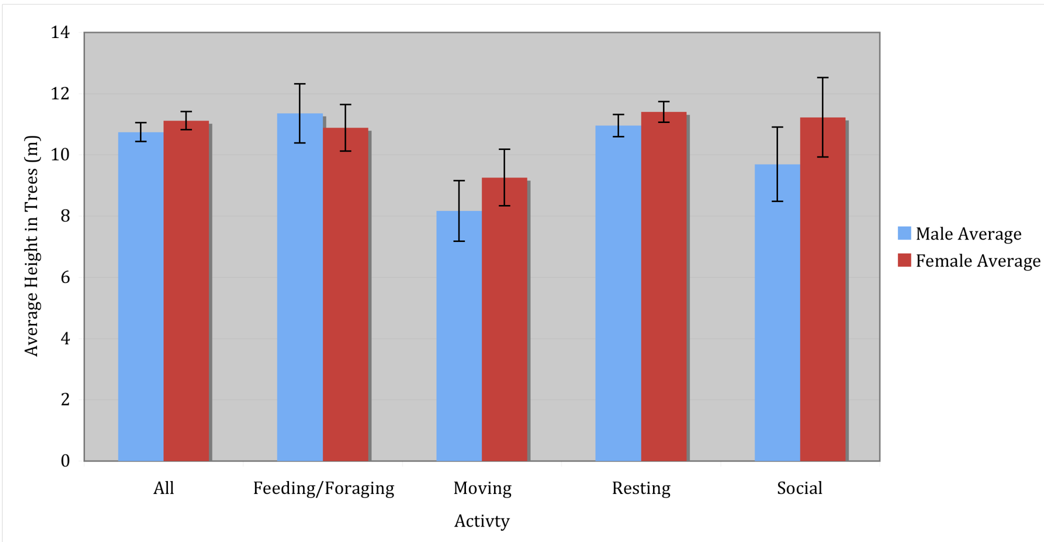


Figure 4. Average height in trees (m) for male and female *E. rubriventer* by activity from April 6 - April 19, 2012. Error bars = 95% CI.

Feeding and Foraging Behavior

Data was compiled on the observed diet composition of Talatakely 5 during the study period **(Table 2)**. The individuals of Talatakely 5 were observed exploiting a total of 23 plant species. The two most commonly exploited food sources were *Cissus pileata* (27.60%) and *Smilax sp.* (21.09%), both fruit-bearing vines. As previously reported for *E. rubriventer*, Talatakely displayed a high rate of frugivory (86.20%, n=384), though they were also observed feeding leaves, stems, bark, and mushrooms (*e.g.* Overdorff 1991) **(Figure 5A)**. Females were observed spending slightly but insignificantly more time exploiting fruit than males ($p>0.05$, $t=1.34$, n=384).

Table 2. Description of plants eaten by *E. rubriventer* group Talatakely 5 from April 6 -April 19, 2012. Parts eaten: F = fruit, L = leaves, S = stems, B = bark. Focal animals refers to individuals observed exploiting the corresponding species: M = adult male, F = adult female, J = juvenile, B = baby.

Vernacular Name	Scientific Name	Parts Eaten	Color of Fruit	Focal Animals	% feeding/ foraging time
Vahirano	*Cissus pileata*	F, L	yellow	M, F, J, B	27.60%
Roindambo	*Smilax sp.*	F, L	red	M, F, J, B	21.09%
Nonoka	*Ficus pyrifolia*	F	red/orange	M, F, J, B	12.24%
Guava	*Psidium littorale*	F	red	M, F, J, B	9.11%
Kalafana	*Oncostemum botryoides*	F, L, S, B	black	M, F, J, B	5.73%
Kalafamba kaka	*Oncostemum nervosum*	F, L	black	M, F, B	5.47%
Hafitrataikalalao	*Grewia sp*	F	green	J, B	3.39%
Hazotoho	*Gaertnera sp*	F	white	J	2.34%
Kimba	*Symphonia*	F	red	J	1.82%
Lalona	*Weinmannia sp.*	L		B	1.82%
Fohaninatsity	*Psychotria sp.*	F	red	J, B	1.82%
??	unidentified tree 2	L		B	1.56%
??	unknown white mushroom species			M, F	0.78%
Randrompody	*Tarenna sp.*	L		F, J	0.78%
Tambonetra	*Ephippiandra madagascarensis*	L		B	0.78%
Vahiherotra	*Landolphia sp*	F	red	J	0.78%
Voararano	*Ficus botryoides*	F	brown/green	J, M	0.78%
Rotramena	*Syzygium sp.*	F	red	F	0.52%
??	unidentified tree 1	L		M	0.52%
Mandravasarotra	*Cinnamosma madagascariensis*	L		F	0.26%
Voara	*Ficus sp.*	F	green	M	0.26%
Fahimandrono	*Plectaneia sp*	F	black	B	0.26%
Velaha	*Ruellia sp.*	L		J	0.26%

To better understand how feeding and foraging behavior might be affected by a color vision polymorphism, food data was divided into categories of green and non-green. Black and white foods were excluded from these categories because they lie in the spectral range absorbed by S-opsins (Yamashita, *et al.* 2005). Gender comparison for exploitation of green and non-green foods revealed that males exploited significantly more non-green food than females ($p<0.005$, $t=3.50$, $n=343$) **(Figure 5B) (Table A8)**.

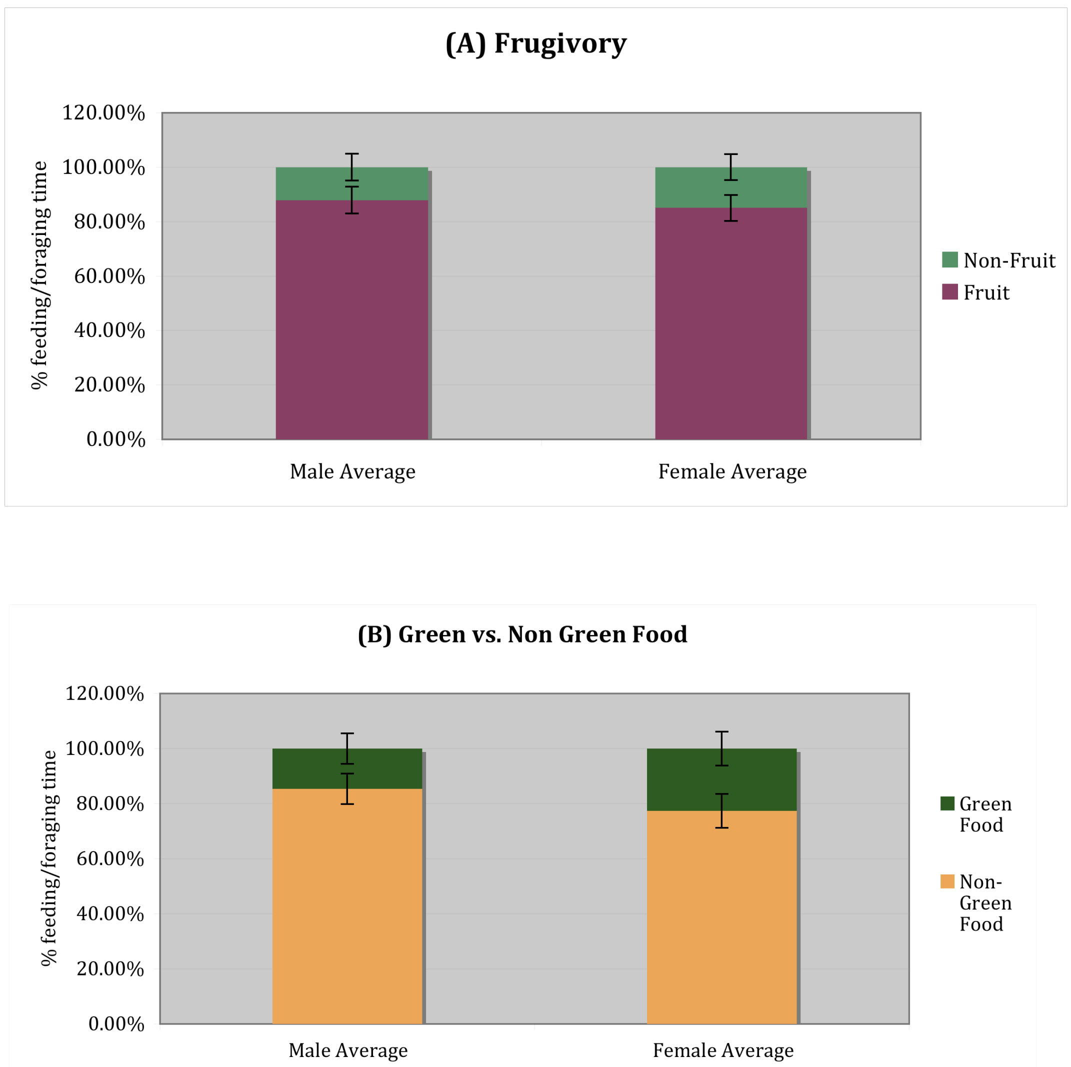
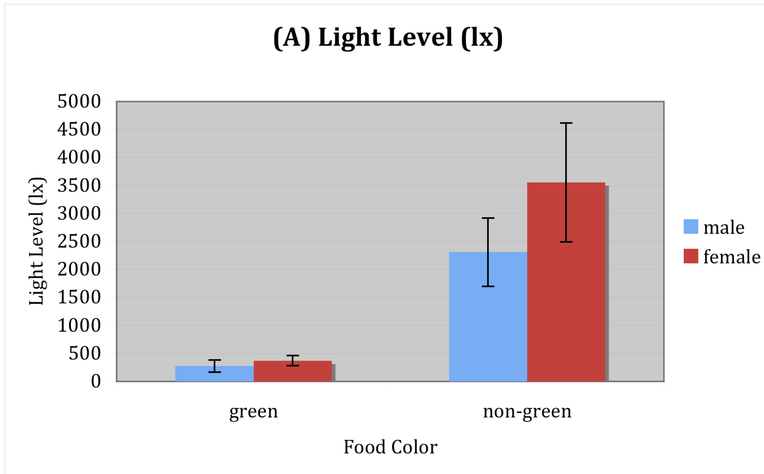
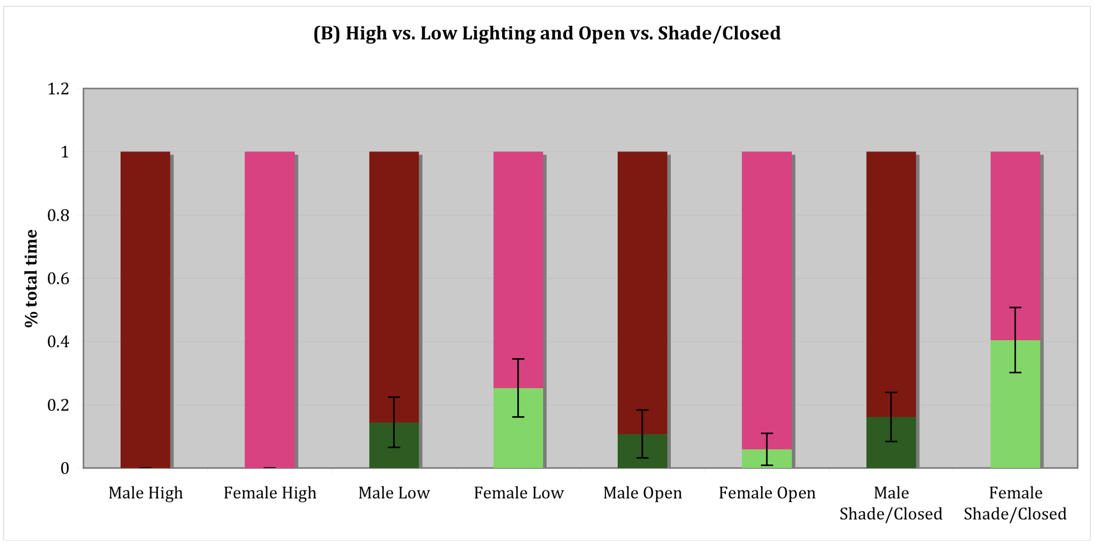


Figure 5. **(A)** Observed frugivory; **(B)** Exploitation of green and non-green foods by males and females of *E. rubriventer* group Talatakely 5 from April 6 - April 19, 2012. Error bars = 95% CI.

To determine the effects of light level on the color of food exploited by male and female *E. rubriventer*, average light level was calculated for instances of green and non-green food exploitation **(Figure 6A)**. This comparison showed that both males and females exploit non-green foods at much higher light levels than green foods and that females exploited non-green food sources at significantly higher light levels than males ($p<0.05$, $t=2.28$, $n=209$). Comparison of total time spent exploiting green and non-green foods under low vs. high light and open vs. shade/closed conditions showed no significant differences between males and females **(Figure 6B)**. However, a trend can still be seen of females feeding on non-green foods in higher light levels than males.

Finally, average height of the focal animal in the trees was calculated for green and non-green food exploitation **(Figure 6C)**. This comparison revealed no significant difference between males and female but further confirmed that across genders exploitation of non-green foods occur at higher light levels than green foods **(Table A9)**.





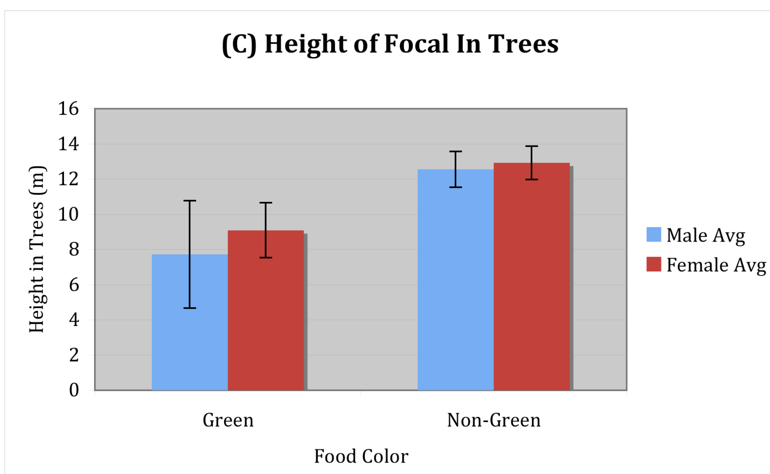


Figure 6. Observed exploitation of green and non-green foods by the males and females of *E. rubriventer* group Talatakely 5 from April 6 - April 19, 2012 with **(A)** average light level (lx); **(B)** in conditions of high vs. low lighting and open vs. closed conditions. Green = green foods, red/pink = non-green foods; **(C)**height of focal animal in trees. All error bars = 95% CI.

DISCUSSION

Home Range

Characterizing the home range of a group or species may lead to important insight into social structure. Overdorff and Tecot (2006) reported that home range sizes for *E. rubriventer* are usually between 12 and 15 ha. The home range size, 13.91 ha, estimated for Talatakely 5 in the present study is well within this previously reported range. More long term data for the home range of Tatlatakely 5 will increase the accuracy of the area estimation and provide more insight on whether or not the group exhibits high site fidelity.

Activity Budget

Activity budgets can be used to understand energy use as it relates to the environment and climate (Coelho 1986; Halle and Stenseth 2000). General activity budget for Talatakely 5 was fairly consistent with previous findings for *E. rubriventer*, with a majority of time devoted to resting, smaller amounts of time devoted to feeding/foraging and moving, and a very small amount of time devoted to social activity. (Tecot 2007) **(Figure 2A)**. The large proportion of time budgeted for resting compared with other activities is suggestive of an energy minimizing strategy. Interestingly, energy minimizing strategies are generally more characteristic of folivorous than frugivorous species (Schoener 1971; Estrada *et al.* 1999, Vasey 2005).

In gender comparisons for general activity budget, females were found to spend significantly more time feeding/foraging than males and significantly less time resting. While this initially seems as though it may be reflective of higher energetic requirements of females for reproduction, a look a activity budget by individual reveals that Fiona, the sexually mature adult female, had a similar general activity budget to the two males. In contrast, baby Pookie was much more active than the older group members and spent much more time feeding/foraging and moving than any other group members. This is not particularly surprising as young primates are generally more active than older primates **(Figure A1)**.

The main objective of activity budgeting in the present study was to understand how activity budget might correspond with light level. For example, if one or both of the group females has trichromatic vision, we might expect that they would be more likely to feed/forage in higher lighting conditions than males. However, low sample sizes made it particularly difficult to assess general activity budgets based on light levels.

Data on average light level for each activity by gender shows that females were found to have participated in feeding/foraging at higher light levels than males on average, but this data is not statistically significant However, it is important to note that females were found to have spent their time in significantly higher light levels than males overall, which suggests that a larger sample size would reveal females budgeting a significantly larger portion of time to feeding/foraging than males under high lighting conditions, in line with expectations for trichromatic vision **(Figure 3A)**.

Data on activity under high and low lighting and open and shade/closed conditions yielded somewhat mixed and inconsistent results due to small sample size. Both were ultimately assessed because while high and low lighting based on light meter readings is a more accurate descriptor of lighting conditions as it is based on light meter data, difficulty with equipment left some light meter data incomplete. Therefore, open and shade/closed conditions could be used to analyze a larger data set. Females spent more time feeding/foraging under high lighting conditions than males but less time in open lighting conditions **(Figure 3B-C)**. Further, although females spent more time feeding/foraging under high lighting conditions than males, males increased the percent of time they budgeted for feeding/foraging in high lighting conditions more than females **(Table 1)**. Due to the many apparent inconsistencies in this data set, it is difficult to suggest even general trends, and larger sample sizes are needed to more accurately assess the situation.

Data on the height of the focal animal in the trees was collected as a final parameter by which to assess modifications of activity budget based on light level. Females spent their time significantly higher in trees overall. There was no significant difference in average height of feeding/foraging behavior between males and females **(Figure 4)**.

Feeding and Foraging Behavior

The overall results for diet composition of Talatakely 5 are unsurprising. As previously reported for *E. rubriventer*, Talatakely 5 was highly frugivorous (Overdorff 1993) **(Figure 5A)**. The four most commonly exploited species - *Cissus pileata*, *Smilax sp.*, *Ficus pyrifolia*, and *Psidium littorale* - each bear non-green fruits **(Table 2)**. The observed diet composition from this study is highly representative of the season. For example, *P. littorale* (Chinese guava) is in season April-May most years but typically has little or no ripe fruit in other months. April is, in fact, generally characterized as fruit-abundant in Ranomafana, while other months might have revealed lower instances of frugivory (Tecot 2007).

The males and females of Talatakely 5 did not display significantly different levels of frugivory **(Figure 5A)**. Further, non-green foods were found somewhat surprisingly to comprise a larger portion of the male diet than the female diet **(Figure 5B)**. There are two possible explanations for this, aside from error due to small sample size: 1) Neither of the females of Talatakely 5 have trichromatic vision, or 2) color vision status does not strongly affect diet composition, at least in terms of frugivory and general exploitation of green vs. non-green food (*ie.* not accounting for ripeness of fruit or foraging efficiency). One reason that color vision status might not strongly affect diet composition might be the nature of *E. rubriventer* group feeding behavior, where males and females of the group almost always feed simultaneously. This may allow dichromatic males to make feeding/foraging decisions based on their association with potentially trichromatic females (Yamashita, *et al.* 2005). This is further supported by the evidence that males and females did not feed at significantly different heights in trees.

To further explore these possibilities, an analysis of the exploitation of green versus non-green foods under various light levels is crucial. Unsurprisingly, non-green foods were exploited at much higher light levels than green foods as a whole **(Figure 6A)**. More interestingly, females exploited non-green foods at much higher lighting levels than males. This matches reports from Yamashita et al. (2005) where females of polymorphic primate species feed on non-green foods in conditions of higher luminosity than males of the same species. It is therefore perhaps the most convincing piece of evidence provided by this study that one or both of the females in Talatakely 5 may have trichromatic vision and that trichromatic vision affects feeding behavior in E. rubriventer similarly to other species with reported color vision polymorphisms. If one or more of the females in Talatakely 5 *does* have trichromatic vision, this makes the second explanation for the results in the paragraph above - that color vision status does not strongly affect diet composition, at least in terms of frugivory and general exploitation of green vs. non-green food - more likely.

CONCLUSION

Data analysis in the present study has provided insight on several aspects of *E. rubriventer* general behavior and the possible interactions of light level, color vision, and feeding behavior. Findings support evidence that one or both of the females in Talatakely 5 may have trichromatic vision and that vision status of *E. rubriventer* may affect feeding behavior as it relates to light level, to an extent. However, activity budget and diet are both highly influenced by season and rainfall, both of which are highly variable at the study site. The short time span and small sample size represented necessitate that the results presented in this study are only suggestive of general trends. This study would need to be repeated year round for at least two years to draw any finite conclusions. Other necessary further work will include genotyping of study individuals and collecting rates for feeding accuracy and efficiency for more in depth feeding behavior analysis. Nevertheless, the present study represents a foundation upon which future work can be built and brings us another small step towards understanding the evolution of primate vision.

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APPENDIX

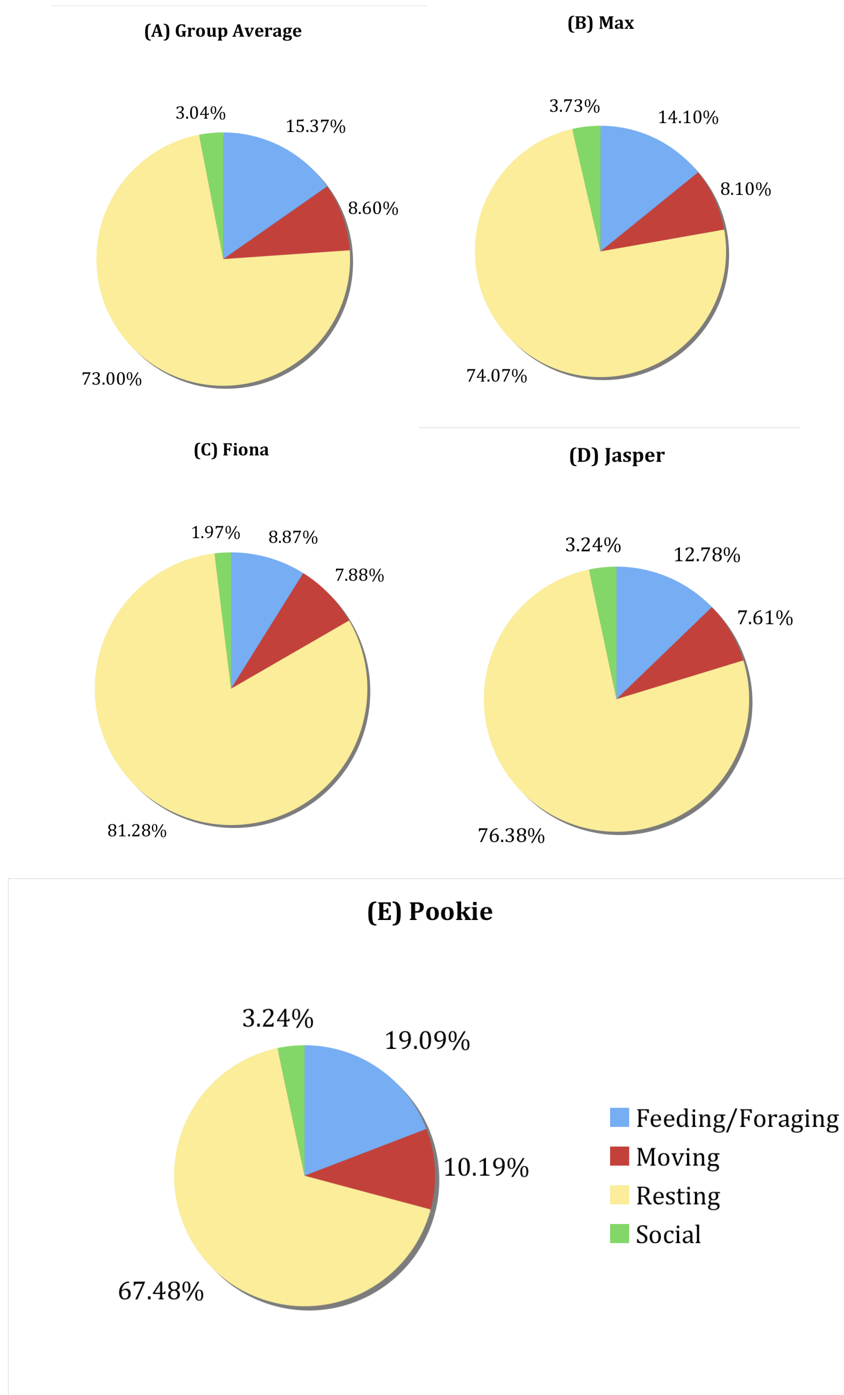

Figure A1. General activity budget of individuals from April 6 - April 12, 2012. **(A)** Group average activity budget, included for comparison **(B)** Max; **(C)** Fiona; **(D)** Jasper; **(E)** Pookie.

Table A1. Activity budget (% total time) for *E. rubriventer* group Talatakely 5, April 6 - April 12, 2012 (n=2466).

	Feeding/Foraging	Moving	Resting	Social
Max	14.10%	8.10%	74.07%	3.73%
Fiona	15.50%	8.48%	74.06%	1.96%
Jasper	12.78%	7.61%	76.38%	3.24%
Pookie	19.09%	10.19%	67.48%	3.24%
Male average	13.44%	7.85%	75.22%	3.48%
Female average	17.30%	9.34%	70.77%	2.60%
p-value	0.0110	0.1176	0.0169	0.1434
t-value	2.9280	1.5654	2.3905	1.4638
Group average	15.37%	8.60%	73.00%	3.04%

Table A3. Activity budget (% total time) for *E. rubriventer* group Talatakely 5 with average light meter readings (lx), April 6 - April 12, 201.

	Feeding/Foraging	Moving	Resting	Social	All
Max	2631.59	2285.24	702.98	672.14	1106.01
Fiona	4149.67	1637.89	695.52	301.25	1208.14
Jasper	1496.67	2100.61	643.31	576.67	841.93
Pookie	1604.11	2706.59	1035.26	1137.27	1297.31
Male Average	2064.13	2192.92	673.14	624.40	973.97
Female Average	2876.89	2172.24	865.39	719.26	1252.73
p-value	0.1699	0.4944	0.0273	0.3192	0.0128
t-value	1.3762	0.6850	2.2096	1.0074	2.4912
n	281	154	1437	45	1917

Table A3. Activity budget (% total time) for *E. rubriventer* group Talatakely 5 in high lighting conditions, April 6 - April 12, 2012 (n=293).

	Feeding/Foraging	Moving	Resting	Social
Max	30.19%	13.21%	55.66%	0.94%
Fiona	38.71%	9.68%	51.61%	0.00%
Jasper	23.81%	16.67%	57.14%	2.38%
Pookie	24.10%	14.46%	59.04%	2.41%
Male average	27.00%	14.94%	56.40%	1.66%
Female average	31.40%	12.07%	55.32%	1.20%
p-value	0.3564	0.3280	0.4850	0.4918
t-value	0.9237	0.9798	0.6992	0.6883

Table A4. Activity budget (% total time) for *E. rubriventer* group Talatakely 5 in low lighting conditions, April 6 - April 12, 2012 (n=1624).

	Feeding/Foraging	Moving	Resting	Social
Max	9.54%	7.22%	79.90%	3.35%
Fiona	8.87%	7.88%	81.28%	1.97%
Jasper	10.66%	5.90%	80.95%	2.49%
Pookie	19.33%	7.47%	71.13%	2.06%
Male average	8.87%	7.88%	81.28%	1.97%
Female average	10.10%	6.56%	80.42%	2.92%
p-value	0.0088	0.1815	0.0192	0.1657
t-value	2.6226	1.3368	2.3444	1.3866

Table A5. Activity budget (% total time) for *E. rubriventer* group Talatakely 5 in open conditions, April 6 - April 12, 2012 (n=413).

	Feeding/Foraging	Moving	Resting	Social
Max	34.02%	13.40%	52.58%	0.00%
Fiona	46.22%	11.76%	41.18%	0.84%
Jasper	49.28%	21.74%	23.19%	5.80%
Pookie	28.57%	21.43%	46.03%	3.97%
Male average	46.22%	11.76%	41.18%	0.84%
Female average	41.65%	17.57%	37.88%	2.90%
p-value	0.2359	0.4856	0.2494	0.4950
t-value	1.1870	0.6980	1.1534	0.6830

Table A6. Activity budget (% total time) for *E. rubriventer* group Talatakely 5 in shade/closed conditions, April 6 - April 12, 2012 (n=2053).

	Feeding/Foraging	Moving	Resting	Social
Max	10.38%	7.12%	78.08%	4.42%
Fiona	8.11%	7.71%	81.95%	2.23%
Jasper	8.20%	5.83%	83.06%	2.91%
Pookie	16.67%	7.32%	72.97%	3.05%
Male average	8.11%	7.71%	81.95%	2.23%
Female average	9.29%	6.47%	80.57%	3.67%
p-value	0.0110	0.1950	0.0423	0.0968
t-value	2.5460	1.2963	2.0317	1.6613

Table A7. Average height in trees (m) for *E. rubriventer* group Talatakely 5 by activity, April 6 - April 12, 2012.

	All	Feeding/Foraging	Moving	Resting	Social
Max	10.24	10.68	7.10	10.60	8.09
Fiona	10.93	10.57	7.87	11.34	11.75
Jasper	11.25	12.04	9.23	11.32	11.30
Pookie	11.31	11.20	10.65	11.47	10.70
Male average	10.74	11.36	8.17	10.96	9.69
Female average	11.12	10.89	9.26	11.40	11.23
p-value	0.0005	0.2602	0.0353	0.0000	0.0384
t-value	3.4694	1.1276	2.1186	8.2587	2.1079
Group average	10.93	11.12	8.71	11.18	10.46
n	2465	378	211	1846	74

Table A8. Food types exploited by *E. rubriventer* group Talatakely 5 from April 6 - April 12 2012: green vs. non-green foods characterized by color, excluding black and white (n=343) and fruit vs. non-fruit (n=384).

	Green	Non-green	Non-fruit	Fruit
Max	11.11%	88.89%	9.20%	90.80%
Fiona	13.75%	86.25%	12.50%	87.50%
Jasper	18.18%	81.82%	15.00%	85.00%
Pookie	31.43%	68.57%	17.36%	82.64%
Male Average	14.65%	85.35%	12.10%	87.90%
Female Average	22.59%	77.41%	14.93%	85.07%
p-value	0.0005	0.0005	0.1820	0.1820
t-value	3.5011	3.5011	1.3369	1.3369
Group average	19.53%	80.47%	13.80%	86.20%

Table A9. Light level, % feeding time during various lighting conditions, and average height of focal animal in trees during exploitation of green vs. non-green foods by *E. rubriventer* group Talatakely 5 from April 6 - April 12 2012.

	Green Foods						Non-Green Foods					
	Light Level (lx)	% feeding time				Heig ht in Tree s (m)	Light Level (lx)	% feeding time				Height in Trees (m)
		High Light	Low Light	Open	Shade / Closed			High Light	Low Light	Open	Shade / Closed	
Max	272	0.00%	15.15%	6.25%	15.22%	5.33	2984.23	100.00%	84.85%	93.75%	84.78%	12.14
Fiona	420	0.00%	11.76%	0.00%	36.67%	4.91	4830.20	100.00%	88.24%	100.00	63.33%	12.68
Jasper	276.7	0.00%	13.95%	15.15%	17.07%	9.50	1447.83	100.00%	86.05%	84.85%	82.93%	13.00
Pookie	361.1	0.00%	33.96%	14.29%	42.37%	10.63	2422.91	100.00%	66.04%	85.71%	57.63%	13.17
Male Average	274.6	0.00%	14.47%	10.77%	16.09%	7.71	2311.14	100.00%	85.53%	89.23%	83.91%	12.55
Female Average	371.8	0.00%	25.29%	5.88%	40.45%	9.10	3557.11	100.00%	74.71%	94.12%	59.55%	12.92
p-value	0.109		0.3356	0.4832	0.3915	0.192	0.0234		0.3356	0.483	0.3915	0.3020
t-value	1.65		0.9657	0.0032	0.8590	1.32	2.2829		0.9657	0.003	0.8590	1.0341
n	33	79	163	150	176	62	209	79	163	150	176	264