# Weight Variability and Social Dominance in Semi-free Ranging Ring-tailed Lemurs

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REVIEW OF LITERATURE

The ring-tailed lemur (*lemur catta*) is a member of the Lemuridae or true lemur family, and belongs to the Lemurinae subfamily (Macdonald 2001). The strepsirrhine species *Lemur catta* was originally proposed in 1758 by Karl Linneaus (Linnaeus 1758). The generum lemur is based on the malagasy term *lemures* meaning "spirits of the night" or "ghosts" referring to their large reflective eyes, and catta referring to the domestic cat, because of the ring-tails' purring vocalizations which sound similar to that of a cat. Lemurs have been studied much less intensively than other primates, primarily because there are so few lemurs in the wild and in captivity. *Lemur catta*, however, have been studied the most in-depth and are the most well known species of lemur because they breed well in captivity and are more common in the wild then many of their close relatives.

The ring-tailed lemur is usually about 400 mm head/body length with a tail that is around 600mm in total length and an adult weighs from 4.6 to 6 pounds. The back is usually a grey to reddish brown, with the rump, and limbs black or grey, and the underparts a cream or off-white color. They have characteristic large triangular dark eye patches, dark snout, and lighter white outer face and throat. The tail, which is the most distinctive part of the *Lemur catta* is long and ringed alternately with black and white, the 13-15 black bands are usually wider then the white bands (Mittermeier et al. 1994). *Lemur catta* are a diurnal species, which means that they are active during the day, which separates them from the majority of lemur species that are nocturnal (Fleagle 1988) and allows for easier observation in the wild. *Catta* are semi-terrestrial and are thought to be the most terrestrial of all lemurs spending more time on the ground then any other lemur

species (Jolly 1966). The ring-tailed lemurs in the wild are found only in the south and southwestern parts of Madagascar. The *Lemur Catta*'s habitat consists of spiny forest, dry scrub, deciduous forest and gallery forest. The average annual rainfall averages around 750 mm, most falling during the rainy season from November to March (temperatures average around 34.5° C) with relatively little rain from June to August (temperatures average around 25° C) (Sussman 1991). The forests ring-tailed lemurs live in are diminishing as a result of fires, overgrazing, wood harvesting for charcoal production, and some lemurs are even hunted for food (Dunham et. al 2008).

The social organization of ring-tailed lemurs is unique in that they group themselves in a matrilineal society, where there is a dominance hierarchy (Jolly 1966). But instead of being a strict hierarchical society like gorillas, ring-tailed lemurs exhibit more complex dominance relationships, with a more fluid and shifting hierarchy (Dunham 2008). Females are routinely dominant over males, and they tend to display size monomorphism (males and females being the same size), and masculinized external genitalia. The reason females are the same size as the males may be in part due to the hormonal masculinization of the females who show increased androstenedione and testosterone levels, especially during mating season (Drea et al. 2008). Because males do not play as large a role in the social hierarchy, the intrasexual competition between males will favor the male that has the ability to win the fight (according to the sexual selection theory). This often results in sexual dimorphism, however *lemur catta* have monomorphism of size so the males use sperm competition and physiological suppression of subordinates as mate guarding behavior instead of physical combat (Kappeler 1990). The dominance in general of the females may be due to the fact females

will get the first priority to food during feeding and foraging and this "female feeding priority" will end up getting a better nutrition and therefore their offspring will be better suited for the sometimes unpredictable environments of Madagascar (Jolly 1966).

The diet of wild lemurs is known to have effects on their growth and maturity, as exhibited between folivorous and frugivorous lemurs of the same size. According to the "ecological risk aversion hypothesis" which predicts that rates of growth and maturation should vary inversely to the amount of feeding competition in the wild (Janson & Van Schaik 1993; Godfrey et al 1994). In recent studies this theory has been contradicted because the folivorous lemurs such as the *Lepilemur*, *Indri*, *Hapalemur* and *Avahi* growth slower and mature in a longer amount of time generally than the more frugivorous counterparts *Lemur catta* and *Eulemurs*. This opposite effect is most likely the result of adaptive evolution and the different species solutions to the problem of environmental volatility (Godfrey, 2004).

While information regarding feeding does come from wild Malagasy ring-tailed lemur populations, much of the nutritional information and feeding ecology is recorded by researchers through meticulous observation and experimentation done on captive and semi-free ranging *Lemur catta* populations. The nutrition of a captive ring-tailed lemur usually consists of monkey chow, fruit such as bananas, apples, oranges, vegetables such as carrots, and greens such as spinach. This varies for each zoo or center and if the lemurs are captive or semi-free ranging (Mowery 2001). The feeding ecology of the semi-free ranging ring-tailed lemur was studied in the Duke Primate Center and on St. Catherines Island, finding that ring-tailed lemurs at Duke ate around 30 different plant species (local), and the lemurs did not pick or avoid certain foods for the effects of the

secondary compounds such as poisons like tannins or increased protein content, showing that they seem to not to factor the secondary compounds of their food into the choice of foraging and feeding at all (Ganzhorn 1986; Sauther 1999).

When ring-tailed lemurs were released into a "natural habitat" (in other words free ranging) in St. Catherine's island they showed decreased obesity, increased agility, and increased ability to forage for novel plants (Keith-Lucas, 1999). They showed an ability to use new forage and habitat, which bodes well for the suitability of *Lemur catta* for reintroduction into new habitats. The time spent foraging in free ranging areas on St. Catherine Island varied depending on the diet, range use, and gender of the lemur and it also seems that a provisioning of food (such as monkey chow) for the semi-free ranging populations will decrease their need to forage on natural plants and fruit (Ganzhorn 1986; Glander 1999).

## RESEARCH OBJECTIVE

The objective of this research was to determine if free range foraging by *Lemur catta* in natural habitat enclosures (NHEs) affects their weight (a factor in their overall health), and whether dominance status affects feeding and foraging time and amount of the food that they are able to get access to and consume.

## HYPOTHESES

$H_1$: *Lemur catta* weight will decrease, which would indicate better health and fitness, during periods of free ranging. This is hypothesized because the lemurs must rely more

on their own foraging skills and are continually exercising and expending more energy in the NHE as compared to when they are provided with all their food in the cages.

$H_2$: The more socially subordinate individuals in groups of free ranging *Lemur catta* will spend more time foraging. This is hypothesized because they do not obtain as large an amount of food from feeding on the supplemental monkey chow provided by the keeper (the dominant lemurs impede them from eating the larger pieces and as much food overall) and instead must acquire their nutrients through other methods such as foraging. The dominant male and female lemurs therefore will achieve significantly more feeding time, but will require significantly less foraging time than their subordinate counterparts.

$H_0$: (Null Hypothesis) No positive or negative effect will be observed for the caged versus free ranging lemurs.

## MATERIALS AND METHODS

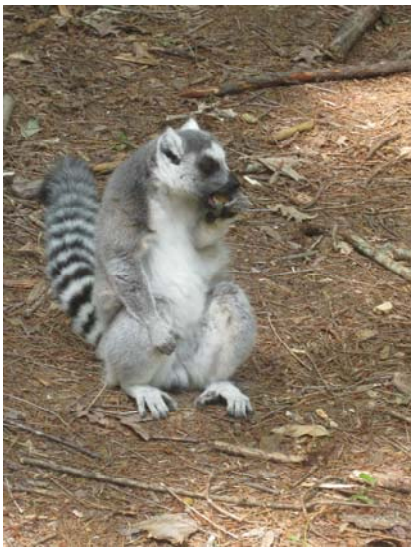
Research was conducted at the Duke Lemur Center (DLC) in Durham North Carolina through twenty-one days of direct field observation and synthesis of data collected previously at the DLC. The subjects were eleven ring-tailed lemurs (five males, six females) that ranged from two years old to twenty years old. Nine of the eleven subjects were born on premises at the DLC, however two males were born in Georgia at the St. Catherines Island Foundation (SCI), and then shipped to the DLC in 2004. The reason these Lemur Catta are semi-free ranging is because during the warmer months they are housed outside and are “free ranging”. During the colder months they are housed indoors and are “caged”. These eleven lemurs are grouped together during the free-ranging months, which are generally 4/15-11/15 each year. During this time they live

(without any other species of lemur present) in the Natural Habitat Enclosure 4 (NHE4), as seen in image 1, and are brought into Cold Shelter Boxes (CSBs) for a few hours every Wednesday and Sunday to make sure they will be able to be secured during the winter months. While in the free ranging habitat they are fed and checked on everyday by a DLC technician, who provides their supplemental diet of around 55g Old World (monkey) Chow per animal (image 2); however the lemurs must obtain the rest of their diet through foraging in the enclosure. NHE 4 is 14.33 acres in total area, includes a pond, and borders several other NHEs and the Duke Forest. During the colder months the ring-tailed lemurs are caged in the triplex enclosure (a building that is connected to NHE 4), in the triplex indoor cell (L – 6.0 ft; W- 5.1-8.0 ft; H – 8.0 ft) and when temperatures allow the triplex outdoor cage (L = 14.0ft; W-6.4-11 ft; H-7.8 ft). During the winter, the lemurs are allowed to free-range when low temperature is >40°F for more than 48 hours; non-free ranging animals are allowed in their outside yards when daytime temps >40°

**Image 1**

Semi-free ranging *Lemur catta* resting together in NHE4

**Image 2**



Male lemur eating supplemental food (monkey chow) provided by technician

**Table 1: Subject Information**

| **Lemur Name** | **Alena** | **Alexander** | **Berisades** | **Cap'n Lee** | **Cleis** | **Dory** | **Fern** | **Fritz** | **Ivy** | **Nicaea** | **Persep-hone** |
|---|---|---|---|---|---|---|---|---|---|---|---|
| **Sex** | F | M | M | M | F | F | F | M | M | F | F |
| **DOB*** | 3/18/05 | 3/18/05 | 3/28/04 | 3/25/00 | 4/09/85 | 3/15/89 | 4/25/07 | 5/15/02 | 5/4/04 | 3/18/04 | 4/25/04 |
| **POB**** | DLC | DLC | DLC | SCI | DLC | DLC | DLC | SCI | DLC | DLC | DLC |

*Date of Birth **Place of Birth

A twenty-one day observational experiment (July-August) during non-breeding season was conducted using the scan (instantaneous) sampling method. Scan sampling is a technique in which the observer records the animal's current activity at a certain moment in time, so it is a sample of its activity state at that moment (Cohen, 1971; Altmann 1973). The lemurs were observed at intervals of five minutes, and the behaviors were recorded for a total of 65 hours (around 32 hours per adult). To record my observations, a behavioral index was used (see table 2), which included the four main activities of lemur, refining them through addition of certain data subsets, however focusing primarily on the feeding aspect of their behavior. The lemurs were separated into two groups each day, with three hour blocks of each a day, in either the morning or the afternoon, switching time intervals every other day to maintain data accuracy (Altmann, 1970).

**Table 2: Behavioral Index**

| **Feeding – F** | ***Social – S*** | ***Resting- R*** | ***Travel – T*** |
|---|---|---|---|
| Monkey chow – *mc* | Groom – *g* | Alone – *a* | Foraging– *for* |
| Young leaves– *yl* | Fighting-*f* | Social– *s* | not foraging- *nf* |
| Mature Leaves – *ml* | Play– *p* | | |
| Water– *h* | | | |
| Stems– *s* | | | |
| Grass – *g* | | | |
| Bark/Wood – *bw* | | | |
| Fruit/flowers/berries/nuts – *f* | | | |
| Ripe – *r* | | | |
| Unripe – *ur* | | | |
| Other* – *o* | | | |

*Other = (dead leaves, mushrooms, insects, dirt)

Discussions with DLC staff and technicians provided information about dominance relationships among the eleven lemurs before observation started. Throughout observation, *ad libitum* sampling (Sade 1966) or "non-systematic sampling" was used. This means that all negative interactions were noted, especially during feeding (when dominance relationships are most noticeable), to assess a hierarchy throughout the group of eleven lemurs. The subordinate lemurs are assessed as the ones that defer to the dominant lemurs in feeding and run away during confrontation with another lemur.

For the analysis of the change in weight of the eleven semi-free ranging *Lemur catta*, previous data collected by DLC technicians was used. The DLC routinely weighs the animals approximately every 2-4 months. Weight records dating back to 1995 were used to identify animal moves, health issues, pregnancies, etc. The data were then compiled, reformatted, and analyzed to test for significance between caged and free-ranging weight.

DATA AND RESULTS

Chart 1 depicts the dominance hierarchy among the females and among the males determined during the observational period. For the females, Dory, Alena, and Persephone were found to be most dominant, whereas Cleis, Fern, and Nicaea were found to be the more subordinate females during feeding and social activities. For the males, Alexander and Ivy were found to be the dominant males, whereas Cap'n Lee and Fritz were the more subordinate male lemurs. Berisades was not subordinate to Ivy or Alex and was not dominant to Cap'n Lee and Fritz, therefore he was dominance neutral and was left out of further analysis of dominant versus subordinate lemurs.

**Chart 1: Dominance Relationship Hierarchy**

***Females***

Dory → Alena → Persephone → Cleis → Fern → Nicaea

***Males****

Alexander → Ivy → Cap'n Lee → Fritz

*Berisades dominance neutral

Significant difference in time spent foraging and time spent feeding between dominant and subordinate individuals was calculated for a 95% confidence interval using a two-sample T-test. Table 3 displays the average percentage of time (and Standard Deviation) spent on feeding and foraging by the males, females, and respective groups of dominant and subordinate lemurs. Figure 1 illustrates the differences between these four groupings in feeding and foraging time, with Table 4 depicting the P-values of all the

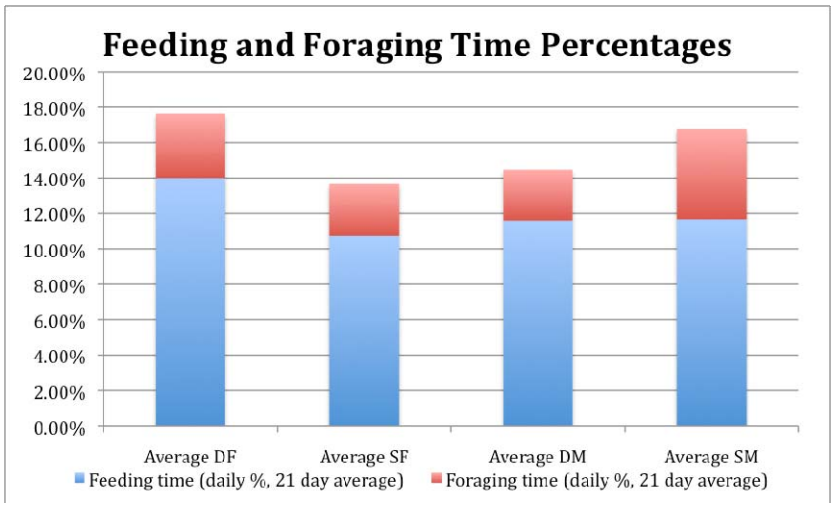
statistical results. The dominant females had an almost significantly (P-value = 0.054) greater percentage total feeding time than the subordinate females, at a 94% confidence interval. However, there was no significant difference in feeding time between dominant males and subordinate males (P-value = 0.565). There was no correlation between differences in the foraging times in dominant females versus subordinate females (P-value = 0.772). There was, however, a significant difference (P-value =0.031) between foraging in dominant males versus subordinate males, in that the subordinate males spent a significantly greater amount of their time foraging.

**Table 3: Observational Percentage Time Data**

| | Average M | Average F | Average DF | Average SF | Average DM* | Average SM* | Average D | Average S |
|---|---|---|---|---|---|---|---|---|
| Feeding time (daily %, 21 day average) | 11.46% (0.47%) | 12.36% (2.56%) | 14.01% (1.94%) | 10.72% (1.98%) | 11.59% (0.18%) | 11.66% (0.47%) | 13.04% (1.29%) | 11.10% (1.63%) |
| Foraging time | 4.57% (1.08%) | 3.29% (1.62%) | 3.63% (1.00%) | 2.94% (1.05%) | 2.88% (0.48%) | 5.09% (0.61%) | 3.33% (0.93%) | 3.80% (1.38%) |
| Feeding and foraging time combined | 16.03% (3.06%) | 15.65% (1.49%) | 17.64% (1.37%) | 13.67% (2.99%) | 14.47% (0.29%) | 16.75% (1.08%) | 16.37% (1.06%) | 14.90% (2.84%) |
| Supplemental (MC) feeding time | 64.09% (7.61%) | 56.11% (5.63%) | 57.34% (6.19%) | 54.89% (8.63%) | 65.17% (8.30%) | 63.95% (2.72%) | 60.47% (10.08%) | 58.51% (8.21%) |
| Other feeding time | 35.91% | 43.89% | 42.66% | 45.11% | 34.83% | 36.05% | 39.53% | 41.59% |

Key: (Standard Deviation) in Parenthesis, M = Male, F = Female, D = Dominant, S = Subordinate, MC =MC
*Berisades left out of comparisons because dominance neutrality

**Figure 1**: **Comparison of Percent Time Spent Feeding and Foraging in Dominant and Subordinate Males and Females**




There was no significant difference in time spent eating the supplemental diet provided, between dominant males versus subordinate males (P-value = 0.436). There was also no significant correlation between dominant females versus subordinate females (P-value = 0.356) in relation to time spent feeding on the supplemental diet. A significant correlation (P-value = 0.039) does exist, however, in comparison of males versus females, in that females spent a greater percentage of their time eating supplemental monkey chow than did the males. The average feeding time of all dominant lemurs was significantly greater than the feeding time versus all subordinate lemurs (P-value = 0.036). There was no statistically significant difference in foraging time between all dominant versus all subordinate lemurs (P-value = 0.555).

**Table 4: P-values of Observational Data**

| | % Time Spent Feeding | % Time Spent Foraging | Time Spent Feeding on Supplemental Chow |
|---|---|---|---|
| DF v. SF | PV = 0.054 | PV = 0.772 | PV = 0.356 |
| DM v. SM | PV = 0.565 | PV = 0.031 | PV = 0.436 |
| M v. F | NA | NA | PV = 0.039 |
| D v. S | PV = 0.036 | PV = 0.555 | NA |

Key: V. = versus, D = Dominant, S = Subordinate, M = Male, F = Female, PV = P-value, NA = Not Applicable, comparison does not test project hypothesis

The weight data for all eleven lemurs was analyzed using a two-sample T-test with a 95% confidence interval, with variables such as juvenile growth, pregnancy, and lactation being factored into the free ranging versus caged period weight difference. Weights taken when animals were growing (under 24 months of age), pregnant, or lactating were removed as these factors will clearly have a strong impact on animal weight. Cleis and Dory were the only lemurs that were pregnant, which was factored into the results by not including the weight data measured when they were pregnant or lactating. Fern was completely removed from this dataset because her entire weight data history was affected by her continuous period of juvenile growth (i.e., had not yet achieved maturity and stable adult weight).

All the females decreased in weight when free ranging, and four out of five of the females had significantly decreased weight when free ranging (P-values = 0.000, 0.009, 0.000, 0.042), with only one female, Nicaea, not significantly changing weights (P-value =0.278). The lemur with the most significant decrease in weight was the dominant female Persephone, as can be seen in Figure 3 boxplot below. On the other hand, only three of five males decreased in weight when free ranging and only one of them, Fritz changed significantly (P-value = 0.012). Weights of two of the males decreased when caged and

increased when free ranging, but neither set of changes were significant (P-values = 0.189, 0.472). The male with the least significant change in body weight was Ivy (Figure 4 boxplot, below). As represented in the box-plot of Figure 2, for all ten lemurs combined there was a highly significant overall decrease in body weight when free ranging (P-value = 0.000).

**Key For Boxplots** CI = Confidence Interval, N=Number of Data Points
SE Mean = Standard Error Mean, DF= Degrees of Freedom , StDev = Standard Deviation

**Significance of All Lemurs**
**Two-Sample T-Test & CI: all-c, all-fr**
Two-sample T for all-c vs all-fr

| | N | Mean | StDev | SE Mean |
|---|---|---|---|---|
| all-c | 115 | 2.486 | 0.288 | 0.027 |
| all-fr | 140 | 2.355 | 0.234 | 0.020 |

95% CI for difference: (0.0671, 0.1957)
T-Test of difference = 0 (vs not =):
T-Value = 4.02, P-Value = 0.000, DF = 253

**Figure 2: Boxplot of all lemurs weight caged versus free ranging**

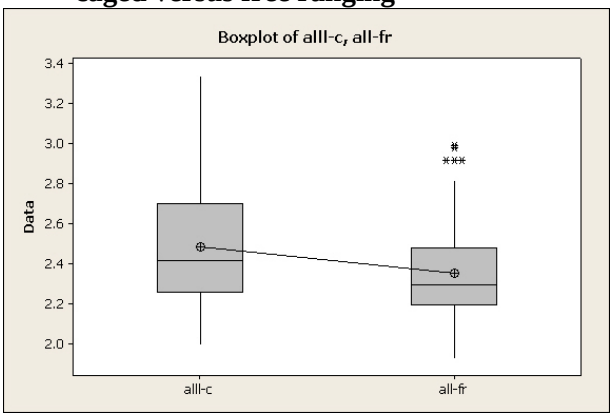
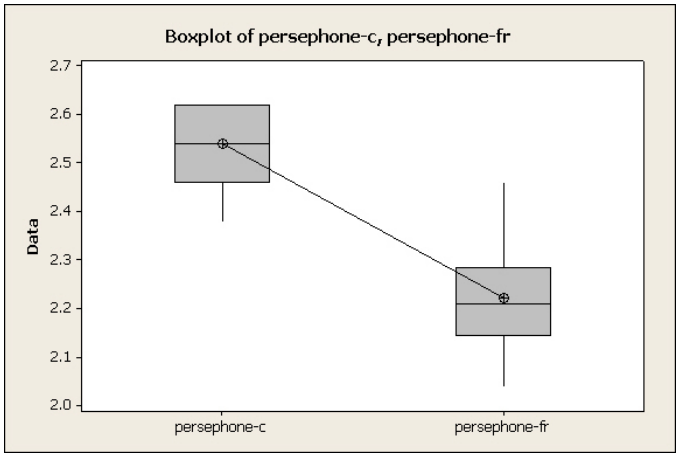



**Figure 3**: **Boxplot of weight of Persephone caged versus free ranging**

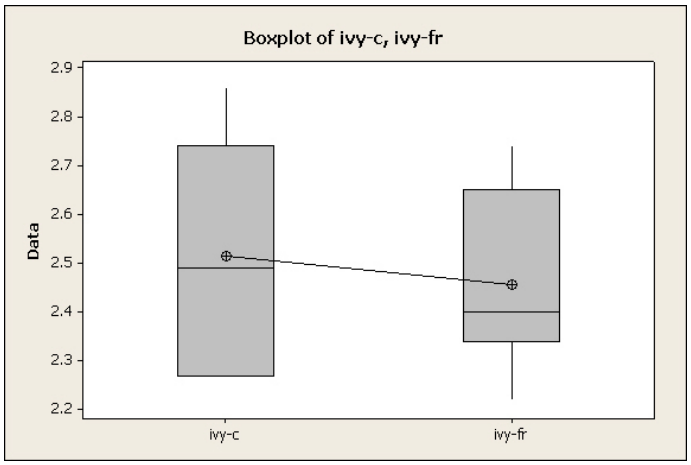



**Most Significant Lemur: Persephone**
**Two-Sample T-Test & CI: pers-c, pers-fr**
Two-sample T for pers-c vs pers-fr

| | N | Mean | StDev | SE Mean |
|---|---|---|---|---|
| pers-c | 5 | 2.5400 | 0.0980 | 0.044 |
| pers-fr | 10 | 2.223 | 0.120 | 0.038 |

95% CI for difference: (0.1828, 0.4522)
T-Test of difference = 0 (vs not =):
T-Value = 5.09 P-Value = 0.000 DF = 13
Both use Pooled StDev = 0.1138

**Figure 4: Boxplot of difference in weight of Ivy caged versus free ranging**




**Least Significant Lemur: Ivy**
**Two-Sample T-Test and CI: ivy-c, ivy-fr**

Two-sample T for ivy-c vs ivy-fr

| | N | Mean | StDev | SE Mean |
|---|---|---|---|---|
| ivy-c | 6 | 2.513 | 0.241 | 0.098 |
| ivy-fr | 13 | 2.457 | 0.170 | 0.047 |

95% CI for difference: (-0.1454, 0.2574)
T-Test of difference = 0 (vs not =):
T-Value = 0.59 P-Value = 0.565 DF = 17

**Table 5: Summary Of Significance of Changes In Lemur Weight When Free Ranging Versus Caged**

| Name | FR change | significant | p-value |
|---|---|---|---|
| all | down | yes | 0.000 |
| Alena (F) | down | yes | 0.009 |
| Alex (M) | up | no | 0.189 |
| Berisades (M) | up | no | 0.472 |
| Cap'n Lee (M) | down | no | 0.485 |
| Cleis (F) | down | yes | 0.000 |
| Dory (F) | down | yes | 0.042 |
| Fern (F) | n/a | n/a | n/a |
| Fritz (M) | down | yes | 0.012 |
| Ivy (M) | down | no | 0.565 |
| Nicaea (F) | down | no | 0.278 |
| Persephone (F) | down | yes | 0.000 |

Females (F): 5/5 females lower when FR (4/5 significantly)
Males (M): 2/5 males higher when free-ranging (not significantly)
3/5 males lower when free-ranging (only 1 significantly)
Outliers: Fritz only male to change significantly
Nicaea only female to NOT change significantly

DISCUSSION

The weight data results indicated that overall the ring-tailed lemurs had significantly lower weights when free ranging than when caged, providing strong support for $H_1$ in this case. The majority of the females (except for one) had significant decreases in weight when free ranging, which again supports $H_1$. However, the males were much more varied in weight, with some decreasing and some increasing in weight when free ranging, with only one male actually showing a significant decrease in weight. The results comparing the males' weights contradict $H_1$ for the overall male study population. The probable reason for the one male outlier's (Fritz) weight decreasing significantly is because he is the most subordinate lemur in the group and most likely is not feeding on supplemental food as regularly when free ranging as when caged. When Fritz is in the cage during the winter, he is separated from the more aggressive dominant lemurs, and therefore the technicians tend to feed him more than is necessarily required for a balanced diet. When in NHE4, Fritz is constantly the last lemur in the troop to eat the supplemental monkey chow, feeding on mostly the remnants of the other lemurs' food and forced to forage for parts of his diet. The rest of the males not having a significant decrease in weight, whereas the majority of the females have a significant decrease in weight, is attributed to the fact that *Lemur catta* are a female dominated society, and the feeding struggle among the female is much more extreme between females than it is between males. Therefore, when females are free ranging they will lose weight because of the increased struggle for food and intrasexual competition (Kappeler 1990).

The observational results revealed that the dominant females spent a greater percentage of their feeding than the subordinate females. While this does not entirely

confirm $H_2$ it suggests that there is a probable correlation between dominance in females and feeding time. There was no significant difference in dominant female foraging time, which suggests that females rely more on the keeper provided monkey chow during feeding time for their diet. The reason for no correlation in the foraging time is further supported by the evidence that females overall spend a greater amount of their time than males feeding on monkey chow, than on foraging and feeding on leaves and fruits. Dominant males, on the other hand, did not spend a significantly greater percentage of time foraging than the subordinate males, which does not support $H_2$. Compared to dominant males, the subordinate males spent a significantly greater percentage of their time foraging for food, which supports $H_2$. This result can be understood by the data demonstrating that males spent a significantly greater amount of time foraging for leaves and fruits than females. This documents that males rely less on the supplemental feeding and more on foraging, which would explain why there was no significant difference between dominant and subordinate feeding time, and a large and significant difference in dominant males foraging less than subordinate males.

These results illustrate that the issue of weight variability and feeding and foraging percentage times in free ranging *Lemur catta* are most likely due primarily to gender identity as supported by $H_1$ and dominance status in the troop of lemurs as supported by $H_2$. Through referencing historical data and observing the *Lemur Catta* while free ranging, the results suggest that dominance and gender play a major role in free ranging population feeding and foraging time. The study also finds the lemurs' weight decreases significantly when free ranging, which indicates an increase in fitness and that free ranging is a healthy way to maintain captive populations and potentially

reintroduce into novel habitats (Keith-Lucas 1999). These findings are novel because studies of this nature have either been done on caged or wild lemurs, but not on semi-free ranging lemurs at the DLC in which conditions can be regularly monitored. This semi-free ranging system of partially caged living/partially free ranging living provided a unique opportunity to replicate both conditions of lemurs in the wild and conditions of lemurs in captivity. When assessing different factors such as the differences in weight between caged and free ranging, one is in essence looking at both the wild and the captive conditions in one lemur. The observational percentage of activity time and dominance data has advantages over wild observation in that one can measure all variables on a regular basis, since there are many unpredictable features of observing and obtaining data in the wild.

For future testing, it would improve the study to use a larger sample size and include additional hours of observation for a more substantial data set to enhance the ability to contradict null hypotheses and increase reliability of the statistical analysis. Included in this study would also be an analysis of the precise nutritional value of the food the *Lemur catta* are eating to observe if weight when free ranging also is affected by the actual nutritional content of the food they are foraging for, not simply by the total amount of food consumed, weight difference, or time spent foraging. Hopefully the results found and future testing can in some way influence both preservation plans for lemurs in captivity, and help make informed decisions about *Lemur catta* diet and feeding provisions in long-term wild habitat conservation.

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WORKS CITED

Altmann, Jeanne. "Observational Study of Behavior: Sampling Methods." *University of Chicago Press* 15 (1973).

Altmann, Jeanne, and S. A. Altmann. "Baboon Ecology: African Field Research." *Bibl. Primatol* 12 (1970): 490-522.

Christine, Drea M., and Weil Anne. "External Genital Morphology of the Ring-tailed Lemur (lemur catta): Females are Naturally "Masculinized"" *Journal of Morphology* 269 (2008): 451-63. Print.Dunham, Amy E. "Battle of the sexes: cost asymmetry explains female dominance." Animal Behavior (2008): 1435-439.

Cohen, J. E. "Social grouping and troop size in yellow baboons." *Int. Congr. Primat.* 3 (1954): 58-64.

Dunham, Amy E., Erhart M. Elizabeth, Overdorff J. Deborah, and Wright C. Patricia. "Evaluating effects of deforestation, hunting, and El NIno events on a threatened lemur." *Biological Conservation* 141 (2008): 287-97.

Ganzhorn, J. U. "Feeding behavior of *Lemur catta* and *Lemur fulvus*." International Journal of Primatology 7 (1986): 1-15.

Glander, Kenneth E., and Dori P. Rabin. "Food Choice From Endemic North Carolina Tree Species by Captive Prosimians (*lemur fulvus*)." American Journal of Primatology 5 (1983): 221-29.

Godfrey, L. R. "Ontogenetic Correlates of Diet in Malagasy Lemurs." AMERICAN JOURNAL OF PHYSICAL ANTHROPOLOGY 123 (2004): 250-76.

Jolly A. 1966. Lemur behavior: a Madagascar field study. Chicago (IL): Univ Chicago Pr. 187 p.

Janson CH, Van Schaik CP. 1993. Ecological risk aversion in juvenile primates: slow and steady wins the race. In: Pereira ME, Fairbanks LA, editors. "Juvenile primates: life history, development, and behavior." Chicago: University of Chicago Press. p 57–74.

Kappeler, Peter M. "Female Dominance in Lemur Catta: More than Just Female Feeding Priority?" Folia Primatol (1990): 92-95.

Keith-Lucas, Timothy, Francis White, Laura Vick, and Lisa Keith-Lucas. "Changes in Behavior in Free-Ranging Lemur catta." American Journal of Primatology (1999): 15-28.

Linnaeus, Carolus. "Systema Naturae." (1758).

Mittermeier RA, Konstant WR, Nicoll ME, Langrand O. 1992. “Lemurs of Madagascar: an action plan for their conservation, 1993-1999. Gland (Switzerland)”: IUCN. 58 p.

Mowery, Christopher B., Colleen McCann, Robert Lessnau, and Ellen Dierenfeld. "Secondary Compounds in Foods Selected by Free-Ranging Primates on St. Catherines Island, GA." Ring-tailed Lemur (Lemur catta) Husbandry Manual: American Association of Zoos and Aquariums (2001).

Sade, D. S. "Ontogeny of social relations in a group of free-ranging monkeys (macaca mulatta Zimmerman)." *Dissertation at University of California, Berkeley*.

Sauther, Michelle L., Robert W. Sussman, and Lisa Gould. "The Socioecology of the Ringtailed Lemur: Thirty-Five Years of Research." Evolutionary Anthropology (1999).

Sussman RW. 1991. “Demography and social organization of free-ranging *Lemur catta* in the Beza Mahafaly Reserve, Madagascar.” Am J Phys Anthro 84(1): 43-58.