

**The Effects of Age on Behavioral Thermoregulation in  
*Lemur catta* and *Propithecus coquereli***

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## Abstract

Older mammals experience a decrease in physiological function that impairs their ability to internally regulate body temperature. Behavioral mechanisms can be used to alleviate thermal stress on the body, and thus could be an effective strategy for coping with such deficiencies that accompany the aging process. I studied geriatric and younger individuals of five semi-free ranging groups of *Lemur catta* and *Propithecus coquereli* to determine whether or not older lemurs were utilizing behavioral thermoregulation more often than younger lemurs across a range of temperatures. Using focal animal sampling, I examined activity level, the use of heat-retaining and heat-dissipating postures, and sun exposure preference. I found that older lemurs changed their own behavior more than younger individuals to utilize low-energy thermoregulatory behaviors, such as decreasing activity level as temperature increased, shifting to utilize heat-retaining postures in cooler temperatures, and shifting to utilize heat-dissipating postures in warmer temperatures. These patterns, however, were not statistically significant and therefore only suggestive of their function in varying ambient temperatures. Still, this information is useful preliminary data, and future study with more focal individuals over a wider range of temperatures may be able to highlight these subtle, but potentially meaningful differences between age classes. By examining the thermoregulatory potential of all members of lemur social groups we can make more informed conservation decisions for these species in changing climatic environments.

## Introduction

Aging in humans impairs an individual's ability to autonomically maintain core body temperature (DeGroot and Kenney 2006) and a similar decline in thermoregulatory ability may be seen in older non-human primates as well (Aujard et al. 2006). In harsh environmental conditions, behavioral adjustments are the most reasonable first response to such age-related physiological deficiencies (Terrien et al. 2011). This study aims to compare the thermoregulatory behavior between older primates and their younger counterparts across a range of temperatures to determine the importance and role of behavior in temperature regulation for two species of lemur.

### Body Temperature Regulation

With regards to core body temperature ( $T_c$ ) regulation, animals are categorized as either homeotherms or poikilotherms. Homeotherms have the ability to maintain a relatively narrow core temperature range despite changes in ambient temperature, whereas poikilotherms lack this ability, causing their body temperature to fluctuate with the environment (reviewed in Tabarean et al. 2009). In order for homeotherms to maintain normal internal temperature (normothermia) in an overly hot or cold environment, they rely on an energetically-costly set of metabolic, endocrine, and muscular responses (Terrien et al. 2011). These autonomic responses are activated mainly by thermoregulatory pathways in the preoptic and anterior hypothalamic area as a reaction to ambient temperatures that are outside an organism's ideal temperature range, or thermoneutral zone (Van Someren et al. 2002). However, autonomic responses are energetically costly and alone they have a limited ability to prevent hyperthermia or hypothermia, so homeothermic species exhibit certain behaviors to supplement these processes when they experience thermal discomfort, minimizing temperature-induced stress on the body (Flouris 2011).

Thermoregulatory behaviors can function to manage activity levels and internal rates of heat production, minimize or maximize heat loss via body-surface radiation, or select/create

microhabitats that better suit thermoneutral conditions (Donati et al. 2011). For example, yellow baboons (*Papio cynocephalus*) are more likely to slow their movement and stop to rest in shady areas in high ambient temperatures (Stelzner 1988). In the cold, Japanese macaques (*Macaca fuscata*) congregate in tight social huddles on cloudy winter days, effectively minimizing surface to mass ratio and thus conserving heat. When the sun comes out, the macaques tend to separate from huddles and open their posture to absorb solar radiation (Hanya et al 2007). Mammals have discovered countless ways to manipulate their thermal condition—other examples include nest building for insulation, increased food consumption for digestion-induced thermogenesis, and panting to dissipate excess heat (Terrien et al. 2011).

These behaviors work in concert with autonomic mechanisms, but are believed to be activated by separate pathways in the *posterior* hypothalamus as it processes information from the body indicating thermal discomfort (Van Someren et al. 2002). Thus, in order for a homeothermic individual to effectively maintain  $T_c$ , it must be able to recognize ambient and internal temperatures that cause thermal stress, activate the proper autonomic mechanisms, and behave appropriately given the nature of the surrounding environment (Van Someren et al. 2002, Donati et al. 2011). Nonetheless, the extent by which each of these components is utilized varies between species, gender, and age-class (Terrien et al. 2009, Terrien et al. 2010).

### Aging and Thermoregulation

The aging process in all living organisms is accompanied by physiological and morphological changes that impair bodily function (Languille et al. 2011). We know that humans and non-human primates experience an age-related decrease in their ability to maintain proper  $T_c$ , but because thermoregulation requires a complex feedback system there could be numerous reasons for this finding (Von Someren et al. 2002, Weinert 2010, Terrien et al. 2009). In a young, healthy homeotherm temperature receptors in the skin identify and trigger “hot” and “cold”

sensations, and receptors in the body core and central nervous system identify thermal stress on the body and activate autonomic responses. Information from all three forms of temperature reception (skin, body core, and central nervous system) is processed by the anterior and posterior regions of the hypothalamus, resulting in the emotional response that is thermal “comfort” or “discomfort” (Van Someren et al. 2002). Aging could have an effect on any or all of these pathways and structures, and by looking at behavior we can gain information as to what the main issues are with thermoregulation for geriatric mammals.

With regards to autonomic factors, older mammals are known to show a decline in basal metabolic rate, ability to produce body heat, and evaporative heat loss capacity (Terrien et al. 2011). If deficiencies such as these were to be the main thermoregulatory problems that arise with aging, we would expect that geriatric animals would utilize behavioral thermoregulation more than their younger counterpart to make up for these impairments. Aujard et al. (2006) found that old mouse lemurs, as compared to prime-aged adults, were much more inclined to choose warmer microhabitats when given access to five temperature controlled chambers (10°, 15°, 20°, 25°, and 30° C), and consistently avoided cold exposure. The results from this study suggest that older mouse lemurs have more costs associated with colder temperatures, and must therefore spend more time alleviating them through behavior.

This is not always seen with senescence in homeotherms. In humans, for example, it has been shown that thermal perception attenuates with age—the elderly do not respond to hot or cold stimuli as sharply as younger individuals, and are particularly less sensitive to warm stimuli (Meh and Denislic 1994). This suggests an increased range of perceived thermal comfort, and results in less behavioral response to temperature change as older individuals are less likely to recognize temperature stress. If this were to be the main thermoregulatory problem that manifests with age, the consequences would be much more detrimental given that they are neither able to recognize nor autonomically compensate for thermal stress. Still, another possibility is that while there are

autonomic deficiencies that develop with age, they remain unnoticed and behavior remains consistent throughout the aging process. A study on found that old and young rats showed an equal amount of behavioral thermoregulation when exposed to cold temperatures and access to a lever that turns on a heater. Here they were unable to find any differences in performance, proposing that aging has no significant effect on thermal perception or behavior (Jakubczak 1966).

Species variation can account for many different factors (surface to mass ratio, basal metabolic rate, social systems, environmental conditions, etc.) but a general lack of data leaves a lot of room for growth in this field of research. This study aims to observe the relative use of behavioral thermoregulation in old and young lemurs, which are known to exhibit a large array of thermoregulatory behaviors in order to cope with harsh environmental conditions in Madagascar. I will be using two different diurnal lemur species as models: *Lemur catta* and *Propithecus coquereli*.

#### *Lemur catta* in the wild

Wild *Lemur catta*, ring-tailed lemurs, reside in multi-male, multi-female social groups, which have been observed to be somewhere between 6 and 24 individuals (Mittermier and Nash 1994). They have been observed in the south, southwest, and western side of Madagascar, occupying a range of habitats that include spiny, scrub, gallery and dry deciduous forest (Gould et al. 2003). Temperatures in these areas typically average between 20-30°C most of the year, but based on their distribution wild ring-tailed lemurs can experience temperatures as low as -7° C and as high as 48°C. (Gould et al. 2003, Goodman et al. 1996, Sussman 1991).

*Lemur catta* have been found to have a relatively low basal metabolic rate (BMR) and energy output for their size, which is likely in order to facilitate fat build-up before the lean dry season (Simmen et al. 2010). The low BMR found in this species implies an increased need for behavioral thermoregulation, especially with harsh and variable environmental conditions. To support this, they have been observed performing a number of behaviors with thermoregulatory

functions. For example, they are known for their characteristic “sunning” behavior, in which they sit with their ventrum facing the sun, arms extended out at their sides, and legs opened with their knees bent in order to absorb as much solar radiation as possible (Gould et al. 2011, Wright 1999, Jolly 1966). During cold months, they spend a significant amount of time in social huddles, minimizing the surface to mass ratio of the total group to avoid heat loss (Jolly 1966, Wright 1999). They have also shown an ability to behaviorally adapt to multiple habitats with varying thermal qualities. *Lemur catta* living in the spiny forests—where there is no actual forest canopy and little shade—have been observed to spend significantly more time resting during hotter months than other groups of ring-tails living in shadier habitats (Gould et al. 2011).

Because ring-tailed lemurs have adapted to a number of different climatic regions in Madagascar, they make a useful model species for gaining thermoregulatory information. However, it is also valuable to look at the thermoregulatory behavior of a species that naturally adapted to a more neutral thermal environment, such as *Propithecus coquereli*. If this species were to be exposed to greater temperature variation than it experiences in the wild, it may elicit certain behavioral responses that are not typically seen. This could shed light on how these lemurs adapt to thermal conditions without as many alternative explanations for why these behaviors evolved.

#### *Propithecus coquereli* in the wild

*Propithecus coquereli*, or Coquerel’s sifakas, are known to occupy the dry deciduous forests of northwest Madagascar where the mean annual temperature falls around 27° C (Demes et al. 1996, Petter 1962). Occasionally temperatures can drop as low as 14°C in the dry season and rise as high as 39.5°C in the wet season, but daily temperature does not fluctuate as much here as it does in the south (Richard 1978). Like *Lemur catta*, *Propithecus coquereli* are known to have a low basal metabolic rate, but have a small thermoregulatory advantage in that they are

slightly larger than *Lemur catta* (3.7-4.3 kg vs. 2.3-3.5 kg), giving them a lower surface to mass ratio (Tattersal 1982, Terrien et al 2011, Richard and Nicole 1987). However, despite their larger size and exposure to milder conditions, *Propithecus coquereli* has been seen to display behavior with thermoregulatory implications.

Evidence of behavioral thermoregulation in this species involves regulating sun exposure and activity level. Richard (1978) observed that *Propithecus coquereli* spent significantly more time high in the canopy during the cooler dry season, and attributes it specifically to an increase in treetop sunning behavior. On most mornings in the dry season, they would spend about an hour sitting or hanging with their arms and legs splayed and their ventrum facing the sun. Then at night they would huddle together for warmth. During the warmer wet season they allocate less time to this form of resting behavior, and spend more time at lower, shadier elevations (Richard 1978). Additionally, *Propithecus verreauxi*, their closest relative, spends the smallest amount of time resting at night during the cold winter months to prevent body temperature from dropping too low (Eckert et al. 2004).

### Hypothesis and Predictions

Although climate in Madagascar can bring about harsh seasonal conditions (with occasional heat waves, droughts, and below-freezing temperatures), there have not been any recorded illnesses or deaths in wild lemurs directly attributed to extreme temperatures (Wright 1999). By taking into account the known physiological consequences of aging, geriatric lemurs may be able to survive these extremes through behavioral adaptations. Therefore, I hypothesize that geriatric lemurs will allocate more time to thermoregulatory behaviors to compensate for autonomic deficiencies and minimize the energy demand imposed by temperature stress.



### *Prediction One: Activity levels*

Physical activity results in an increase in internal heat production, which can be detrimental in extreme heat. I predict that geriatric lemurs will show a significant decrease in physical activity levels in hotter ambient temperatures, relative both to their own personal activity levels in neutral and colder temperatures, and to the activity levels of their younger counterparts. While the converse (increase in activity level in cooler ambient temperatures to produce more internal heat) may be an effective thermoregulatory strategy for young, healthy lemurs, there are too many other age-related factors that may prevent excessive movement in older individuals (joint pain, reduction in muscle strength, etc) for this to be a viable prediction.

### *Prediction Two: Heat loss via surface radiation*

Since higher surface to mass ratios correspond to greater heat loss radiating from the skin, I predict that geriatric lemurs will spend more time in a closed, tucked position or in a social huddle than will younger lemurs in colder temperatures. They will start to display this behavior even when temperatures are at the lower end of their thermal neutral zone, before temperatures have dropped to stressful levels. In hot weather, I believe older lemurs—as compared to younger—will more frequently rest in open, extended positions to help dissipate heat from their body and prevent overheating. As a separate component of this open, extended position, I predict older lemurs will engage in specific sunning behavior (with an open posture and their ventrum facing the sun to absorb solar radiation rather than dissipate heat) more often than younger lemurs in cold weather.

### *Prediction Three: Selected sun exposure*

In hotter temperatures, I predict geriatric lemurs will be more selective with regards to sun exposure, staying in the shade as much as possible. Similarly, during the colder months I predict they will position themselves in sunlight more often than younger individuals.

The Duke Lemur Center in North Carolina provides a unique setting in which to study *Lemur catta* and *Propithecus coquereli* because there are great seasonal fluctuations in temperature conditions, yet the lemurs have the freedom to adjust their behavior and thermal setting at will. To test these predictions, I performed a focal-sampling study of these two lemur species, analyzing behavior between old and young individuals.

## Methods

### Subjects and Housing

A total of 22 lemurs, 7 of which were geriatric (>19 years of age) were observed at the Duke Lemur Center (Tables 1-5). This consisted of two groups of *Propithecus coquereli* and three groups of *Lemur catta*. All individuals were identified using collars, natural markings, and physical features.

**Table 1: *Lemur catta* group 1**

<b>Name</b>	<b>Age (years)</b>	<b>Sex</b>
Aristodes*	20	M
Sosiphanes	16	F
Lilah	8	F

**Table 2: *Lemur catta* group 2**

Dory*	24	F
Fritz	11	M
Alena	8	F

**Table 3: *Lemur catta* group 3**

Aracus*	22	M
Shroeder*	21	F
Leisl	5	F
Johan	3	M
Rolfe	2	M
Brigitta	2	F
Gretl	1	F

**Table 4: *Propithecus coquereli* group 1**

Jovian*	19	M
Pia	14	F
Conrad	4	M
Ferdinand	.5	M

**Table 5: *Propithecus coquereli* group 2**

Drusilla*	20	F
Julian*	20	M
Martinianus	5	M
Arcadia	2	F
Pontius Pilate	.5	M

(\*) = Geriatric individual

The subjects were primarily observed in natural habitat enclosures within the Duke Forest; a fenced in section of mixed forest (deciduous and coniferous) with trees averaging a height of 30 m (Taylor and Sussman, 1985). The subjects also had access to a temperature-controlled building (maintained at approximately 22°C), containing multiple, connected enclosures with dimensions measuring 2.1 X 2.3 X 3 m. Each enclosure had a small doorway that allowed for access to an outdoor, “yard,” enclosure, which mirrored its indoor counterpart in dimensions but had a fenced roof and walls and concrete flooring. The outdoor yard enclosures opened to a fenced in hallway that led out to the forest, allowing the lemurs to transition freely between these three forms of housing. All lemurs are restricted from outdoor access once nightly temperatures drop below 4°C.

### Protocol

Observations were collected using 20-minute focal animal samples, with continuous recording. Samples were collected between the hours of 8 AM and 4 PM over the course of six months (May-October, 2013). During each focal session, the subject’s behavior (Table 6) and exposure to the sun (Table 7) were recorded. Data was recorded on a Pasion Workabout Pro event recorder, programmed with The Observer XT (v.11.5; Noldus 2013) software. A change in any of these variables was recorded after three seconds of a new behavior-- inputting a single entry into

the Psion Workabout takes approximately three seconds on average, so excluding rapid behavioral changes (<3 seconds) that could be missed during this time frame prevented observer error.

Following each focal sample, a Kestrel hand-held weather station was used to note ambient temperature, humidity, heat index, and wind-speed. Cloud cover was also noted (overcast, scattered, clear), as well as whether or not it was raining. In addition, there were two infant lemurs in the study groups, so an estimate of the percentage of time they spent clinging onto their mother or another individual in the group was also noted.

**Table 6:** Behaviors Observed

<b>Behavior Type</b>	<b>Surface to mass classification</b>	<b>Behavior</b>	<b>Description</b>
Inactive	High	Seated: extended limbs	Weight resting on haunches or lower back with at least one or more limbs extended outwards away from the body. Ventrums not exposed to sun.
		Lay	Resting flat on a substrate while on ventrum
		Lounge	Resting flat on a substrate on dorsal side with ventrum exposed
	Neutral	Seated	Weight resting on haunches with arms resting at sides or on the ground. Ventrums not opened to the sun.
		Stand	Resting with weight supported by hands and/or feet touching substrate
	Low	Seated: tucked	Body resting on posterior with ventrum not exposed, arms and hands tucked in to the body, tail either curled or wrapped around the torso
		Huddle	Extensive body contact (such as torso to back or torso to torso) with one or more conspecifics
	High: Sunning	Seated: open sunning	Weight resting on haunches with ventrum exposed towards sun and arms extended away from torso
		Suspensory: facing sun	Hanging from a substrate with at least two hands and/or feet, body opened up so that ventrum is exposed to the sun
Active	--	Social Play	Non-aggressive wrestling, jumping on another individual, playful biting, or rolling around with another individual.
		Locomotion	Movement such as bipedal galloping, quadrupedal walking or running, climbing, or leaping
Consumption	--	Eat	Consuming food
		Drink	Consuming water
Out of view	--	--	Subject cannot be seen at all or is too obscured for observer to confidently identify activity
Other	--	--	Behavior not identified above

**Table 7: Selected Sun Exposure**

Sun	Full exposure to sunlight
Sun/Shade	Partly located in the shade, with over half of the body exposed to sunlight
Shade/Sun	Partly located in the shade, with less than half of the body exposed to sunlight.
Shade	Full enclosure in the shade, with no light filtering through.
Cloud	Positioned completely out of the shade, but the sun is covered by clouds
Cloud/Shade	At least partially located in the shade while clouds cover the sun.
Indoor	Animals retreat indoors for a portion of the observation. (Note: no observations were <i>started</i> while the animal was indoors)

### Analysis

To analyze the results, I separated observations into three temperature bins based on the ambient temperature at the time of the observation: cooler temperatures (23° C or below), neutral temperatures (between 23° C and 28° C), and warmer temperatures (28° C or below). Once separated, all of the results obtained throughout analysis were calculated within these temperature bins for each individual.

To analyze activity levels, I categorized each behavior as “active”, “inactive”, or “consumption” (Table 6). I separated “consumption” from “active” and “inactive” behaviors because of the different thermoregulatory implications of eating and drinking (i.e. food consumption to increase rates of digestion-induced thermogenesis, or hydrating to aid in autonomic regulation of thermal stress). For analysis of heat loss via surface radiation, I only included resting postures in which the animals were not moving. I categorized each behavior as either having a high, neutral, or low surface to volume ratio. Sunning behavior is characteristic of a high surface to volume ratio, but it was separated due to the fact that it is a strategy employed to absorb solar radiation, rather than dissipate excess body heat. For my analysis of selected sun exposure, each variable was analyzed as its own behavioral category. No observations were

started while the focal animal was indoors, but if the subject retreated indoors during the sample the behaviors were included in analysis with the reasoning that their body would still be acclimated to the influence of outdoor temperatures for the duration of the focal session.

In each analysis, I calculated the percent time an individual spent on each broader category defined above, based on the total time they were observed within each temperature bin. I then found the group mean and standard deviation for prime-aged and geriatric lemurs, separating the calculations by species. Residual values were calculated to note individual changes in behavior across a range of temperatures. For each individual, three comparisons were made:

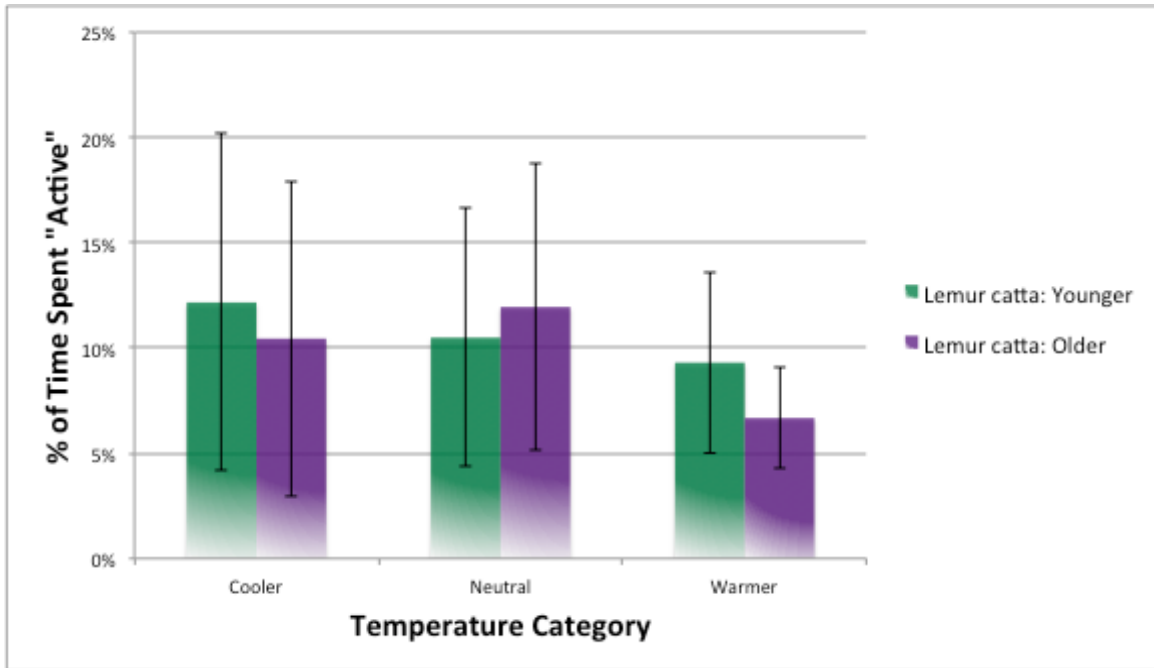
1) subtracting values in neutral conditions from those in warmer conditions; 2) values in cooler conditions from those in neutral conditions; and 3) values in cooler conditions from those in warmer conditions. Individual residual figures were averaged across the older and younger groups of both species separately, as well as the standard deviation for each group. I conducted Mann-Whitney U tests to evaluate whether or not results between age groups of each species were significantly different. Because there were only three geriatric *Lemur catta* and three *Propithecus coquereli* in my study, I was unable to perform Wilcoxon sign-ranks tests to determine if average change in behavior was significant across temperature bins.

## Results

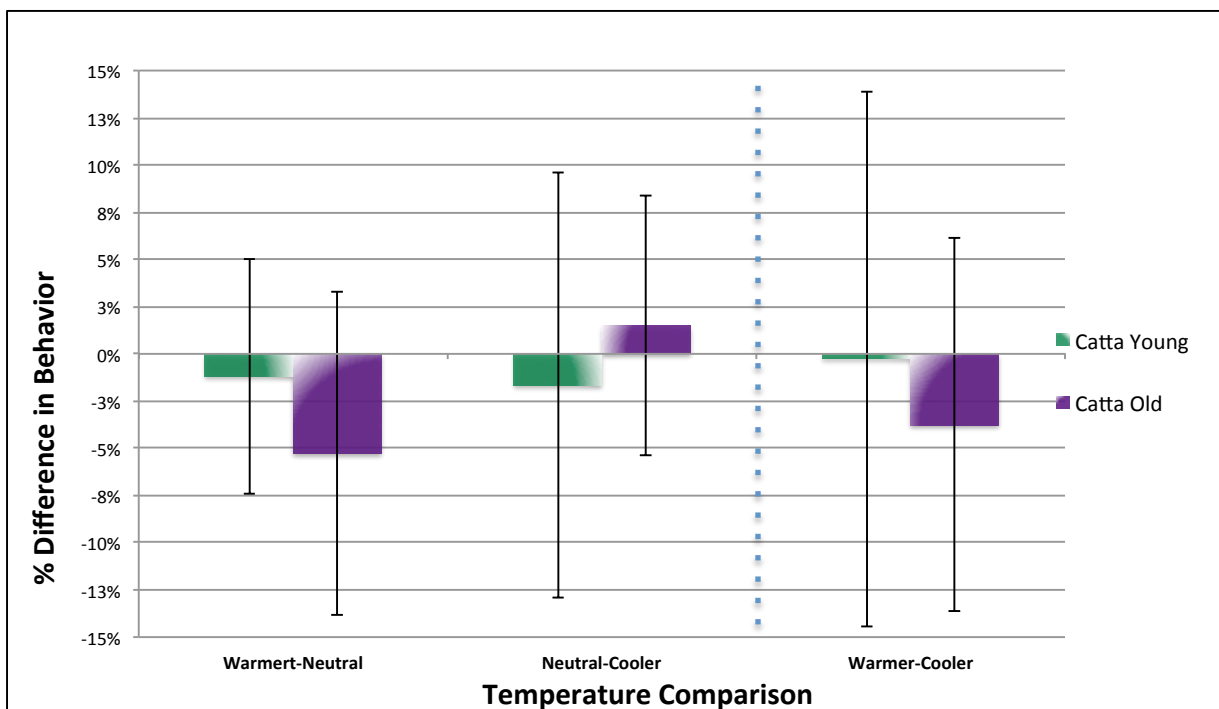
### Activity level

Among *Lemur catta*, the least amount of activity was observed with geriatric individuals in warmer temperatures, but the difference between old and young individuals was not significant ( $6.68\% \pm 2.41$  vs.  $9.31\% \pm 4.28$ , n.s.; Figure 1). When looking at average change in behavior across a range of temperatures, the residual values show that older *Lemur catta*, as compared to younger, will decrease their individual activity level more when temperatures rise above or fall

below the neutral range, with the greatest decrease in activity occurring as temperatures rise above the neutral range (Figure 2, Appendix 15-16).

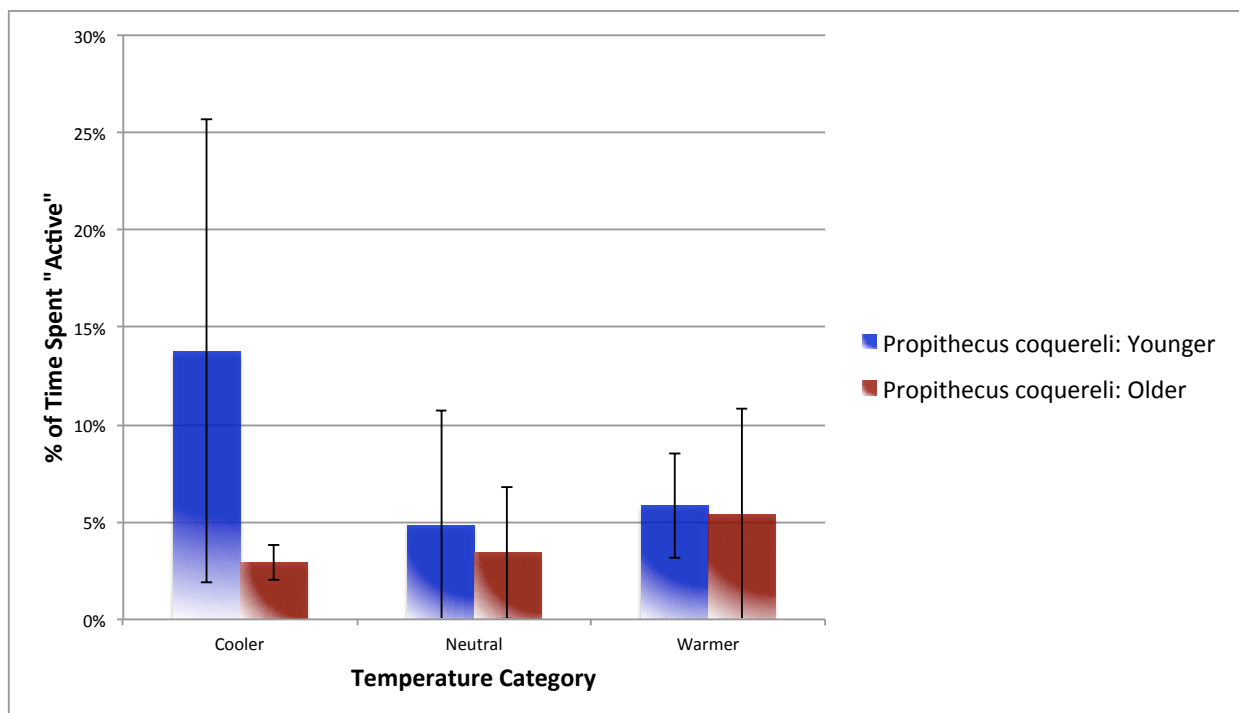


**Figure 1:** *Lemur catta*: Percent time active under different temperature conditions. Younger n=9, Older n=4. % time: average of all individuals in each group. Error bars = standard deviation



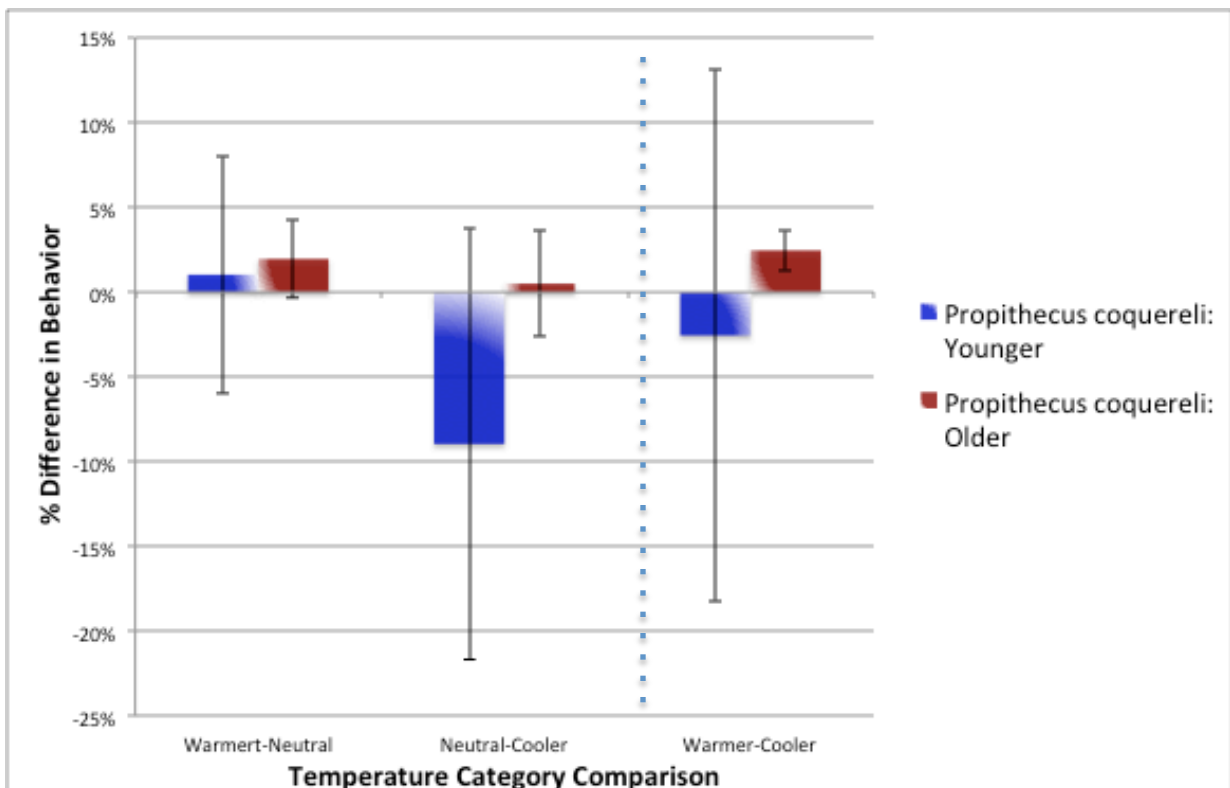
**Figure 2:** *Lemur catta*: Change in active behavior between temperature categories. % difference: average of all individuals in each group. Error bars = standard deviation

For *Propithecus coquereli*, older individuals were less active in the cold than their younger counterparts, but the difference was not significant ( $2.9\% \pm 0.9$  vs.  $13.7\% \pm 11.9$ , ns, Figure 3, Appendix 3- 4). As temperatures dropped from neutral to colder temperatures, on average the younger group increased their activity level by  $8.95\%$  ( $\pm 12.75$ ), while activity level of older individuals did not change ( $0.5\%$  increase  $\pm 3.08$ , ns, Figure 4). There was no clear pattern in general activity in warmer temperatures. Outside of my initial predictions, I observed that geriatric *Propithecus coquereli* spent increasing amounts of time eating and drinking as temperatures declined. At the extremes, they spent an average of  $11.6\%$  ( $\pm 4.11$ ) more time eating in cooler temperatures than in warmer temperatures, whereas younger individuals on average did not adjust consumption and had much more variability in individual change in consumption rate (Appendix 5-6, Figure 5). Both groups of *Lemur catta* showed the opposite trend, increasing consumption as temperatures rose, and the younger individuals of both species showed much more variation in behavior (Figure 5).

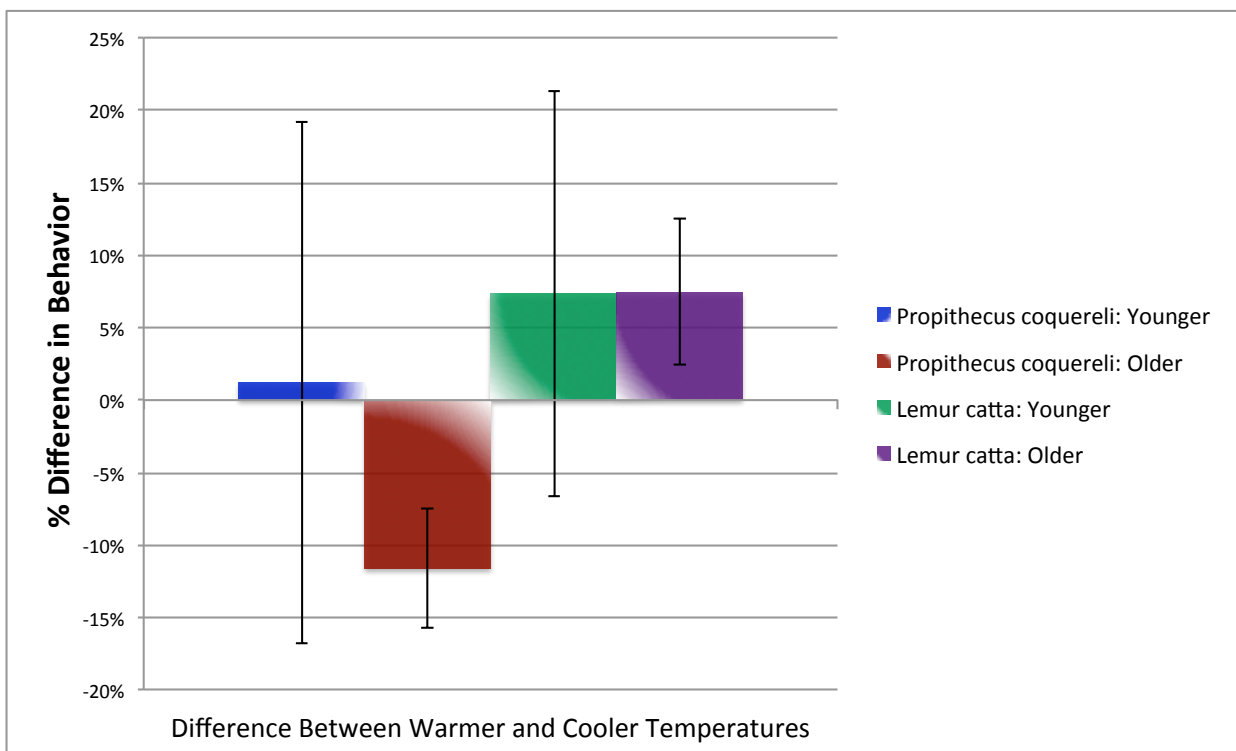


**Figure 3:** *Propithecus coquereli*: Percent time active under different temperature conditions. Younger n=6, Older n=3. % time: average of all individuals in each group. Error bars = standard deviation





**Figure 4:** *Propithecus coquereli*: Change in active behavior between temperature categories. % difference: average of all individuals in each group. Error bars = standard deviation

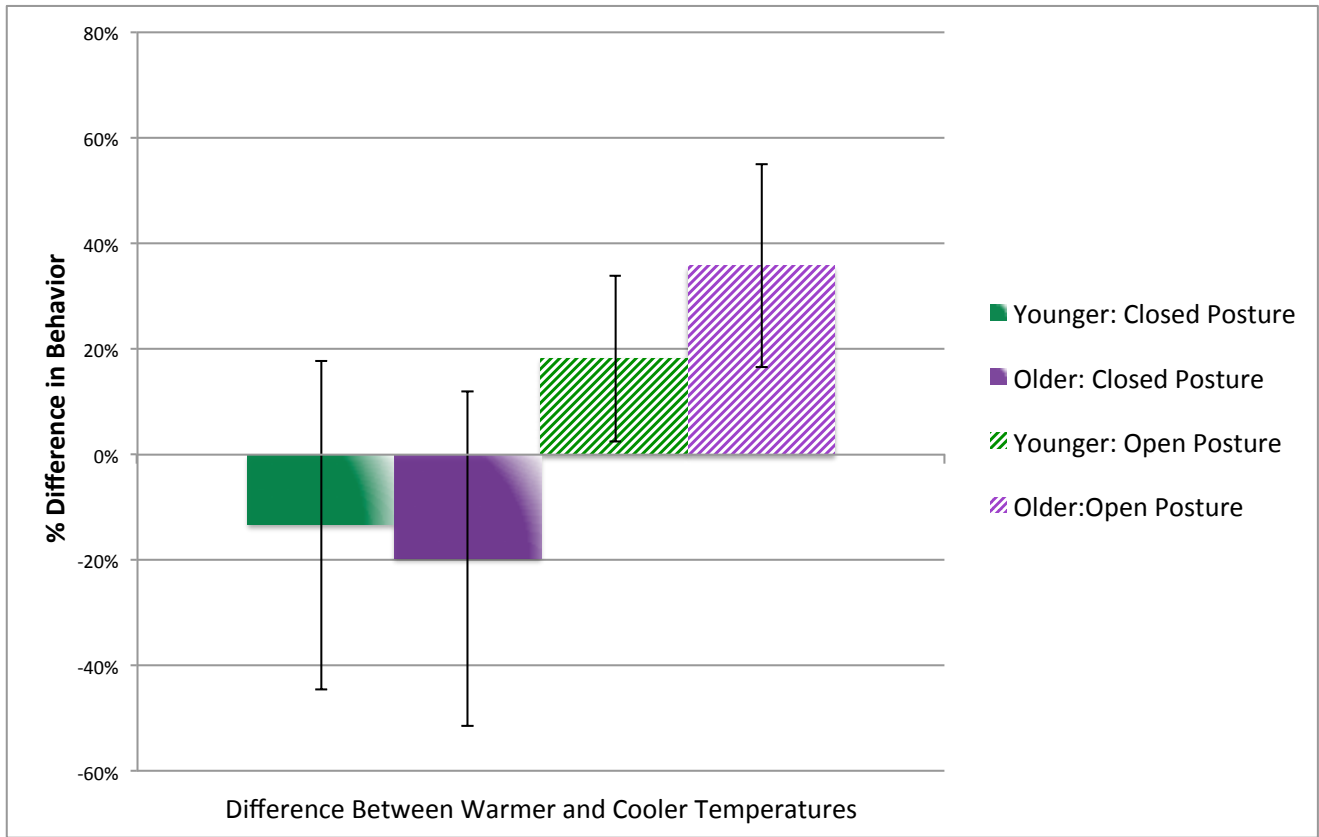


**Figure 5:** Change in eating behavior between warmer and cooler conditions. % difference-average residual values of all individuals in each group. Error bars = standard deviation.

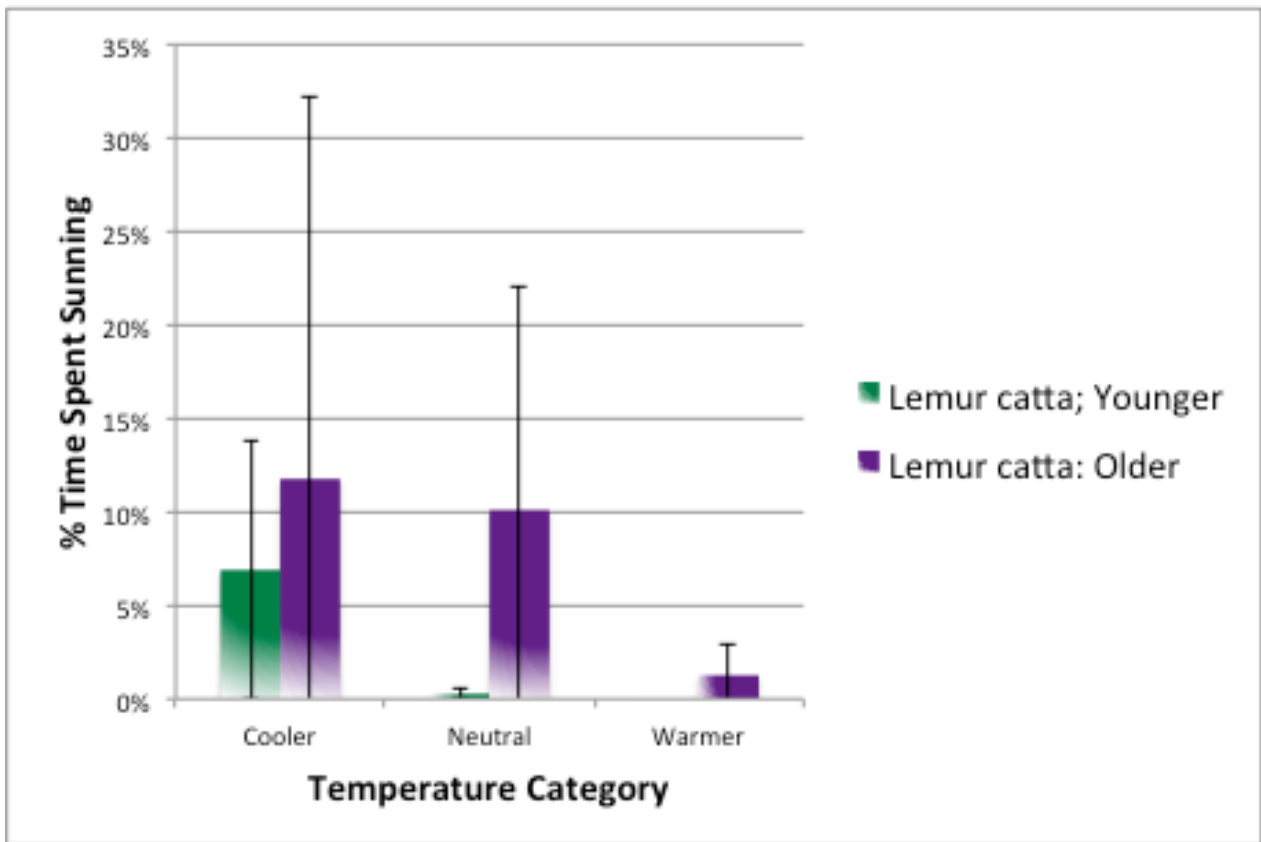
## Heat loss via surface radiation

Older and younger *Lemur catta* individuals rested in heat retaining (closed) postures in essentially equal amounts in cooler weather. However, relative to their own behavior, on average older *Lemur catta* showed a bigger change in their resting behavior (shifting to utilize this closed posture more often) than did younger subjects, in cooler vs. warmer temperatures (19.67% difference  $\pm$  31.65 vs. 13.27% difference  $\pm$  31.15, ns, Figure 6, Appendix 7-10). With regards to heat dissipating (open) postures, on average geriatric individuals—as compared with younger individuals—rested in this position more often in all temperature bins, but the difference was not significant (Appendix 7-8). Similarly, across temperature bins, older *Lemur catta* showed a greater change in this behavior (increased use with increasing temperatures) on average than did the younger, although the data between groups was, again, not significant (Appendix 7-10). Specifically, on average they spent 35.65% ( $\pm$  19.16) more time resting with an open posture in warmer temperatures than they did in cooler temperatures, whereas younger individuals only spent 18.2% ( $\pm$  17.53) more time (ns, Figure 6). During analysis of sunning behavior in *Lemur catta*, I had to remove six individuals (five younger and one older) because the sky was completely overcast during all cold weather observations for these individuals. Older *Lemur catta* were observed sunning more than the younger in neutral temperatures (Appendix 17-18, Figure 7), but the average percent time spent sunning in cooler temperatures (11.76%) is the result of only one of the three lemurs sunning for 35.30% of the observations.

On average, older *Propithecus coquereli* rested in closed postures more often in cooler temperatures than did younger (41.03%  $\pm$  14.71 vs. 21.05%  $\pm$  20.34, ns). As temperatures dropped to the cooler category, on average they spent 38.30% ( $\pm$  11.19) more time in this posture relative to their own behavior in warmer temperatures, whereas the younger group only spent 21.05% ( $\pm$  20.34) more time in this posture (ns). They were observed resting with an open posture more often than did younger in neutral and warmer temperatures, but were never observed in this

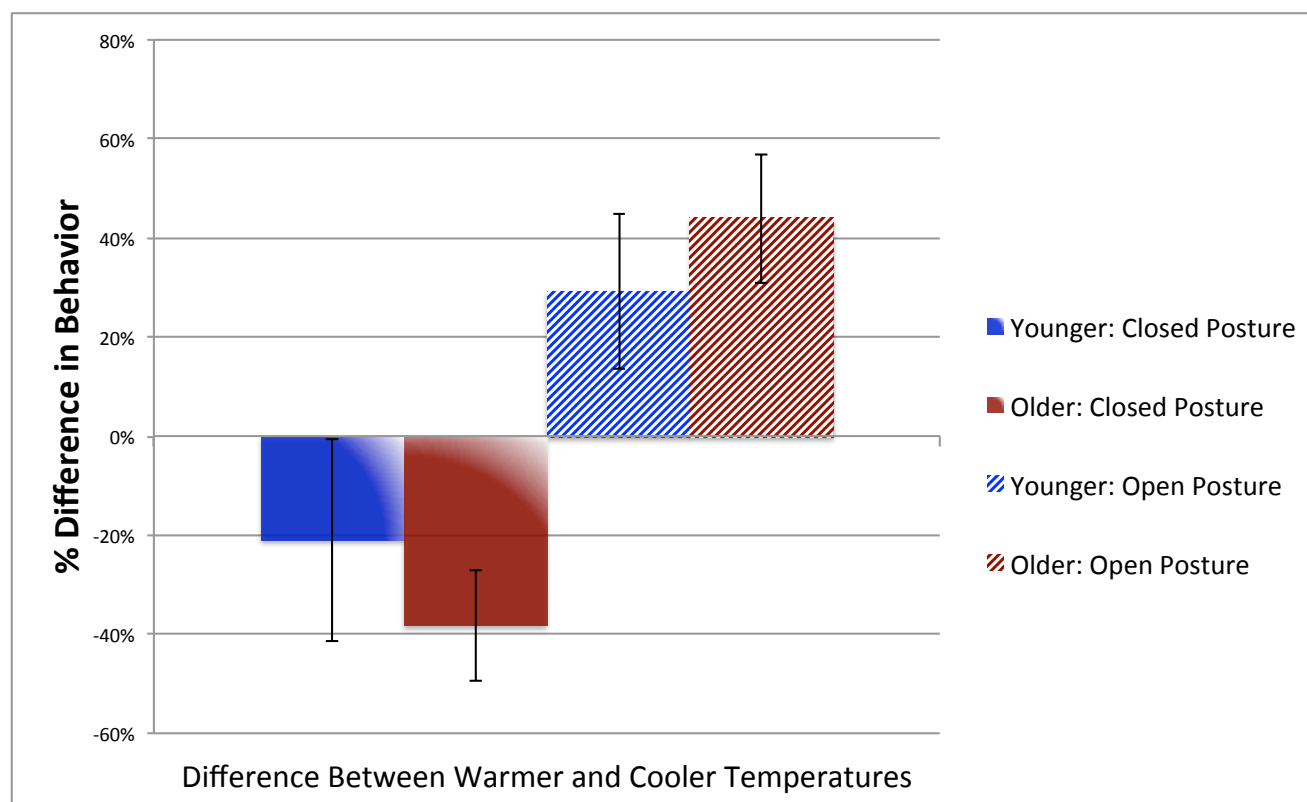


**Figure 6:** *Lemur catta*: Change in resting posture between warmer and cooler temperatures. % change- average residual values of all individuals in each group. Error bars = standard deviation

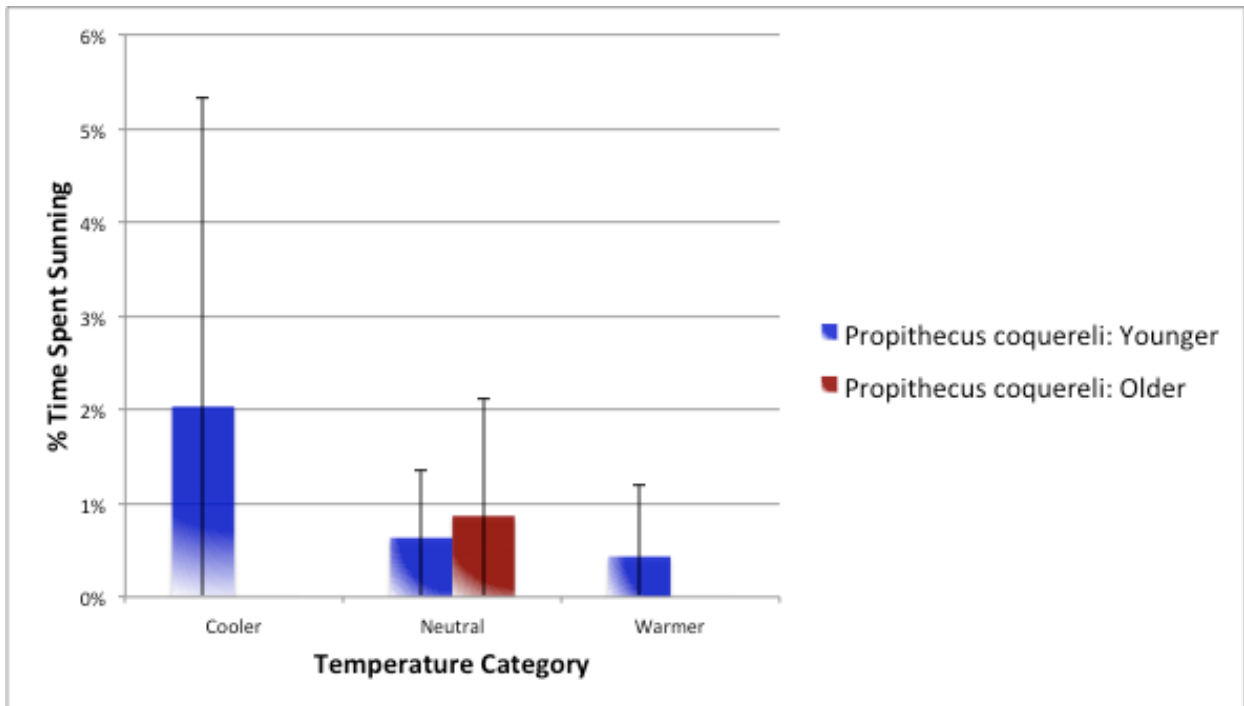


**Figure 7:** *Lemur catta*: Percent time spent sunning under different temperature conditions. Younger n=4, Older n=3. % time: pools data of all individuals in each group. Error bars = standard deviation

posture during cooler observations. Similar to the trends seen with heat retaining postures in cooler temperatures-- as compared to their younger counterparts, geriatric *Propithecus coquereli* also changed their own behavior more drastically to utilize this open position more often as temperatures increased (Appendix 11-14, Figure 8), and they spent 43.83% ( $\pm 12.87$ ) more time resting with this posture in warm temperatures than they did in cooler temperatures (as compared with 29.3%  $\pm 15.68$  more for the younger group). With regards to sunning behavior, *Propithecus coquereli* were observed exhibiting this behavior much less than *Lemur catta*. Geriatric *Propithecus coquereli* were never observed sunning in cooler or warmer temperatures, whereas the younger individuals were seen sunning an average of 2.03% ( $\pm 3.32$ ) of the time (Figure 9, Appendix 19-20) As was the case with *Lemur catta*, I had to exclude one geriatric and one younger individual from analysis because they were never observed in cooler temperatures when the sun was out.



**Figure 8:** *Propithecus coquereli*: Change in resting posture between warmer and cooler temperatures. % difference- average residual values of all individuals in each group. Error bars = standard deviation



**Figures 9:** *Propithecus coquereli*: Percent time spent sunning under different temperature conditions. Younger n=5, older n=2. % time: pools data of all individuals in each group. Error bars = standard deviation.

### Selected Sun Exposure

The ability to analyze selected sun exposure was greatly reduced due to the fact that on many “cooler” days, the sky was completely overcast and no sun was available for thermoregulatory use. A total of nine individuals (7 *Lemur catta*, 2 *Propithecus coquereli*) were never with the sun available in cooler temperatures, which impaired analysis between younger and older groups as well as analysis between temperature bins. For the individuals who were able to be included in these analyses, there were no trends observed between variables. In neutral and warmer conditions, younger and older individuals of both species avoided the sun and utilized shady patches equally.

## Discussion

Though aging in mammals is accompanied by the attenuation of a number of different physiological processes, regulating internal body temperature through behavioral mechanisms could be used to account for difficulties in maintaining ideal core body temperature in a changing thermal environment. My study shows overall behavioral trends are present between older and younger lemurs in both model species, but these differences were not significant. Below I discuss these patterns in behavior and the limitations of this study.

### Activity Level

Changes in activity patterns observed within *Lemur catta* are consistent with my initial prediction that older individuals will be less active in warmer temperatures relative to their younger counterparts, but these trends were not significant. At the same time, geriatric lemurs reduced individual activity levels by an average of 5.28% between neutral and warmer temperatures, as compared to an average reduction of only 1.19% by younger lemurs. Because geriatric individuals changed their own personal activity levels between temperature bins more dramatically than the younger, this would suggest that they are capable of recognizing thermal discomfort associated with increased activity in warmer temperatures. This is in contrast with what was found by Meh and Denislic (1994), regarding the elderly humans and their inability to recognize hot or cold stimuli as effectively as adults. Explanations for a reduction in total energy expenditure in elderly humans have been attributed to nutritional deficiencies, lowered metabolic rate, and a greater susceptibility to diseases and disorders (Elia et al. 2000). However if any of these factors were to be impacting lemur energy expenditure, then the expected result would be overall lower rates of activity across all categories for geriatric lemurs, which was not a trend for either species. Because older *Lemur catta* decreased their own activity level more as temperatures rose out of the neutral category, thermoregulatory response is likely the acting mechanism.

Older *Propithecus coquereli* did not show this same trend—activity level varied only slightly between neutral and warmer temperatures for both age classes. Natural ranges for this species in Madagascar have temperatures typically falling in the upper 20's (°C), and these conditions do not fluctuate as much annually as they do in *Lemur catta* ranges (Demes et al. 1996, Petter 1962, Richard 1978). Species that experience more seasonal variation tend to adopt a larger array of thermoregulatory strategies (Terrien et al. 2011), which may explain this intraspecies variation, and *Propithecus coquereli* may simply be more tolerant of the neutral-warmer temperature boundary defined in this study (28° C), because it is so close to average annual temperature of the western dry deciduous forest of Madagascar (27° C).

On the opposite end of the thermal range, younger *Propithecus coquereli* had a more notable response to cooling temperatures, which was not seen with geriatric individuals. The younger group showed an average increase in activity level of 8.95% between neutral and cooler temperatures, a strategy that was unemployed by geriatric *Propithecus coquereli*. Thermoregulatory implications of this behavior follow that this is used to increase internal thermogenesis, however this behavior is energetically costly and it is not the only mechanism that could be used to achieve a similar result. Older *Propithecus coquereli* showed a notable increase in consumption rate as temperatures declined, a trend not seen in the younger group. Increasing consumption not only helps meet energy demand imposed by autonomic regulation in the cold, but digestion-induced thermogenesis can represent 5-15% of total energy expenditure in colder weather (Westerterp 2004). This strategy may be a more passive mechanism used to achieve a similar goal—to increase production of body heat—when raising activity level may be too stressful on an older body. One consideration is that the captive lemurs at the Duke Lemur Center are provisioned with food, and thus have the luxury of minimizing foraging activity while maximizing intake. However, this does show that thermoregulatory behavior is still being utilized by older *Propithecus coquereli* in a different way, which is favorable given physical limitations.

## Heat Loss via Surface Radiation

Analyzing activity level as a thermoregulatory strategy is limiting in that general physiological capabilities are reduced with aging (Languille et al. 2011), but resting behavior is equally accessible across age classes and thus may have fewer influencing variables. Older *Lemur catta* and *Propithecus coquereli* both changed their resting posture more dramatically across temperatures than did their younger counterparts. Specifically, older lemurs adjusted their own behavior to a greater degree to utilize: 1) a closed posture more often as temperatures dropped from neutral to cooler, and 2) an open posture more often as temperatures rose from neutral to warmer. While these differences were not significant, the consistency between species reinforces the conclusion that aging in lemurs is accompanied by a greater behavioral response to temperature variation, that they have sufficient ability to recognize changing thermal conditions.

Cutaneous vasoconstriction in cold temperatures is important in reducing heat loss through the skin, and the ability to activate and maintain this reduction of peripheral blood flow is greatly diminished in older humans and animals (Florez-Duquet and McDonald 1998). The trend observed with the geriatric lemurs in this study suggests that they are supplementing these deficiencies by behaviorally decreasing surface to mass ratio. With a decrease in ability to metabolically produce body heat (Florez-Duquet and McDonald 1998, Terrien et al. 2011) it becomes increasingly important to preserve existing heat in cooler temperatures, and it makes sense why geriatric individuals would prioritize this thermoregulatory strategy over increasing activity level to increase thermogenesis (the latter being a strategy employed by younger *Propithecus coquereli*). A similar pattern is seen in elderly humans with regards to vasodilation—peripheral blood flow capabilities are not only reduced compared to adults, but the temperature threshold for vascular dilation is raised (Van Someren et al. 2002). Increasing surface to mass



ratio by resting in open postures likely compensates for this inability, and a complementary reduction in activity level (as seen with older *Lemur catta*) may be influenced by their decreased ability to dissipate the body heat that would result from excessive movement.

### Sunning Behavior and Selected Sun Exposure

Trends in sunning behavior did not yield the predicted results—there were not any patterns suggesting age-related differences in behavior. This is likely resulting from limitations of this particular study—nine individuals had to be excluded from analysis because they were only observed in cooler temperatures when the sky was completely overcast, and thus they were unable to exhibit sunning behavior in the temperature category most relevant to this thermoregulatory strategy. Free ranging lemurs at the Duke Lemur Center have access to an indoor, temperature-controlled building, and retreat into this thermal refuge proved to be the most popular thermoregulatory strategy in cold temperatures. Observations were only begun when the lemurs were outside, and there were limited opportunities to observe lemurs outside at lower temperatures when the sky was not completely overcast. As a side note, both these species of lemur have been noted to portray sunning behavior in the mornings (Jolly 1966, Richard 1978)—observations in this study were spread evenly throughout the day, but with additional morning sampling there may be more opportunities to record sunning behavior.

While analyzing selected sun exposure, I came across a similar difficulty in that the cooler temperature bin had to be excluded from analysis. In warmer temperatures, the sun was greatly avoided by both young and old lemurs of both species. Takemoto (2004) described microclimate selection within the forest as a group behavior for chimpanzees, and similar assumptions could be applied to social groups of lemurs. Within the forest, permeating light is consistent enough to be fairly uniform across the area encompassing an entire group of lemurs, and individual variation in

these conditions would likely require an individual to stray from the group. However, the alternative explanation for these results is that there simply are no differences in preference across age-classes with regards to sun exposure.

## **Conclusions and Further Study**

While testing my three predictions of age-related differences in lemur thermoregulation, I was able to see a few trends that supported my initial hypothesis. Older lemurs did show evidence of a greater use of thermoregulatory behaviors, with specific propensity towards low-energy thermoregulation. These involve decreasing activity levels in the heat (*Lemur catta* only), adjusting resting posture in both warmer and cooler temperatures, and increasing consumption rate in cooler temperatures (*Propithecus coquereli* only, with low-energy foraging being a possibility in a captive scenario). While none of the results were statistically significant, preliminary study suggests that further observations with more focal subjects may find significance in these subtle patterns. Because of the limited sample size, only the most extreme differences between groups would have yielded significant results.

Analysis of sunning behavior and selected sun exposure did not show any specific trends, but a more extensive study with more observations on sunny, cooler days would set up more complete results for analysis of these behaviors. Similarly, food-provisioning stations located within the forest may have influenced sun avoidance as most groups maintained close proximity to these areas. Finally, during observations the summer was mild and the lemurs were quick to retreat indoors when temperatures began declining in the fall. Thus, the “warmer” and “cooler” temperature bins described in this study had to be cautiously defined because the range of temperatures experienced through the course of the study did not rise or fall enough to induce a great amount of thermal stress. Comparing shifts in behavior across the observed ranges did,

however, show trends that would likely be strengthened if ambient conditions were to stray farther from the thermoneutral zone for these species.

Observing lemur behavior in thermally stressful conditions is useful for determining their vulnerability to a global shift in climate. Madagascar is being deforested at an alarming rate, which only adds to the pre-existing geographic limitations that this island environment imposes on a species attempting to broaden its range to find suitable climatic conditions. Adjustments in the use of behavioral thermoregulation would have to be the first step in managing a change in annual temperatures, as genetic adaptation would take much longer to become fixed within a gene pool. As social species, older members of *Lemur catta* and *Propithecus coquereli* are important to the functionality of social groups, and their ability to cope with thermal stress is an important factor to incorporate into the knowledge base that we draw from when deciding how to properly conserve these species.

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## Appendix

Reference Table 1- *Lemur catta*: Geriatric, % Active

	<b>Cooler</b>	<b>Neutral</b>	<b>Warmer</b>
<b>Mean</b>	10.45%	11.95%	6.68%
<b>SD</b>	7.49	6.82	2.41

Reference Table 2- *Lemur catta*: Prime-aged, % Active

	<b>Cooler</b>	<b>Neutral</b>	<b>Warmer</b>
<b>Mean</b>	12.17%	10.5%	9.31%
<b>SD</b>	8.00	6.13	4.28

Reference Table 3- *Propithecus coquereli*; Geriatric, % Active

	<b>Cooler</b>	<b>Neutral</b>	<b>Warmer</b>
<b>Mean</b>	2.93%	3.43%	5.4%
<b>SD</b>	0.90	2.28	1.15

Reference Table 4- *Propithecus coquereli*: Prime-Aged, % Active

	<b>Cooler</b>	<b>Neutral</b>	<b>Warmer</b>
<b>Mean</b>	13.78%	4.83%	5.87%
<b>SD</b>	11.91	5.88	2.72

Reference Table 5- *Propithecus coquereli*; Geriatric, % Eat Residuals

	<b>Warmer-Neutral</b>	<b>Neutral- Cooler</b>	<b>Warmer- Cooler</b>
<b>Mean</b>	-2.6%	-8.97%	-11.6%
<b>SD</b>	5.2	9.30	4.11

Reference Table 6- *Propithecus coquereli*: Prime-Aged, % Eat Residuals

	<b>Warmer-Neutral</b>	<b>Neutral- Cooler</b>	<b>Warmer- Cooler</b>
<b>Mean</b>	-0.5%	1.73%	1.23%
<b>SD</b>	14.38	11.78	17.97

Reference Table 7: *Lemur catta*: Geriatric, High Surface/Mass Posture

	<b>Cooler</b>	<b>Neutral</b>	<b>Warmer</b>
<b>Mean</b>	9.75%	20.13%	45.40%
<b>SD</b>	10.95	19.01	19.42

Reference Table 8: *Lemur catta*: Prime-Aged, High Surface/Mass Posture

	<b>Cooler</b>	<b>Neutral</b>	<b>Warmer</b>
<b>Mean</b>	5.39%	8.58%	23.6%
<b>SD</b>	10.29	8.38	11.61

Reference Table 9: *Lemur catta*: Geriatric, High Surface/Mass Residuals

	<b>Warmer-Neutral</b>	<b>Neutral- Cooler</b>	<b>Warmer- Cooler</b>
<b>Mean</b>	25.28%	10.38%	35.65%
<b>SD</b>	15.29	26.10	19.16

Reference Table 10: *Lemur catta*: Prime-Aged, High Surface/Mass Residuals

	<b>Warmer-Neutral</b>	<b>Neutral- Cooler</b>	<b>Warmer- Cooler</b>
<b>Mean</b>	15.01%	3.19%	18.2%
<b>SD</b>	12.12	11.94	17.53

Reference Table 11: *Propithecus coquereli*: Geriatric, High Surface/Mass Posture

	<b>Cooler</b>	<b>Neutral</b>	<b>Warmer</b>
<b>Mean</b>	0%	25.3%	43.8%



<b>SD</b>	0	17.24	12.87
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Reference Table 12: Propithecus coquereli: Prime-Aged, High Surface/Mass Posture

	<b>Cooler</b>	<b>Neutral</b>	<b>Warmer</b>
<b>Mean</b>	3.03%	24.12%	32.33%
<b>SD</b>	3.26	13.97	16.40

Reference Table 13: Propithecus coquereli: Geriatric, High Surface/Mass Residuals

	<b>Warmer-Neutral</b>	<b>Neutral- Cooler</b>	<b>Warmer- Cooler</b>
<b>Mean</b>	18.53%	25.30%	43.83%
<b>SD</b>	5.45	17.23	12.87

Reference Table 14: Propithecus coquereli: Prime-Aged, High Surface/Mass Residuals

	<b>Warmer-Neutral</b>	<b>Neutral- Cooler</b>	<b>Warmer- Cooler</b>
<b>Mean</b>	8.22%	21.08%	29.30%
<b>SD</b>	14.08	12.94	15.68

Reference Table 15: Lemur catta: Geriatric, % Active Residuals

	<b>Warmer-Neutral</b>	<b>Neutral- Cooler</b>	<b>Warmer- Cooler</b>
<b>Mean</b>	-5.28%	1.5%	-3.78%
<b>SD</b>	8.59	6.87	9.88

Reference Table 16: Lemur catta: Prime-Aged, % Active Residuals

	<b>Warmer-Neutral</b>	<b>Neutral- Cooler</b>	<b>Warmer- Cooler</b>
<b>Mean</b>	-1.19%	-1.67%	-0.25
<b>SD</b>	2.25	3.08	1.25

Reference Table 17: Lemur catta: Geriatric, % Sunning

	<b>Cooler</b>	<b>Neutral</b>	<b>Warmer</b>
<b>Mean</b>	11.18%	10.10%	1.23%
<b>SD</b>	20.38	11.96	1.55

Reference Table 18: Lemur catta: Prime-Aged, % Sunning

	<b>Cooler</b>	<b>Neutral</b>	<b>Warmer</b>
<b>Mean</b>	6.90%	0.28%	0%
<b>SD</b>	11.24	0.49	0

Reference Table 19: Propithecus coquereli: Geriatric, % Sunning

	<b>Cooler</b>	<b>Neutral</b>	<b>Warmer</b>
<b>Mean</b>	0%	0.87%	0%
<b>SD</b>	0	1.25	0

Reference Table 20: Propithecus coquereli: Prime-Aged, % Sunning

	<b>Cooler</b>	<b>Neutral</b>	<b>Warmer</b>
<b>Mean</b>	2.03%	0.63%	0.43%
<b>SD</b>	3.33	0.7	0.8