Activity Budgets and Behavior of Captive Black-handed Spider Monkeys (Ateles geoffroyi) at the Central Florida Zoo and Botanical Gardens

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ACTIVITY BUDGETS AND BEHAVIOR OF CAPTIVE BLACK-HANDED SPIDER MONKEYS (*ATELES GEOFFROYI*) AT THE CENTRAL FLORIDA ZOO AND BOTANICAL GARDENS

by

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ABSTRACT

Establishing baseline activity budgets for zoo-housed captive animals can be important in tracking behavior changes that may indicate medical or other concerns, as well as assessing overall welfare and the need for implementation of interventions such as increased amounts of enrichment. This study sought to calculate activity budgets for the current spider monkeys residing at the Central Florida Zoo, a father-daughter pair of *Ateles geoffroyi*. Having a baseline activity budget is also valuable because major changes in behavior may accompany the upcoming introduction of new individuals to this particular group of spider monkeys. BORIS behavior coding software was used to log behavior continuously over 58.3 hours of observation. The individuals in this zoo setting spent significantly more time stationary (resting or still and awake) and less time engaged in feeding behavior than wild spider monkeys. However, they spent as much or more of their time moving than *Ateles* species in natural settings. Temperature and exhibit renovation had minimal to no observed effects on activity budgets. Human presence usually has the effect of increasing activity and vigilance of animals while decreasing resting time, but on busier days at the zoo, one subject (a pet-reared male spider monkey) spent more time resting and less time moving than when there were fewer zoo visitors. No aggression was observed, but affiliative social behavior like allogrooming and embracing was observed infrequently. The study animals appeared to lack the bimodal pattern of activity (with activity peaking early and late in the day) common in wild spider monkeys, a finding that is consistent with activity budgets of other spider monkeys that are frequently exposed to humans. Time of day affected activity budgets to a small degree; the monkeys became more active later in the day and spent more time resting in the morning.

INTRODUCTION

Life History

Ateles geoffroyi geoffroyi, commonly known as the Black-handed Spider Monkey, is one of seven currently extant subspecies *of Ateles geoffroyi* (Cuarón et al. 2008). It is native to Central America, specifically the southeastern region of Nicaragua, and may also inhabit northern Costa Rica (Cuarón et al. 2008). Populations of *Ateles geoffroyi* have sharply fallen due to habitat loss and deforestation over the past five decades (Cuarón et al. 2008). *Ateles geoffroyi* is currently listed as Endangered by the International Union for Conservation of Nature's Red List, with habitat fragmentation and loss acting as principal threats to their survival (Cuarón et al. 2008). They also face risks via hunting and the pet trade (Cuarón et al. 2008). Since they live mostly in lowland rainforest, almost always traveling and foraging above the understory, they rely heavily upon suspensory modes of locomotion such as climbing and brachiating (Cuarón et al. 2008). The diet of *Ateles geoffroyi* consists mostly of fruit, although they will consume other plant parts (flowers, leaves, seeds, bark) and infrequently, insects, in the dry season when fruit is scarce (Cuarón et al. 2008). Their frugivory makes them essential as seed dispersers for over 138 species (Cuarón et al. 2008). After reaching sexual maturity at around 4-5 years of age (Gorog 2002), they typically produce one infant per breeding season after a lengthy gestation (Cuarón et al. 2008). Spider monkeys' interbirth interval can be exceedingly long, up to 30 months, which contributes to their population often struggling to rebound after threats and setbacks (Cuarón et al. 2008). The oldest known spider monkey lived to approximately 47 years of age in captivity (Gorog 2002). While spider monkeys have generally been thought of as a species that exhibits female dispersal and male philopatry, recent findings have suggested their dispersal mechanisms

may be more flexible, documenting cases in which males immigrated to other territories (Aureli et al. 2013). Also, while males in a troop would be expected to be more closely related to each other than females if they were indeed the philopatric sex, Aureli et al. (2013) demonstrated no significant difference in relatedness amongst males compared to relatedness amongst females.

Social Behavior

Despite having communities of as many as 30 spider monkeys, *Ateles geoffroyi* are most often seen in groups of only a few individuals (Cuarón et al. 2008). This is because spider monkeys display a unique fission-fusion society (Cuarón et al. 2008). This type of social system is characterized by variable and fluctuating group size and composition, in which subgroups of individuals may join and split off from one another in response to several factors, such as food availability and variability, and at times rejoin the larger group (Aguilar-Melo et al. 2018). Fission-fusion dynamics serve as an adaptive form of social organization that simultaneously allow a species to enjoy the advantages of living in groups while minimizing the drawbacks that often come with it, such as competition over food and other resources (Aguilar-Melo et al. 2018). One typical subgroup is the "party," which usually has a size of 2-4 monkeys (Aguilar-Melo et al. 2018). Although fruit availability is expected, under the ecological-constraints model, to be a predictive factor of subgroup size, with higher availability resulting in larger subgroups, Aguilar-Melo et al. (2018) found that social grouping can be affected by various habitat qualities, and that the effects of fruit availability on subgroup size can be mediated by climate-related variables such as rainfall. In their study, a rainforest site with rainfall patterns that were more constant and not as seasonal as many previously studied areas showed the opposite relationship: subgroup size and fruit availability were negatively correlated (Aguilar-Melo et al. 2018).

It is common for primates brought up by people to exhibit abnormal levels of attachment towards humans and possibly impaired sexual and parental behavior (Anaya-Huertas and Mondragón-Ceballos 1998). However, in black-handed spider monkeys raised as pets, Anaya-Huertas et al. (1998) found that even among a group of recently introduced individuals that had grown up in atypical environments there was little evidence of the monkeys being socially "handicapped." They displayed mostly normal social behavior, mirroring that of free-ranging spider monkeys in the wild (Anaya-Huertas and Mondragón-Ceballos 1998). Even though several in this study group were raised in total isolation from conspecifics and even showed fear of conspecifics at the start of the study, overall the researchers demonstrated that affiliative social behavior (grooming, play, and physical closeness) was 17x as common as aggression (Anaya-Huertas and Mondragón-Ceballos 1998). There was slightly more aggression observed among these pet-reared spider monkeys than in groups of wild spider monkeys, but many other factors, such as females grooming males more frequently than vice versa, held true to what has been found in wild populations (Anaya-Huertas and Mondragón-Ceballos 1998).

In wild troops of *Ateles geoffroyi yucatanensis*, Slater et al. found affiliative behavior such as allogrooming, embracing, approaching, and being near one another was common in male-male interactions and relatively infrequent in female-female interactions (Slater et al. 2009). Males embraced more often in subgroups that included both sexes (Slater et al. 2009). Embraces possibly function to mitigate conflicts; therefore, this finding may have been the result of males' attempts to handle conflict over females (Slater et al. 2009). However, aggression between males was quite uncommon (Slater et al. 2009). These factors led Slater et. al to conclude that males have "high quality" relationships with each other based on the high frequency of affiliative social behavior and low frequency of agonistic behavior occurring

between males (Slater et al. 2009). Slater et al. (2009)'s study showed low percentages of time spent grooming, regardless of the sex of the monkey doing the grooming or the sex of the recipient, with grooming taking up a maximum of 0.5% of their time (in male-male pairs) and as little as 0% of their time (females virtually never groomed other females). Allogrooming occurred the most in male-male pairs, but males also groomed females fairly often (Slater et al. 2009). Although females almost never groomed each other, they did occasionally groom males (Slater et al. 2009). By far the highest rate of agonistic behavior observed in the study was aggression instigated by males and directed towards females (Slater et al. 2009). This is likely impacted by relatedness as adult males were never observed to be aggressive towards their mothers (Slater et al. 2009). Males displayed the highest rates of aggression toward females presumed to be in estrus (Slater et al. 2009). Allogrooming in male-female pairs was observed at a level between that of same-sex pairs of males or females (Slater et al. 2009). Aggression between female spider monkeys peaked when food was involved, and in that scenario, it occurred much more frequently than hypothesized (Slater et al. 2009). The researchers called female-female relationships "low quality" because of this and females' apparent preferences to not engage in affiliative behaviors with one another (Slater et al. 2009).

In a study by Pastor-Nieto et al. (2001), monopolizing access to food was common in a group of monkeys that were unfamiliar with one another, and social grooming and embraces were rare. Pastor-Nieto (2001) showed that in captive spider monkeys, co-feeding and kinship were not significantly related, but food sharing was correlated with rates of social grooming. This suggests that allogrooming facilitates social bonding that makes individuals more tolerant and permissive of sharing food with other conspecifics (Pastor-Nieto 2001).

Activity Budgets of Wild Spider Monkeys

Seasonal variation in activity budgets in wild *Ateles geoffroyi* is primarily related to variation in food availability across wet versus dry seasons (Chaves, Stoner, Arroyo-Rodríguez 2011). Since captive monkeys in a zoo are provisioned with food on a constant basis, this can reliably be taken out of the equation and seasonality would not have much of an effect on their behavior. The communities of spider monkeys observed in a study undertaken by Chaves et al. (2001) in Mexico spent the majority of their time either feeding (44%) or resting (34%). Traveling accounted for only 12% of their daily activities, and other behaviors (such as social activities) took on average 10% of their time (Chaves, Stoner, Arroyo-Rodríguez 2011). They spent more time eating in fragmented forests, but more time traveling in continuous forest compared to fragmented forest (Chaves, Stoner, Arroyo-Rodríguez 2011). More time was devoted to feeding in the rainy season and conversely, more time was allocated to resting in the dry season (Chaves, Stoner, Arroyo-Rodríguez 2011). Spider monkeys ate more leaves in the dry season (Chaves, Stoner, Arroyo-Rodríguez 2011). Previous studies have shown that resting time is related to season, proportion of leafy matter in diet, and temperature (Chaves, Stoner, Arroyo-Rodríguez 2011). More resting has been shown to occur with a higher percentage of leaves consumed and higher temperatures (Chaves, Stoner, Arroyo-Rodríguez 2011). Since resting did not vary with forest type but did vary with season, researchers suggest the amount of resting time may be a factor of temperature changes, not food availability (Chaves, Stoner, Arroyo-Rodríguez 2011).

According to Slater et al., activity budgets are quite similar across sexes (Slater, Schaffner, Aureli 2009). The only significant differences found were in feeding time (females spent more time feeding than males, particularly when they were in subgroups with other

females) and social behavior (males spent more time engaged in social behaviors, especially affiliative gestures, and aggression was rare between males; Slater et al. 2009).

Effects of Humans on Spider Monkey Activity Budgets

Many primate species, such as howler monkeys, gorillas, chimpanzees, and tamarins were included in the species studied by Quadros et al. (2014), investigating the effects of noise from crowds of guests at the zoo on behavior. On days with high human activity at the zoo (and thus significant amounts of noise), almost all of the individual primates showed an increase in vigilance (awake and actively paying attention to the environment), and some of them also showed an increase in locomotion behavior and decreased time spent resting (Quadros et al. 2014).

Muñoz-Delgado et al. (2018) found that activity of tourist-exposed spider monkeys (measured by accelerometer readings) living on an island peaked on weekend days when the most people were visiting. Similarly, in a group of spider monkeys living in a natural enclosure with no tourists around, a decrease in activity was observed on days when animal care staff and researchers were not as active (Muñoz-Delgado et al. 2018). In contrast to spider monkeys housed in a natural forest enclosure without tourist presence, which consistently showed a bimodal activity pattern with a low point in the middle of the day, spider monkeys frequently exposed to tourists on an island had highly variable levels of activity throughout the day, some with multiple peaks in activity and some with only one peak or no discernible peak (Muñoz-Delgado et al. 2018).

Importance of Enrichment for Captive Primates

Captive non-human primates frequently show increased aggression towards conspecifics, as well as stereotypies (Márquez-Arias et al. 2014). Stereotypic behavior includes repetitive, unusual behaviors and motions with no apparent function, such as pacing, rocking, or self-harm (Márquez-Arias et al. 2014). Primates in captivity are typically less active and spend more time sleeping than members of the same species in the wild (Márquez-Arias et al. 2014). Use of environmental enrichment can improve welfare by decreasing stress and heightening activity levels (Márquez-Arias et al. 2014). Enrichment also increases the amount of time spent engaging in locomotion behaviors and playful or exploratory behaviors (Márquez-Arias et al. 2014). The purpose of enrichment is to make a captive animal's environment more engaging and mentally stimulating, allowing them to engage in natural behaviors that emulate the way they would spend their time in the wild (Márquez-Arias et al. 2014). Márquez-Arias et al. group enrichment into three categories: physical (increasing habitat quality, such as adding climbing structures), dietary (increasing amount of time spent feeding and foraging by providing food in puzzle feeders or other devices), and introduction to new objects (Márquez-Arias et al. 2014). In *Ateles geoffroyi*, enrichment has been demonstrated as an effective way of lowering incidents of aggression, coprophilia, and stereotyped behavior, while increasing time spent exploring and playing (Márquez-Arias et al. 2014). Santillán-Doherty et. al. (2010) found that among captive *Ateles geoffroyi*, males tended to have more novel-seeking personalities than females, which could contribute to them being more "adventurous" with exploration of new and unfamiliar enrichment.

Tina Torstensson showed that Colombian black spider monkeys (*Ateles fusciceps rufiventris*) stay in a given part of the enclosure longer when there is enrichment there

(Torstensson 2009). They also seem to have a preference for food puzzles that they could manipulate with their hands to obtain food over other types of enrichment such as ice blocks that require the monkeys to wait until they melt to retrieve the food (Torstensson 2009). This was evidenced by the monkeys spending a much greater amount of time in rooms containing food puzzles versus other enrichment types or no enrichment at all (Torstensson 2009). They were occupied with feeding and foraging for the longest time when food puzzles were present and spent the least amount of time eating when enrichment was not available (Torstensson 2009). The activity budgets of these spider monkeys revealed that they also spent by far the most time eating and the least time inactive when they had access to food puzzles (Torstensson 2009).

Purpose and Significance

The Central Florida Zoo currently houses a two spider monkeys, Big Guy, a 37-year-old male, and Zsa-Zsa, Big Guy's 19-year-old daughter, and plans to add several older female spider monkeys to the troop in the near future. Especially with only two animals currently inhabiting the enclosure, the enclosure is very spacious and is the largest primate enclosure at the Central Florida Zoo. It contains an artificial pond and a wide variety of surfaces, climbing structures, and places to perch at different elevations, including but not limited to a platform adjacent to the front window where guests can view them, a network of branches, tree stumps of varying heights, covered huts, natural plants, and artificial structures such as a "temple" and a large stone archway.

The primary purpose of this study is to create an activity budget for each individual monkey so it can be used as a baseline to further examine changes in each monkey's behavior as they continue to age, especially for the geriatric monkey at the Central Florida Zoo, a male called

Big Guy. Monitoring changes in his daily activities is important to ensuring his ongoing health and well-being, particularly as the longest-lived spider monkey in captivity was estimated to be just over 47 years old (Gorog 2002). At an age of 37, Big Guy is reaching the upper limit of his lifespan. Little is currently known on aging in spider monkeys. The research that does exist focuses on the reproductive decline associated with senescence in males of this species, not behavior changes, so information gained by studying the behavior of an elderly individual can be valuable. This study will contribute data that can not only help assess the ongoing health and well-being of these individual monkeys but assist in gathering an overall understanding of how activity budgets may change with age in this species.

The comparison of activity budgets for captive spider monkeys to those of wild spider monkeys can also be helpful in determining if the zoo is meeting their welfare needs by utilizing enrichment and other enclosure features to encourage natural behaviors. These activity budgets can be used to assess if the behavioral repertoire and frequency of behaviors in captive monkeys are approximately equal to those in the wild. If there are significant differences in captive versus wild spider monkey activity budgets, knowledge of wild spider monkey activity budgets can be utilized to inform management decisions to better approximate the behaviors of wild monkeys (e.g. providing more feeding opportunities throughout the day or more food enrichment to increase time spent feeding, foraging, and moving about the enclosure). Since new spider monkeys will likely be introduced to the Central Florida Zoo's troop in the near future, results from this study can also be used as a baseline for behavior prior to this upcoming event when new social relationships may cause temporary stress, disrupt routines, or changes in typical daily behavior.

The primary goal of this study is to establish activity budgets for two zoo-housed spider monkeys which can then be used to help the zoo make welfare assessments by comparing the behavior of these captive individuals to that of wild spider monkeys, guiding them towards specific areas of the spider monkeys' daily life that could be altered to better mimic the behavior of their wild counterparts and improve welfare. Having a baseline activity budget for each individual can also assist the zoo in analyzing how the upcoming integration of new spider monkeys into the troop changes behavior patterns, evaluating the success of the introduction of new group members, and assessing the impacts of aging and health decline on geriatric monkeys like Big Guy. Secondary objectives include assessing the impacts of variables such as time of day, visitor presence/crowd intensity, exhibit construction, and temperature on behavior.

METHODS

Study Site and Subjects

The study site is Central Florida Zoo and Botanical Gardens in Sanford, FL. This zoological facility is currently home to two black-handed spider monkeys, a father-daughter pair. They previously housed a small troop of four spider monkeys but lost two individuals in the last few years due to old age. There are plans to add three older adult females to the Central Florida Zoo troop soon.

The study subjects are "Big Guy," a 37-year-old male with a history of being a pet, and his daughter, "Zsa-Zsa," a 19-year-old female who was born in captivity at the zoo. As reported by the keepers, Big Guy is more drawn to people (perhaps due to his human-centric upbringing), whereas Zsa-Zsa is more "aloof" and "acts more like a typical monkey," preferring other activities over paying attention to humans.

Data Collection

The spider monkeys at the Central Florida Zoo and Botanical Gardens were mainly observed twice per week for 2-3 hours at a time, and sometimes once per week for 5 or more hours at a time. Visits were made on 25 days September through December 2018 and in March 2019, during periods approximating three defined temporal ranges, together covering the entirety of the zoo's open hours: morning (9:00-12:00), midday (12:00-2:00), and late afternoon (2:00-5:00). The time ranges of observations were not always exact due to weather, monkeys being out of sight, or keepers cleaning the enclosure. Three observation days at the beginning of the study were considered a "pilot study," were used to identify and discriminate between the individuals

and to decide which behaviors to include or exclude from the ethogram. Because the "pilot study" did not include the full extent of the ethogram, data collected during that time were excluded from the results. The ethogram was input into BORIS 6.3.7 (Behavior Observation Research Initiative Software) and each behavior was assigned a key-code so that behaviors could be easily recorded instantaneously during an observation session. The ethogram used for observation is provided in Table 1. BORIS only allows data collection for one focal individual at a time. Therefore, one focal individual was chosen at the start of each observation period and that individual's behavior was logged continuously in BORIS 6.3.7. The choice of focal individual for the day was as random as possible to accumulate approximately equal amounts of observation for each monkey, but if one monkey was out of sight at the beginning of the observation period, the other monkey automatically became the focal individual. In total, after discarding observations with errors, 31.7 hours of observation were used in activity budget calculations for Big Guy and 26.6 hours for Zsa-Zsa.

After several weeks, observations in the back area of the enclosure was also included since the monkeys sometimes spent time resting "behind the scenes." For example, they would be shifted into this area when keepers were cleaning the main enclosure. The focal subject of the day was followed if it went into the back and did not reemerge for 5-10 minutes (the monkeys often went in the back holding area for short periods of 1-2 minutes, during which their behaviors were not observed). Activity budgets were only calculated using time the monkey was in sight and its behavior observable, which for some days may be less than the typical 2-3 hour observational period.

Table 1 *- Ethogram used to log behavior in BORIS software.*

Behavior	Definition
Rest	Monkey is apparently sleeping, in a sitting or laying position, with its head down, i.e. resting on a surface or tucked inward towards the body.
Sit	Monkey sits on haunches, awake, with head up and alert. Back can be upright or hunched in posture, as long as the head is not bowed inward towards the body.
Lay/Lounge	Monkey lays awake with body outstretched on a surface, either in a prone position with head elevated, or on its side, with its head propped up by a folded arm (termed "lounging")
Self-groom	Monkey strokes or scratches itself with its hands and fingers
Eat	Monkey brings food to mouth with hands, masticates, and swallows
Vocalize	Monkey emits any of several types of sound, e.g. a "whinny"
Drinking	Monkey consumes water
Allogroom	Monkey grooms, or is groomed by, another conspecific. Details of which monkey was doing the grooming were logged as "modifiers" in BORIS.
Walk	Monkey traverses a flat surface such as the ground or a relatively horizontal branch on all four limbs
Climb	Monkey travels along a vertical or near-vertical surface, such as the walls of the enclosure, or a steeply angled branch/post
Brachiate	Monkey travels along a surface above its head ("ceiling" of the enclosure, hanging ropes, etc) swinging by its forearms
Near conspecific	Monkey's position in the enclosure is within approximately a meter of the other monkey, or their bodies are against each other/touching
Embrace	Monkey wraps arms around a conspecific's body briefly
Forage	Monkey walks or stands while looking at the surface underfoot and occasionally pushing substrate aside and sifting through it with hands as if searching
Interact with Enrichment	Monkey grabs, holds, touches, pushes, reaches inside, bites, or otherwise interacts with a designated enrichment item
Urinate	Monkey urinates
Defecate	Monkey defecates
Yawn	Monkey opens mouth wide in a non-aggressive context
Mouth Open	Monkey opens mouth in a non-aggressive manner while gazing at guests. Often paired with curious head tilting. This behavior is unique to Big Guy.

Ethogram Notes

Behaviors such as play and aggression were initially included in the ethogram, but since no instances of either were observed, they were removed. For resting behavior, it was often

difficult to determine when the monkeys' eyes were closed due to their location in the rear of the enclosure. For this reason, the definition of resting used in the study is a readily observable posture. For eating, a "modifier" was used in the BORIS software to specify what the monkey was consuming if the food item was visible (if not, it was marked "unknown"). Food categories include primate biscuit, fruit, vegetables, and leafy greens. A "modifier" was added for vocalization behavior partway through the study to record a probable cause of the vocalization by attempting to determine an antecedent (e.g. another conspecific vocalizes or a species housed near the monkeys vocalizes, food is presented, a keeper walks by or acknowledges the monkeys). Since normal locomotion was often indistinguishable from locomotion while foraging, foraging was given a narrow definition and the "foraging" behavior was most commonly observed on the ground. As a result, the majority of the food-finding activity of the monkeys will show up as locomotion behaviors in their activity budgets.

Since early on in the study enrichment use was not logged for interaction with natural browse, such as a beautyberry branch placed in the enclosure (this was instead considered foraging and eating), enrichment related behavior was only recorded for times when the monkeys interacted with artificial, manmade enrichment toys such as a KONG Wobbler, clear food box with holes, or dish of straw with food scattered throughout. Another behavior, "look at" was recorded if monkeys appeared to be watching something or someone in particular while they were static, along with modifiers for where the monkey's gaze was directed (e.g. a keeper, a guest, the other monkey). For ease of comparison with other time budget studies of wild and captive spider monkeys, the behaviors in the ethogram can instead be categorized instead into the behavioral groups most commonly used in these studies:

- *Inactive (Resting)*: all stationary behaviors such as resting, sitting, laying, standing in place, or hanging/clinging to the enclosure walls without moving
- *Traveling*: locomotion behavior (walk, brachiate, climb)
- *Feeding*: eating, foraging
- *Other*: all other behaviors, including social interaction, enrichment use, self-grooming, and allogrooming

HYPOTHESES

Because food is provisioned, captive spider monkeys are expected to spend less time foraging and feeding. On a related note, since they would have to traverse long distances in rainforests to find fruiting trees or other suitable food sources, it is expected that the proportion of time captive monkeys spend traveling or moving will be smaller due to the limited confines of their enclosure, compared to a very large home range in their native habitat, up to 400ha, with core areas of up to 84ha (Asensio, Schaffner, Aureli 2012). There is simply less space to move around in, so even if food is scattered, encouraging the monkeys to forage, it will take them less time to find than in a more expansive environment. Captive spider monkeys are expected to spend a greater fraction of their time resting and being still, since they will likely not need to spend as much time searching for food; however, because she is younger, Zsa-Zsa is expected to spend more time active and less time resting than Big Guy.

At the Central Florida Zoo, the spider monkeys are given food scattered throughout the enclosure and in enrichment devices at two main mealtimes (before the zoo opens at approximately 8:00am, and an hour before the zoo closes, at approximately 4:00pm). They are also usually given a smaller amount of food as a "snack" when a keeper cleans the enclosure sometime between 11:00am and 1:00pm. Therefore, instead of leveling off as it did in Wallace's study of *Ateles chamek* in the wild (Wallace 2001), feeding behavior in captive spider monkeys may see a sharp decline to nearly 0% of their time after food from keeper-provisioned feedings is mostly or entirely consumed, since new food will not be given again until the next feeding. Also per Wallace's findings on the activity budgets of black spider monkeys, if there are any unusually cold days during this study, the monkeys may be expected to rest more early in the day

and delay their feeding until late morning or early afternoon (Wallace 2001). However, this effect will presumably be minimized by the fact that their food arrives via the keepers at approximately the same times each day, regardless of weather and temperatures.

In terms of space limitations, a zoo enclosure is more analogous to "fragmented forest" than continuous forest. However, the increased feeding time observed in fragmented forest by Chaves et al. was likely due to low quality or low abundance of suitable food such as fruits (Chaves, Stoner, Arroyo-Rodríguez 2011), and problems of diet abundance and quality are not an issue in a zoo environment, so it is unlikely the monkeys will show high amounts of time feeding.

RESULTS AND DISCUSSION

Overall Activity Budgets

Total activity budgets for the 58 hours and 21 minutes of observations that were used after excluding the three pilot study days and observations with errors (totaling approximately 75 minutes, from three days in which behaviors were coded incorrectly or the BORIS software crashed) can be seen in Figure 1. Contrary to predictions, geriatric Big Guy spent less time inactive (63.3%) and more time engaged in locomotion behaviors (22.7%) than his much younger daughter, who spent 69.2% of her time resting and only 13.2% moving (Figure 1). Activity budgets for Big Guy and Zsa-Zsa supported previous findings that females spend more time feeding (Slater et al. 2001). Overall, Zsa-Zsa spent almost twice as much of her time feeding (11.7%) as did Big Guy (6.3%). Post-construction was the only individual condition in which she spent less of her time feeding than Big Guy. Even so, this was a slight difference and likely attributable to unusual factors impacting her behavior in the post-construction observations, which are discussed in more detail in the section on the impacts of exhibit renovation.

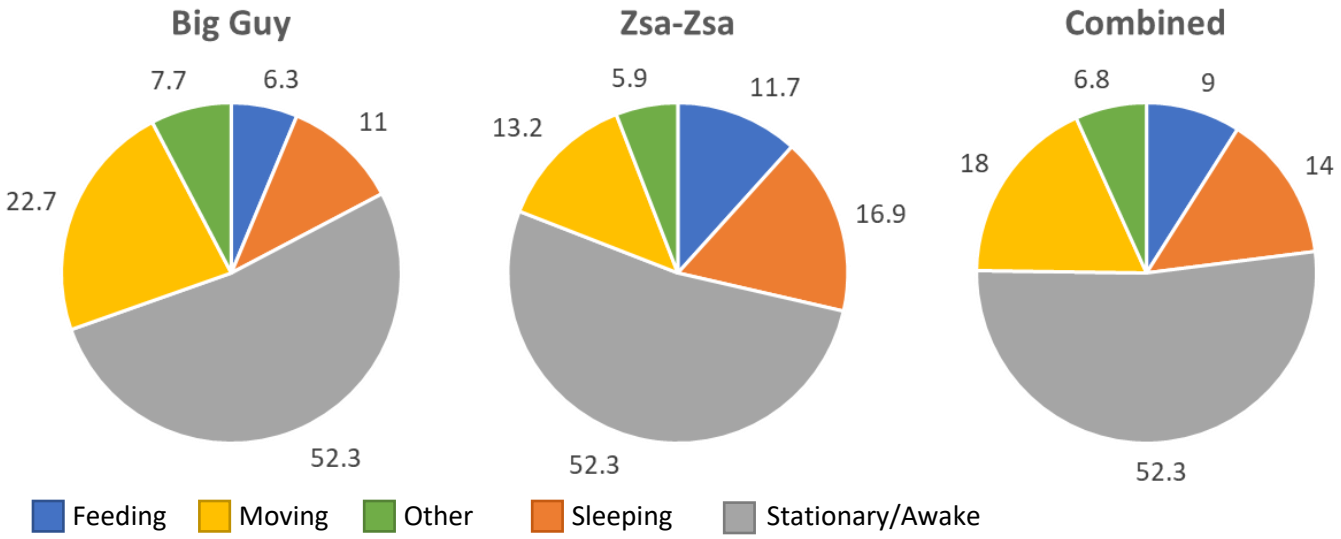

Figure 1 *- Overall activity budgets for each individual and a combined (averaged) activity budget, calculated from 58.3 hours of observation data collected between September and December 2018, and in March 2019.*

Compared to wild *Ateles geoffroyi* studied by Chaves et al. (2011), these captive individuals spent much more time inactive (66.3% for Big Guy and Zsa-Zsa, versus 34% in the wild) and less time eating and foraging (44% in wild populations but only 9% in these zoo-housed monkeys). However, a majority of their inactive time was when they were stationary and awake, not sleeping, and studies on spider monkeys in the wild do not make this distinction, so a comparison is not possible to determine if Big Guy and Zsa-Zsa are actually sleeping as much as wild spider monkeys would. They also spent less time eating and more time inactive than members of a related species, *Ateles chamek*, studied by Wallace (2001). This finding could have been exaggerated due to discrepancies in terminology between the ethograms of the studies, because in Chaves et. al (2011) and Wallace (2001) the behavioral categories of resting, feeding, moving, and other were not clearly defined, and as mentioned in the Ethogram Notes, "foraging" behavior had a narrow definition in this study and was seldom recorded. Instead, the equivalent of "foraging" was expected show up in their locomotion behaviors (moving) as they navigated

their exhibit, walking, climbing, and brachiating to look for scattered meals. The studies by Chaves et al. (2011) and Wallace (2001) may include foraging behavior (moving in search of food) in the "feeding" category. Surprisingly, both individually and when averaged, Big Guy and Zsa-Zsa spent as much of their time moving as the wild spider monkeys studied by Chaves et al (2011). To help captive spider monkeys spend more time being active (foraging and moving through the enclosure), they could be given more enrichment devices, which have been shown by Torstensson (2009) and others to successfully increase time spent eating and decrease inactive resting behavior. However, with regard to enrichment use, Big Guy was observed interacting with enrichment for less than a third of the time Zsa-Zsa spent using enrichment. Big Guy spent 5.9 minutes with enrichment, whereas Zsa-Zsa interacted with enrichment items for 21.3 minutes. Big Guy used enrichment such as food scattered in a mulch bin but was not observed using any enrichment that required him to reach his fingers inside something to pull food out (e.g. Kong Wobbler, acrylic box feeder with small holes, etc). Because Big Guy did not seem to be as readily accepting of some enrichment devices as Zsa-Zsa, it may be difficult to get him to utilize more difficult and time-consuming food puzzles. In this case, a larger number and variety of simple enrichment puzzles could be provided around the enclosure.

Social Behavior: Proximity, Embraces, and Allogrooming

No instances of aggression or play behavior were observed, nor were any conflicts over resources. Proximity to the other monkey was the most common social behavior observed, usually when the monkeys were laying still or resting together on the same exhibit prop, but because it was a co-occurring behavior that was recorded simultaneously with other behavior such as resting or being still and awake, it was not recorded in the “other” category like

allogrooming was. Out of the total time observed (58.3 hours), the monkeys spent 6.6% of their time near each other. Zsa-Zsa typically initiated social contact, as she was often the one who came over to join Big Guy when he was laying on the arch or the temple and would often get up and follow Big Guy if he left their resting spot. Interestingly, the amount of time these spider monkeys spent near one another is higher than what Slater et al. (2009) found in opposite-sex pairs of *Ateles geoffroyi yucatanensis* in the wild, which spent about 2.5-3.0% of their time near each other. Instead, this study's observations of proximity align more with what Slater et al. (2009) found for male-male pairs of spider monkeys, who spent 6.8% of their time near each other. This may be because at this time Big Guy and Zsa-Zsa are each other's only source of conspecific social interaction and they do not have the option of interacting with monkeys of other sexes. Future research on this captive group of spider monkeys may observe different patterns of social interaction once new individuals are added to the troop.

Embraces were observed on occasion (n=19 total), most frequently when the monkeys would encounter one another when traveling in opposite directions. At their meeting, they would briefly embrace, then cross paths and keep moving away from one another. Embraces did not occur following other forms of social interaction, nor did they seem to predict occurrences of other social interaction soon afterward. The frequency of embraces seen in Big Guy and Zsa-Zsa is consistent with observations from Slater et al. (2009) that saw very low rates of embraces in opposite-sex pairs compared to same-sex pairs, with male-male pairs engaging in embrace behavior twice as often as female-female pairs. Based on Slater et al. (2009)'s findings, Zsa-Zsa may be expected to embrace more often once new female monkeys join their group. When allogrooming occurred, it was usually after the monkeys had been laying near each other for several minutes.

Overall, very little allogrooming was observed; however, Zsa-Zsa spent almost twice as much time grooming Big Guy as she did being groomed by him. Over the course of 3,501 minutes of useable behavioral observations, Big Guy was only recorded grooming Zsa-Zsa for 9.23 minutes (0.5% of the total time he was observed), whereas Zsa-Zsa was observed grooming Big Guy for a total of 18.33 minutes (1.2% of the total time she was observed). Big Guy and Zsa-Zsa both spent slightly more time engaged in allogrooming activities than would be expected based on Slater et al. (2009)'s observations of wild spider monkeys, who groomed each other less than 0.5% of the time regardless of sex of the initiator or recipient of grooming. Scheel and Edwards (2012) demonstrated the prevalence of certain behaviors, like arm-raising, that spider monkeys engage in to "request" grooming from other conspecifics. Although the instances of arm-raising behavior were not formally recorded in the present study, Big Guy frequently engaged in arm-raising behavior either in an initial solicitation of grooming from Zsa-Zsa or to encourage Zsa-Zsa to continue to groom him if she had momentarily stopped. Zsa-Zsa was seldom seen engaging in arm-raising behavior. Her preferred method of soliciting grooming from Big Guy appeared to be to lay down near him and roll slightly onto one side, exposing her underside and/or neck.

Vocalizations

In total, 1,117 vocalizations were recorded for Zsa-Zsa, and only 340 for Big Guy. The majority of vocalizations were "whinny" type vocalizations, which are generally considered to be contact calls (Ordóñez-Gómez et al. 2015). Zsa-Zsa was much more likely than Big Guy to vocalize in response to the presence of food or enrichment (which could be a call to "notify" other troop members that she has found food, or simply related to her own excitement), and also

occasionally vocalized in response to noises emitted by other species housed nearby, such as Hyacinth macaws. Out of Zsa-Zsa's vocalizations that occurred after specification of a "motive" for the vocalization was added as a modifier to the ethogram, and excluding vocalizations that occurred for an "unknown" reason, 72% of her whinnies were in response to food or enrichment, and 19% were responding to a vocalization of another species near her enclosure. Big Guy would often greet keepers or other zoo staff he recognized with a vocalization similar to a whinny but a bit lower in pitch and gruffer sounding than Zsa-Zsa's typical whinny. Excluding vocalizations where the motive was "unknown," 76% of his vocalizations were related to the presence of a keeper or zoo staff. The monkeys occasionally vocalized right after one another in quick succession (accounting for between 4-6% of vocalizations that had an assumed "reason" associated with them), but vocalizations did not seem to predict an approach of either monkey towards the other.

Impact of Time of Day on Behavior

At the Central Florida Zoo the spider monkeys usually have food scattered around the enclosure and in enrichment devices three times per day by the keepers: in the morning around 8:00, midday between 11:00-1:00, and at 4:00 in the afternoon. Because the observation timeframes did not align perfectly with feeding times, observations that by chance did not include the monkeys getting a meal would display a much smaller percentage of time spent feeding and moving (foraging). Provisioning of food around midday likely explains Zsa-Zsa's increase in feeding and foraging behavior at that time of day. However, this does not offer an explanation for why Big Guy's feeding behavior was less frequent during midday. A plausible reason might be that when Big Guy was observed during midday happened to be at a time when

food had already been provisioned and finished (for example, if the observation was from 12:00 to 2:00 but food was given at 11:00 or 11:30). If this study were to be replicated the timeframes should be aligned so that a feeding can reliably happen during as many observations as possible.

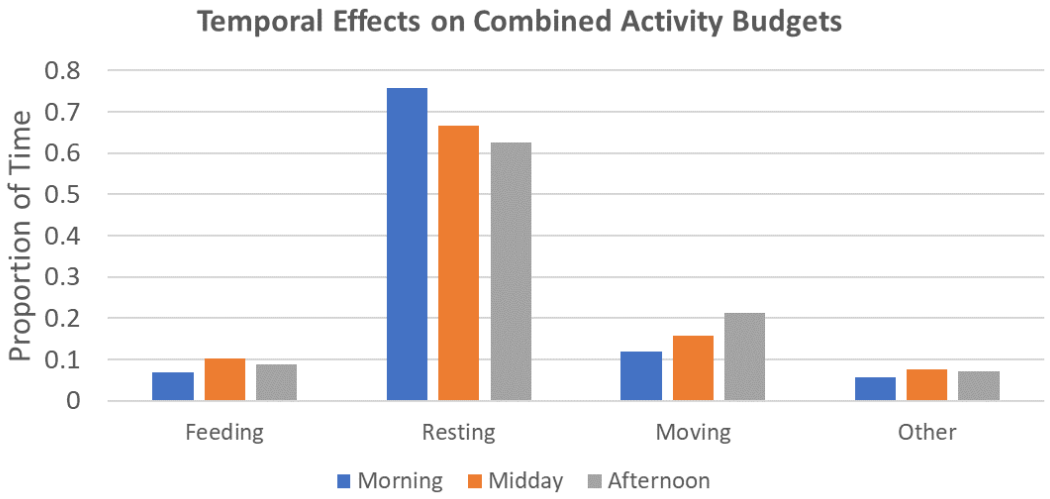

Figure 2 *- Variance in activity budget categories for Big Guy and Zsa-Zsa together, according to time of day: morning (approximately 9:00-12:00), midday (approximately 12:00-2:00), and afternoon (approximately 2:00-5:00).*

Both of the Central Florida Zoo spider monkeys were the least active in the mornings and their locomotion activity peaked in the late afternoon (Figure 2). Increased resting behavior and decreased moving activity in the morning makes sense for these individuals; if the monkeys were fed before the zoo opened then their food would be gone by the time morning observations began at around 9:00. These captive spider monkeys mirrored the findings of Muñoz-Delgado et al. (2018) for the monkeys living on a tourist-exposed island, in that (at least with the broad time blocks used in this study to investigate temporal effects on behavior) they appear to lack the bimodal activity pattern associated with wild spider monkeys. Results may have differed and a bimodal activity pattern may have emerged for the spider monkeys if the day was split more finely and data was collected for 1-hour blocks throughout the day instead of 2-3 hour blocks. It

is likely, however, that their level of activity versus rest is highly dependent on feeding times, and since they are fed at the beginning, middle, and end of the day, this may discourage a natural pattern of resting midday. For future studies obtaining access to the zoo before it opens to the public for the day and/or using cameras to collect data prior to the 9:00 opening time might be valuable. If it had been possible to record the feeding and moving activity they likely displayed when eating their 8:00 meal then the midday time frame may have emerged as a trough in activity.

Impact of Zoo Visitors on Behavior

The number of people visiting the exhibit during the observation periods were not recorded. That is because these data could not be collected while simultaneously collecting accurate behavioral data, especially when large groups of visitors stopped at the enclosure at once. However, the day of the week can be used as a proxy of how many visitors were at the zoo. Observations were grouped by day according to assumed and qualitatively observed numbers of people. The "high crowds" condition (Saturday and Sunday), "moderate crowds" condition (Friday), and "low crowds" condition (Monday through Thursday) were used to analyze possible visitor effects on the spider monkeys. Contrary to Muñoz-Delgado's 2018 study which showed higher spider monkey activity on days with more human activity and Quadros' 2014 study which showed primates tend to rest less and move more when large, noisy crowds are present, Big Guy showed the most active (moving) behavior on days with low crowds, and the least active behavior on days with high crowds (Figure 3). He also spent more time inactive on days with moderate and high crowds (Figure 3). It is possible that Big Guy’s interest in coming to the window platform frequently to sit or lay while watching or interacting with guests contributed to

an increase in stationary behavior on days with more guests. He often engaged in an “open mouth” behavior towards guests at the window that appeared affiliative and curious and was usually accompanied by head-tilting. More data collection would be helpful to confirm that effects seen could be attributed to increased or decreased zoo guest presence, especially because on some "low crowds" days the zoo may have been busy due to school field trips. Zsa-Zsa did not seem to show consistent or pronounced patterns of behavior related to guest presence (see Figure 4).

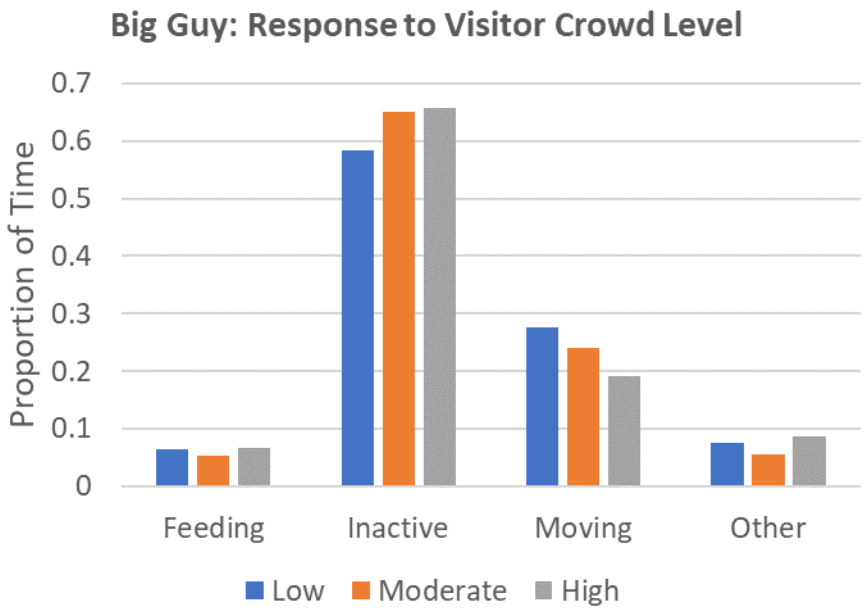

Figure 3 *- Variation in Big Guy’s activity budget according to day of the week (used as a proxy for number of visitors).*

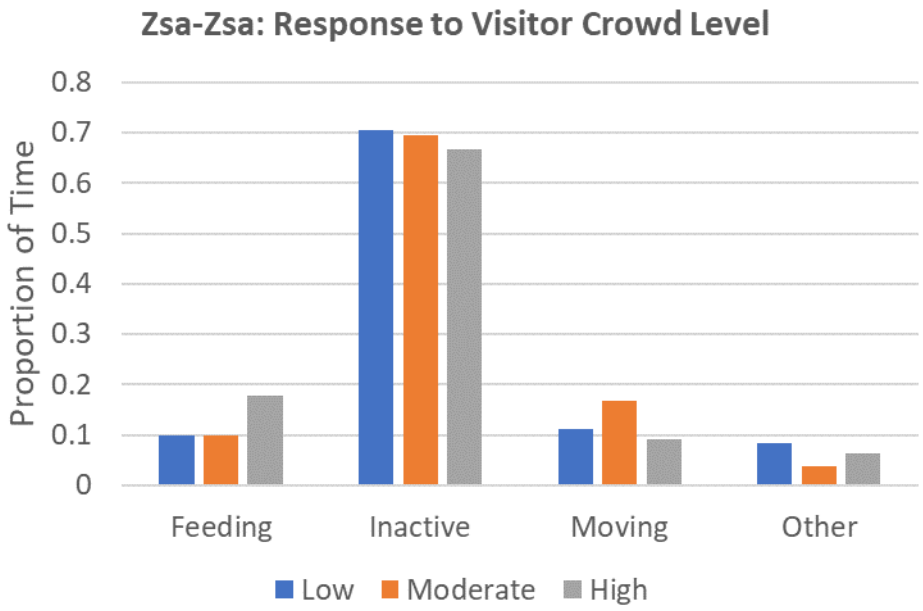

Figure 4 *- Variation in Zsa-Zsa's activity budget according to day of the week (used as a proxy for number of visitors).*

Response to Exhibit Renovation

Definite conclusions cannot be drawn about behavior before and after exhibit renovations because construction (mid-February to mid-March) took longer than expected and allowed very little time to conduct observations after construction, and because cold weather prior to construction prohibited opportunities for observation during January and early February. Because of the large time gap between "pre-construction" observations done mostly in the fall of 2018 and the "post-construction" observations undertaken in the spring of 2019, differences in behavior could also be attributable to seasonal changes. This study used 49 hours of behavioral data that were collected prior to construction (September to December 2018), and 9.5 hours of data collected after the exhibit renovations (March 2019). Relative to the before construction period, Big Guy had an increase in the amount of "other" behaviors he performed after construction was completed. This percentage is likely not representative of his true behavior,

because fewer observations were conducted after construction ended. In one post-construction observation period he demonstrated an abnormally high amount of self-grooming (which would be categorized as "other"). There is a possibility that this spike in self-grooming could have been stress-related, but if it was an anomaly on this particular day, more hours of observation would have likely brought his amount of grooming time down to normal levels. Due to a lack of a large sample of observation days for post-construction no strong conclusion can be made about changes in his behavior after construction occurred. In the observations of Zsa-Zsa post-construction atypical outside factors impacted her behavior so that this also was likely to not be an accurate representation either. During one observation of her, construction on the holding area was beginning, which meant that keepers were standing around the enclosure for hours at a time supervising the construction workers who were in close proximity to spider monkeys. During this time, she exhibited higher levels of activity (locomotion) and spend less time resting than she typically would at that time of day. She spent a long time alert and vigilant, moving around and looking at the keepers. For Zsa-Zsa, time spent inactive decreased slightly and time spent moving increased relative to pre-construction levels. Like Big Guy, she also engaged in more "other" behavior. The increase in "other" behavior could be because 48% of the allogrooming observed during the study took place after construction. In Figure 5, activity budgets for both monkeys pre-construction and post-construction are combined to mitigate the effects of some

abnormal patterns of activity in each monkey after construction.

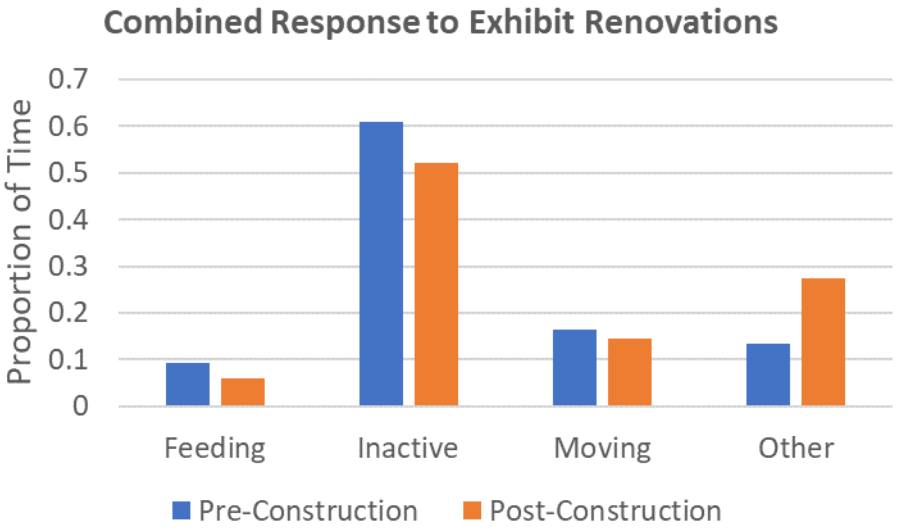

Figure 5 *- Combined activity budget for Big Guy and Zsa-Zsa before and after construction occurred.*

Impact of Temperature on Behavior

Although based on Wallace's investigations into seasonality and activity budgets (Wallace 2001) it was anticipated that these observations would show more time spent resting and less time feeding in cold weather, no clearly discernible relationship between temperature and activity budget was found. However, it should be taken into account that the monkeys were not observed on very cold days and it was likely they spent significant amounts of time resting as they rarely, if ever, emerged from the holding area and their heat lamp.

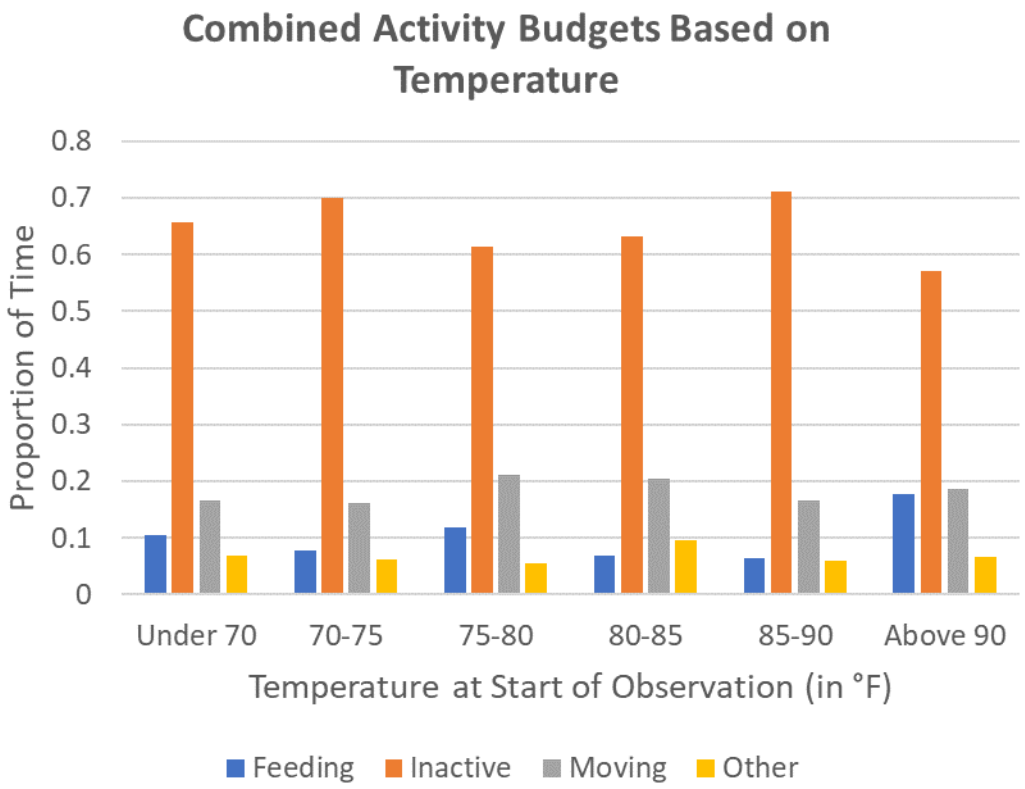

Figure 6 *- Combined activity budgets for Big Guy and Zsa-Zsa for various temperature ranges (°F) showing no particular pattern. The temperature was determined at the start of an observation period.*

FINAL RECOMMENDATIONS AND FUTURE INVESTIGATIONS

Because the activity budgets of the captive spider monkeys in this study showed less time eating and foraging than wild spider monkeys, increased amounts of food-based enrichment are advised to encourage natural feeding behavior. More frequently changing the arrangement of exhibit props and swapping out some items for novel props could also encourage the monkeys to spend less time stationary and resting, so their activity level better matches that of wild spider monkeys. Regulating guest presence in front of the enclosure is likely unnecessary, as the activity budgets for busier weekend days at the zoo saw little to no change from those on less busy weekdays, suggesting these individuals are very well-habituated to crowds. The social behavior of these individuals seems normal, with no aggression or conflicts over resources observed. They exhibited species-appropriate amounts of affiliative behavior like embracing, social grooming, and spending time in close proximity to each other. Exhibit renovation did not drastically impact their activity, suggesting that they adapted well and quickly to the new exhibit.

Future studies should utilize cameras if possible to get a more comprehensive idea of the monkeys' behavior at all times of day, even when the zoo is not open or when the monkeys are out of sight in the holding area. Splitting the day into smaller blocks of time when collecting observational data could yield more detailed insights into behavior changes throughout the day and perhaps reveal activity consistently waning in the middle of the day like it does in wild *Ateles* populations. Investigating social interactions in more depth when there are more individuals present after the introduction of new monkeys is advised. Rates of allogrooming between existing residents and new monkeys can be an indicator of how well the introduction is going, as it is indicative of bonding that allows spider monkeys to tolerate sharing of food

without aggression. Based on Pastor-Nieto et al.'s 2001 study of social grooming, kinship, and co-feeding, when new spider monkeys are introduced at the Central Florida Zoo, monopolizing food access will be frequent at first, but co-feeding will increase as they become more familiar with one another and build social bonds through grooming, despite being unrelated to the current resident monkeys.

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