Hand Use in Juvenile and Adult White-faced Capuchins (*Cebus capucinus)* in Costa Rica

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ABSTRACT

Previous studies have shown varied results in white-faced capuchins (*Cebus capucinus)* hand preference for certain behaviors, such as carry, forage, and eat. In this study, I observed the adults and juveniles of the 24 member troop at Estación Biológica La Suerte in northeastern Costa Rica for 45 contact and 12.1 observation hours to see if hand preference occurs in eat, forage, grab, scratch, carry, groom, and allogroom. Grab, groom, and allogroom were not included in analysis due to low frequencies of usable occurrences. Eat held consistent with prior studies that state adult males use their left hand for hand-eye coordination behaviors more often than their right hand, adult females use both hands more frequently and for longer periods of time than either hand due to a lack in strength to hold large fruits in one hand, and juveniles may not be as consistent due the prolonged developmental period. Forage showed a preference to use both hands across all age/sex classes, but this may be due to fruit size. Carry was inconsistent with some prior studies that showed adults to use their left hand more than their right hand or mouth to carry, but agreed with others that there is no hand preference for carry for any age/sex class. More research must be conducted to determine hand preference for these behaviors. Travel should also be looked at as a measure of handedness, and hand use preference should be looked at at the individual level, rather than just the population level to see if individuals have a personal preference for hand use in certain behaviors.

INTRODUCTION

White-faced capuchins (*Cebus capucinus*) are medium sized new world monkeys that are found from Honduras to the northwest coast of Ecuador, have a large home range and a variable diet, have a 20% body size difference between the sexes, with males being larger than females, and live in multi-male/multi-female groups with both an alpha male and an alpha female (Jack 2011). *C. capucinus* have a large brain to body ratio, don't have much grasping ability in their prehensile tails, and are extractive foragers and make use of tools. (Jack, 2011). They have pseudo-opposable thumbs (Jack,

2011) which allows them to hold an object in one or both hands (Spinozzi, et al,. 2004). Many factors, such as age, strength, and nutritional needs, influence the amount of time expended on and how an individual forages (Izawa and Mizuno, 1977; Collins and McGrew, 1987; McGrew, 1992; Boesch and Boesch, 1993; Boinski et al., 2000 as cited by O'Malley and Fedigan, 2006). Both male and female adult *C. capucinus* have similar positional and hand use behaviors (Doran, 1993; Garber 2007 as cited by Bezanson, 2009; Bezanson, 2009), and infant white-faced capuchins begin to show adult position behavior and similar patterns of hand use by six months of age (Bezanson, 2009). Thus, juveniles may show similar patterns of hand preference for eating and foraging to adults, but may not be as consistent as adults, due to an extended period of learning.

Various studies (Panger, 1998; Spinozzi, et al,. 2004) have found conflicting results when looking at hand preference in *C. capucinus.* One study found that hand use varies across tasks, simple tasks do not have conclusive results because either hand could be used, and that all age and sex variations in the group resulted in similar hand preference, except juveniles use their mouth to carry items more often than adults (Panger, 1998). Other researchers, however, found that their study group had no hand preference for certain tasks (Spinozzi, et al,. 2004). Because so many papers have been published on the subject of handedness in primates, all with varying results, it is important to collect more data to be analyzed.

Does the *C. capucinus* troop at Estación Biológica La Suerte show preferential hand use for behaviors such as forage, eat, carry, grab, scratch, allogroom and groom? The right hemisphere of the brain is associated with hand-eye coordination, meaning the left hand is used primarily to reach for food and to bring it to the mouth (Falk, 2000), while the right hand is used primarily for manipulation tasks (Panger, 1998). Because the left hand is used primarily for hand-eye coordination (Falk, 2000), I expect to find that behaviors such as grabbing and eating will be performed with the left hand, while the right hand will be used for behaviors such as foraging, as the right hand is used more for manipulation (Panger, 1998). I expect behaviors such as grooming will be performed with both or

either hand due to the simplicity of the task. I don't expect that there will be a difference in hand preference for specific tasks between the sexes, nor will there be a great difference between adults and juveniles as juveniles are older than 6 months of age, when infants begin to mimic hand use patterns of adults, but there may be slight differences due to the long developmental period of primates.

Hypotheses

H_0: There will be no hand preference for any tasks in adult males, adult females, and juveniles.

Ha: There will be hand preference for specific tasks, such as eating, foraging, carrying, scratching, allogrooming, grooming, and grabbing, with no difference between adult males, adult females, and juveniles due to juveniles showing adult positional behaviors by 6 months of age (Bezanson, 2009).

Hb: There will be hand preference for specific tasks, such as eating, foraging, carrying, scratching, and grabbing, but not for allogrooming or grooming, with no difference between adult males, adult females, and juveniles due to juveniles showing adult positional behaviors by 6 months of age (Bezanson, 2009).

Hc: There will be hand preference for specific tasks, such as eating, foraging, carrying, scratching, and grabbing, but not for allogrooming or grooming, and there will be a difference between adults and juveniles due to age variation in juveniles, as some juveniles may not have developed hand-eye coordination or be large enough to carry objects with only one hand.

Hd: There will be hand preference for specific tasks, such as eating, foraging, carrying, scratching, and grabbing, but not for allogrooming or grooming, with a difference between adult males and adult females due to males being stronger/larger and therefor able to more easily carry certain objects with only one hand more often than females, but not a difference between adults and juveniles.

METHODS

Study site and study animals

Research was conducted at Estación Biológica La Suerte in northeastern Costa Rica (10º26'N,

83º47'W). This site is a tropical pre-montane wet forest that includes primary forest, advanced secondary forest, and areas that have been selectively logged in the past. Rainfall in this region averages 3,962 mm per year (Sanford et al., 1994). Two areas of the research center, Large Forest and Small Forest, have trails allowing researchers to enter the forest. Five adult females, four adult males, one sub-adult male, eleven juveniles, one independent infant, and two dependent infants make up the 24 member white-faced capuchin study group. This group was rarely present in its entirety during observations, except for in the case of travel, and fission was suspected due to the large group size. The most common observation location was at a mamone tree at the edge of Small Forest, while most travel behavior took place in Large Forest, or between Large Forest and Small Forest.

Data collection

Data were collected from August 30th to July 9th 2014 between the hours of 5am and 2pm, with one collection day lasting until 3:30pm. I was in contact with the troop for a total of 45 hours, and recorded 12.1 observation hours. Data were collected on adult males, adult females, and juveniles. Infants were not recorded due to limited visibility, the sub-adult was recorded as an adult male for simplicity purposes, and juvenile sexes were not distinguished due to difficulties in identification. Due to time constraints, I was unable to identify individuals in each age/sex class, thus all adult males were lumped into the same group, and the same with adult females and juveniles. Individuals that were carrying small juveniles or infants were noted, but not separated into their own group for analysis.

Data were collected using 5 minute continuous focal animal sessions (Altmann, 1974) after an individual was first identified as an adult male, an adult female, or a juvenile. If the focal animal went out of view for longer than one minute, the sample was thrown out, and not included in any analysis or total frequencies. Each behavior was recorded, along with which hand was used at the beginning of the behavior, if applicable. Hand use has six categories: left hand, right hand, both hands, mouth, back foot, or null. Mouth was only applicable to eat and carry, and back foot was only applicable to scratch. If a behavior did not require a specific hand, such as rest, null was recorded. Null was also recorded if

hand use was not seen or if I was uncertain about which hand was used. For scratch, which part of the body that was scratched was recorded along with what hand was used. A behavior ended if a different hand was used or if the individual engaged in a new behavior. The duration of each behavior was recorded using a stop watch, and binoculars were used to aid in hand use differentiation and age/sex class identification.

Data analysis

All behaviors that an individual engaged in were recorded and activity budgets made for each age/sex class, but only seven behaviors that required hand use are included in the analysis. Null hand use is excluded from total usable instances of seen hand use for each behavior. Travel was originally intended to be a focus of this study, but insufficient data on which hand was used at the beginning of travel excluded this behavior from analysis. Frequencies of which hand was used for each behavior was totaled, and, due to unequal amounts of data collected on each of the age/sex classes, proportions of duration of hand use per behavior was calculated. Average amount of seconds that each age/sex class used what hand for seven behaviors was also calculated. These seven behaviors include eat, grab, forage, scratch, carry, groom, and allogroom. I chose to focus primarily on eat and forage hand use, as I was able to record the highest instance of these behaviors.

RESULTS

An activity budget for each age/sex class was created (Figure 1). Adult males spend 35% of their time foraging and eating, adult females spend 34% of their time foraging and eating, and juveniles spend 43% of their time foraging and eating.

During the 12.1 observation hours, an accumulated total of 427 usable instances of eat occurred, 23 usable instances of grab occurred, 237 usable instances of forage occurred, 127 usable instances of scratch occurred, 50 usable instances of carry occurred, 35 usable instances of groom occurred, and 21 usable instances of allogroom occurred (Table 1). Grab, groom, and allogroom behaviors were not

analyzed due to the small number of usable instances of each behavior. Duration for these behaviors was recorded during observations, and proportions of time in seconds that each age/sex class spent using a specific hand for each behavior, excluding grab and scratch, was calculated (Table 2). Grab and scratch were excluded from the proportion of time calculations due to most instances of scratch and grab being too quick to record duration accurately. Adult males use their left hand to eat 47% of the total time they spend eating, adult females use their left hand 30% of the time, and juveniles use their left hand 23 % of the time. Adult males use both of their hands to eat 31 % of the time, adult females use both of their hands 51% of the total time they spend eating, and juveniles use both hands 48% of the total time they spend eating. Adult males use their right hand 10% of the time, adult females use their right hand 13% of the time, and juveniles use their right have 25% of the total time they spend eating. When foraging, adult males use both hands 97% of their total time foraging, adult females use both of their hands 96% of total forage time, and juveniles use both of their hands 92% of total forage time. Adult males carry with their right hand 65% of carrying time, adult females carry with their right hand 35% of carrying time, and juveniles carry with their right hand 43% of the time. Adult males use their left hand to carry 19% of the time, adult females carry with their left hand 35% of the time, and juveniles use their left hand 47% of carrying time. Adult males use both hands to carry 8% of the time, females use both to carry 27% of the time, and juveniles spend no time carrying with both hands. Adult males carry with their mouth 9% of carrying time, adult females carry using their mouth 16% of the time, and juveniles carry with their mouth 10% of carrying time.

Out of the total 127 usable instances of scratch that occurred, 106 scratches were preformed on the same side of the body as the hand that was used. Sixteen scratches were performed with either both hands or with a back foot. Only one instance of across body scratching was observed in a juvenile who used their right hand to scratch the left side of their body. One instance of using the right hand to scratch the mouth was observed in a juvenile, one instance of a juvenile using their left hand to scratch their head, and two instances of a juvenile using their right hand to scratch their head were observed.

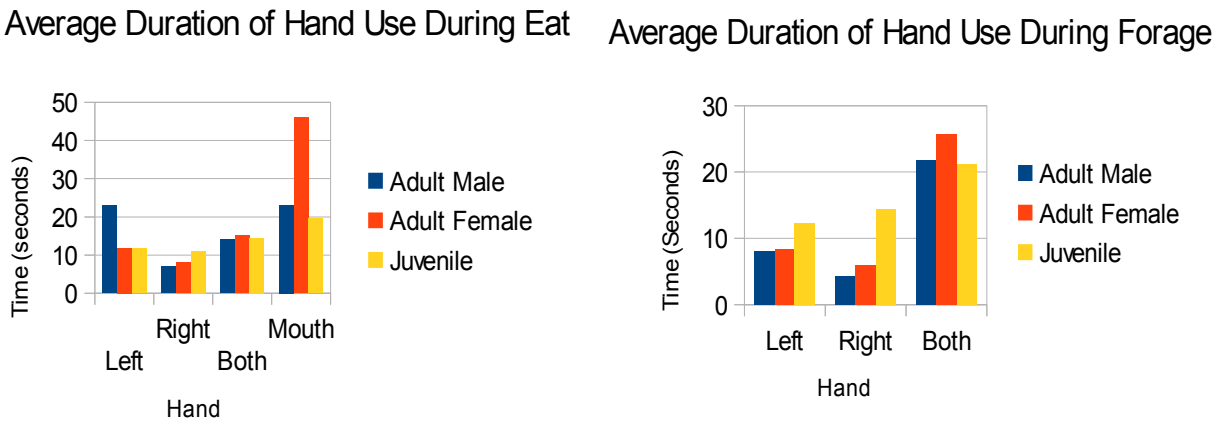

Figure 2: Average duration of hand use for eat and forage for each age/sex class.

Average amount of seconds that each age/sex class used what hand for eat and forage were calculated (Figure 2). Adult males will use their left hand while eating for an average of 23 seconds and their mouth directly on the food source for an average of 23.1 seconds of eating time. Adult males will use their right hand to eat for 7.05 seconds and both hands for 14.1 seconds of total eating time. On average, adult females eat with their mouth directly on the food source without using one or more hands to bring food to their mouth 46 seconds of total eating time. Adult females will use their left hand for 11.8 seconds, their right hand for 8 seconds, and both hands for 15.1 seconds of total eating time. Juveniles use their mouth directly on the food source on average for 19.6 seconds of total eating time, and use their left hand for 11.7 seconds, their right hand for 11 seconds, and both hands for 14.5 seconds of total eating time. Adult males use both hands to forage on average for 21.8 seconds, their left hand for 8 seconds, and their right hand for 4.3 seconds of total forage time. Adult females use both hands to forage on average for 25.7 seconds, their left hand for 8.3 seconds, and their right hand for 6 seconds of total forage time. Juveniles, on average will use both hands to forage with for 21.2 seconds, their left hand for 12.3 seconds, and their right hand for 14.4 seconds of total forage time.

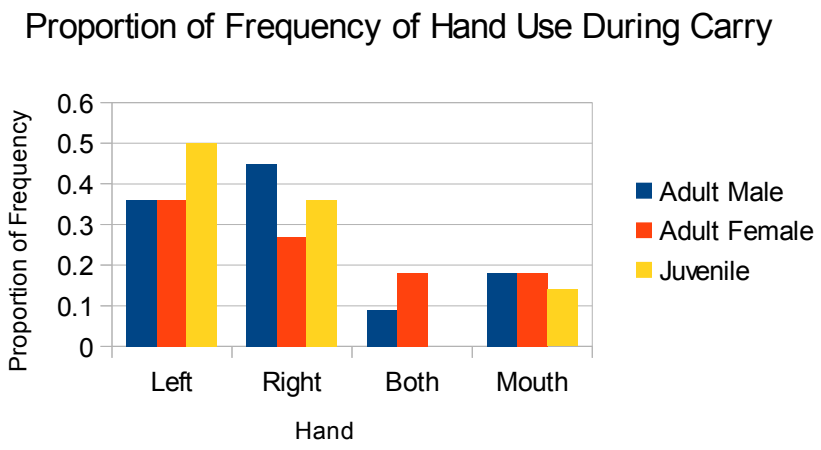

Figure 3: Proportion of frequency of hand use during carry for each age/sex class.

Hand use during carrying was looked at as proportions of total carrying frequency (Figure 3). Adult males carry with their left hand 0.36, their right hand 0.45, both hands 0.09, and their mouth 0.18 of total carrying frequency. Adult female carry with their left hand 0.36, their right hand 0.27, both hands 0.18, and their mouth 0.18 of total carrying frequency. Juveniles carry with their left hand 0.5, their right hand 0.36, both hands 0, and their mouth 0.14 of total carrying frequency.

DISCUSSION

When looking at the time budgets (Figure 1), we find that juveniles spent the most time foraging, adult male and females spend a relatively equal amount of time foraging. This is consistent with prior studies (O'Malley and Fedigan, 2006) that juveniles forage more often than adults because juveniles have a higher metabolism, thus they need to eat more often than adults, and juveniles are more inexperienced than adults at foraging, and so will devote more time to the behavior (Janson and van Schaik, 1993 as cited by O'Malley and Fedigan, 2006). Juveniles will also engage in risk aversion behaviors when forging to avoid dropping food due to inexperience and not having the strength as their adult troop members (O'Malley, personal observation, as cited by O'Malley and Fedigan, 2006).

Despite being older than 6 months of age, the previously stated supports the idea that juveniles, while already beginning to mimic adult hand use preference for behaviors such as eating and foraging, would show inconsistencies of hand use when compared to adults. Results from this study show that adult males use their left hand to eat 17% more than females and 24% more than juveniles do. It makes sense that males would eat most often with their left hand as it is used primarily for hand-eye coordination tasks, which juveniles are still developing. Adult males have larger hands than adult females, so eating with one hand may be easier for males than for females. Adult females use both hands to eat 51% of eating time, as apposed to males, who only eat with both hands 31% of the time, but similarly to juveniles, who eat with both hands 48% of eating time. This is due to females having smaller hands than males, making eating with only one hand difficult. Juveniles are similar to females because they, too, have smaller hands than adult males, but also because juveniles are inexperienced at handling food, and thus will use both hands to avoid dropping it. Juveniles use their right hand for more time during eating than either adult sex, which is consistent with the hypothesis that juveniles may not be as consistent with using their left hand for eating as adult males because they are still in the process of developing hand-eye coordination and becoming more experienced with eating.

When looking at foraging, there is not much difference between the age/sex classes, as all use both hands primarily. This could be due to the large size of the fruits (coconuts and mamones), requiring them to use both hands to forage. This could also be due to the fact that some tasks require both manipulation (right hand) and coordination (left hand), making the use of both hands necessary (Lacreuse and Fragaszy, 1996, 1997, 1999; Parr et al., 1997; Spinozzi and Cacchiarelli, 2000 as cited by Spinozzi et al., 2004), or could be due to the simplicity of the task, allowing either hand to be used (Panger, 1998). This data holds true with a study that found foraging patterns not to differ between the sexes in pre-adult individuals (Fragaszy, 1990; Rose, 1994, MacKinnon, 1995 as cited by O'Malley and Fedigan, 2006).

Carrying data produced by this study is inconsistent with a previous study that states that all

age/sex classes use their left hand to carry equally, while adults use their right hands and mouths less than juveniles do to carry (Panger, 1998). However, another study found that there was no hand preference for carrying at the population level (Panger and Wolfe, 2000).

Scratching data held consistent with a prior study that concluded that primates prefer to use the hand to carry out a task on the same side of their body, and tend not to cross they body with their arm (Panger, 1998). Only one instance of scratching across the body was recorded in a juvenile.

Some of my results are consistent with prior studies, while others are not. This could be improved with additional hours, and equalizing the amount of hours recorded for each age/sex class. Due to time restraints and a group that seemed to be in the process of fissioning, most of my samples are of juveniles, with much fewer adult female samples. If this study were to be carried out again, more time must be devoted to collecting data, and identifying individuals of each age/sex class would strengthen the data as I would be able to determine individual hand preferences as apposed to population hand use. More data could be used to allow for more data analysis of behaviors such as grab and forage.

CONCLUSION

1. Hand use during scratching occurs on the same side of the body as the hand in almost all cases.
2. Eating with the left hand occurs most often in adult males due to strength and developed hand-eye coordination.
3. Foraging occurs equally as often between all age/sex classes with both hands, but could be due to the size of the fruits.
4. Carrying data held consistent with varying results from multiple studies, proving that much more research must be done on the matter.
5. More data should be collected to strengthen the previously mentioned conclusions and for other behaviors, such as grab, to be analyzed.

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APPENDIX

Table 1: Total Usable Occurrences of Hand Use by Behavior and Age/Sex Class

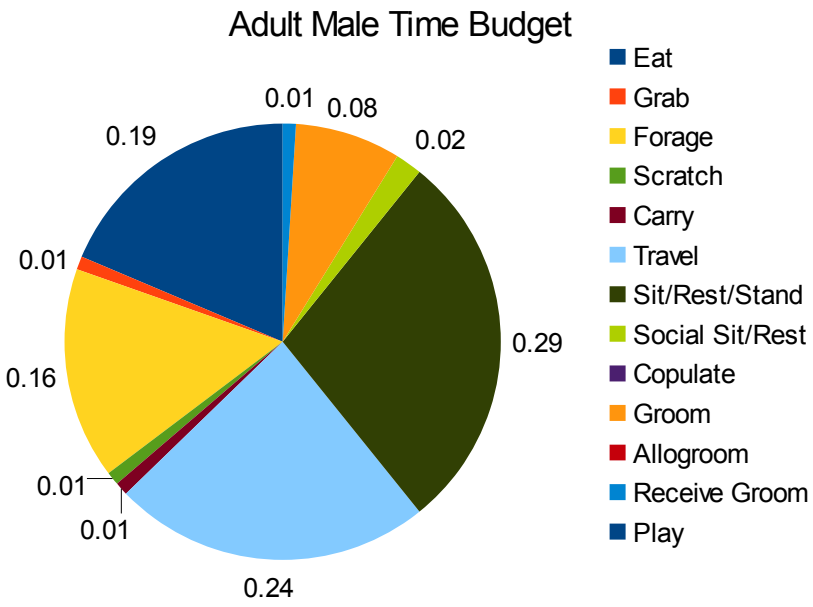
Age/Sex Class	Behavior	Left Hand	Right Hand	Both Hands	Mouth	Back Foot
Adult Male	Eat	30	20	33	8	n/a
	Grab	7	1	2	n/a	n/a
	Forage	3	3	50	n/a	n/a
	Scratch	13	10	1	n/a	2
	Carry	4	5	1	2	n/a
	Groom	1	0	16	n/a	n/a
	Allogroom	0	0	0	n/a	n/a
Adult Female	Eat	20	13	27	1	n/a
	Grab	1	3	0	n/a	n/a
	Forage	3	1	27	n/a	n/a
	Scratch	8	14	0	n/a	4
	Carry	4	3	2	2	n/a
	Groom	0	0	9	n/a	n/a
	Allogroom	0	0	9	n/a	n/a
Juvenile	Eat	69	79	116	7	n/a
	Grab	5	1	4	n/a	n/a
	Forage	6	11	131	n/a	n/a
	Scratch	27	39	0	n/a	9
	Carry	14	10	0	4	n/a

	Groom	0	0	9	n/a	n/a
	Allogroom	0	0	12	n/a	n/a

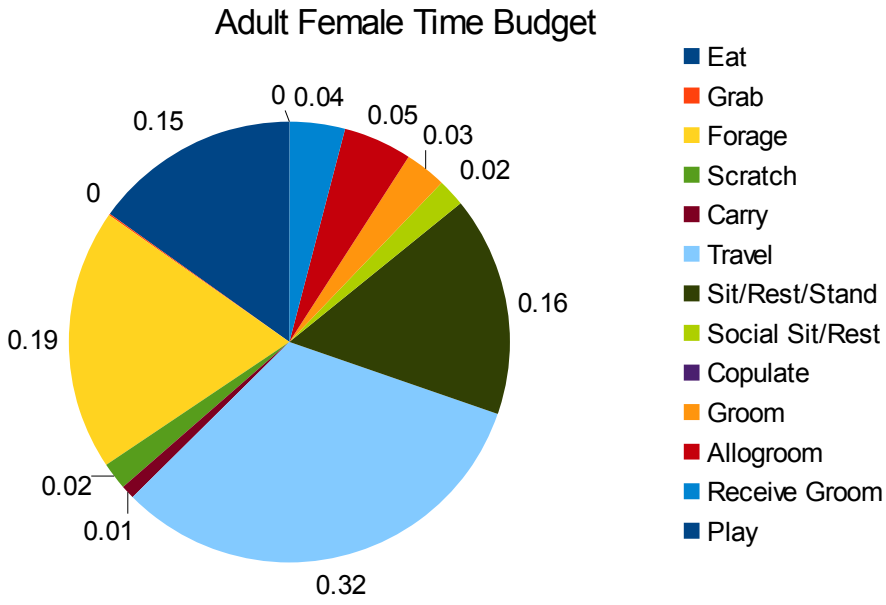
Table 2: Proportion of Time (Seconds) of Hand Use for Behavior and Age/Sex Class

Behavior	Age/Sex Class	Left Hand	Right Hand	Both Hands	Mouth	Back Foot
Eat	Adult Male	0.47	0.1	0.31	0.13	n/a
	Adult Female	0.3	0.13	0.51	0.06	n/a
	Juvenile	0.23	0.25	0.48	0.04	n/a
Forage	Adult Male	0.02	0.01	0.97	n/a	n/a
	Adult Female	0.03	0.01	0.96	n/a	n/a
	Juvenile	0.02	0.05	0.92	n/a	n/a
Carry	Adult Male	0.19	0.65	0.08	0.09	n/a
	Adult Female	0.21	0.35	0.27	0.16	n/a
	Juvenile	0.47	0.43	0	0.1	n/a
Groom	Adult Male	0.06	0	0.94	n/a	n/a
	Adult Female	0	0	1	n/a	n/a
	Juvenile	0	0	1	n/a	n/a
Allogroom	Adult Male	0	0	0	n/a	n/a
	Adult Female	0	0	1	n/a	n/a
	Juvenile	0	0	1	n/a	n/a

(A)


Adult Male Time Budget
0.01
0.08
0.02
0.19
0.01
0.29
0.16
0.01
0.01
0.24
Eat
Grab
Forage
Scratch
Carry
Travel
Sit/Rest/Stand
Social Sit/Rest
Copulate
Groom
Allogroom
Receive Groom
Play

(B)


Adult Female Time Budget
0
0.04
0.05
0.03
0.02
0.15
0
0.16
0.19
0.02
0.01
0.32
Eat
Grab
Forage
Scratch
Carry
Travel
Sit/Rest/Stand
Social Sit/Rest
Copulate
Groom
Allogroom
Receive Groom
Play

(C)

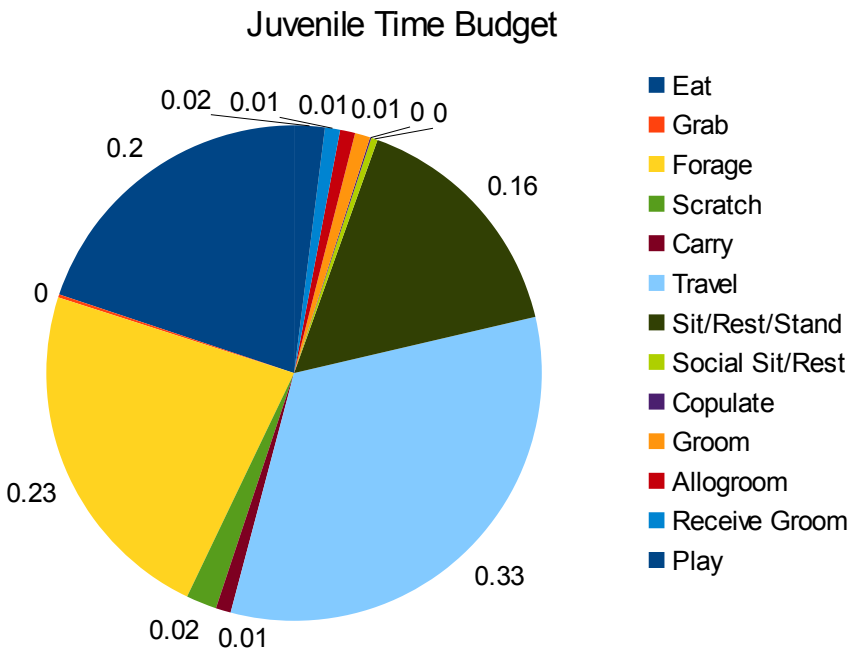


Figure 1: Time budgets for adult males (A), adult females (B), and juveniles (C).

Ethogram

Category	Behavior	Description	Abbreviation
Food Related	Carry	To move an object from one place to another via the use of travel.	C
	Eat	To bring any food object to their own mouth for consumption. Opening fruits is included in eat due to difficulty in determining when an individual is eating rather than opening a fruit from a distance.	E
	Forage	To look for food with the use of hands.	F
	Grab	To take a food item in one or more hands or mouth from a substrate. Follows forage and preludes eat or carry.	Gr
Solitary	Groom	To pick through own body hair with hands.	SG
	Scratch	To rub hand or hands on body in a quick repetitive moment. Must be repeated at least twice to be counted as scratch.	Sc
	Sit/Rest/Stand	Any inactive behavior where no other defined behavior is being performed.	Si/R/St
	Travel	To move from one location to another. Distances beyond 1 body length are counted as travel.	T

Social	Allogroom	To groom another individual.	Allo
	Copulate	Any behavior involving mounting.	Cop
	Play	Affiliative play behavior between two or more individuals. May include play-chase, play-wrestle, or any other play behaviors.	P
	Receive Groom	To be allogroomed by another individual during Sit/Rest/Stand.	ReGr
	Social Sit/Rest	To Sit/Rest in proximity or in contact with one or more individuals.	SS/SR
Other	Out of View	To be out of view from the observer.	OOV

Data Sheet Example

Date: 8/8/14	Juvenile		
Time	Behavior	Hand	Notes
0	E	Null	
5	St	Null	
8	Sc	Null	
10	St	Null	
14	F	B	
35	E	L	
36	T	Null	
56	Si	Null	
59	T	Null	
1.11	F	Null	
1.17	Sc	R	R
1.24	Si	Null	
1.34	T	Null	
2.11	Si	Null	
2.17	T	Null	
3.55	E	B	
4.16	E	R	
4.25	T	Null	
4.3	Sc	Null	
4.32	St	Null	
4.41	F	Null	
4.55	E	Null	