INFLUENCE OF FOREST FRUIT PRODUCTIVITY AND HIERARCHY ON BEHAVIORAL PATTERNS AND BODY WEIGHT OF CAPUCHIN MONKEYS ***(Sapajus apella)***

DANIELA RODRÍGUEZ PEDRAZA

Trabajo de Grado para optar por el título de Ecóloga

Pablo R. Stevenson Díaz, PhD
Director del Trabajo de Grado

PONTIFICIA UNIVERSIDAD JAVERIANA
FACULTAD DE ESTUDIOS AMBIENTALES Y RURALES
CARRERA DE ECOLOGÌA
BOGOTÁ, D.C.
2019

Índice

Anexos

Título del Trabajo de Grado

Influence of forest fruit productivity and hierarchy on behavioral patterns and body weight of capuchin monkeys (*Sapajus apella*)

Pregunta de investigación

¿Cómo se ve afectada la fluctuación de patrones comportamentales y el peso corporal de *Sapajus apella* por la productividad de bosque y jerarquía de la población, en un periodo de tiempo de 5 meses?

Objetivos

- Objetivo General

Determinar la manera en la que afecta la productividad de frutos del bosque y la jerarquía de una población las variaciones comportamentales y de peso corporal de individuos de *Sapajus apella,* en un periodo de 5 meses en la reserva biológica "Tomo Grande"- Vichada, Colombia.

- Objetivos Específicos

Determinar la productividad de frutos mensual en un bosque de galería, en una temporada de escasez y una de abundancia.

Determinar la fluctuación que presenta la población de *Sapajus apella* en términos comportamentales y de peso corporal.

Determinar el orden y rangos jerárquicos de la población de *Sapajus apella.*

Influence of forest fruit productivity and hierarchy on behavioral patterns and body weight of capuchin monkeys (*Sapajus apella*)

Daniela Rodríguez Pedraza
Faculty of Environmental and Rural Studies, Pontificia Universidad Javeriana

Abstract
Wild neotropical primates face several threats that are exponentially decreasing their populations, constant changes in their natural habitats have forced them to adapt to natural and anthropogenic changes. Because of this, is important to know how primate species respond to habitat changes that have been affecting them. Changes in forest fruit productivity is one of them, and this study focused on a population of *Sapajus apella* to test the hypothesis that fruit abundance affects behavior and body weight, and that dominant individuals will be less affected by periods of fruit scarcity. Fruit production was estimated using 60 fruit traps, body weight was measured using baited scales and behavioral patterns were observed for 5 months, (four months during the scarcity season, and one additional month in fruit abundance). Body weight was relatively stable during scarcity, but in abundance all individuals gained weight. Variation in behavior was not significantly different between months ($p > 0.05$), although correlations with fruit production were found in some behaviors, such as in feeding and foraging ($r = -0.88$, $p < 0.04$), grooming ($r = 0.91$, $p < 0.02$) and displacement ($r = 0.89$, $p < 0.04$). Differences in behavior were found within hierarchical ranks as well, dominants were more aggressive, groomed more, were seeing feeding more frequently and in longer periods of time and the alpha male usually expelled others from the feeding trees. Also, the alpha male had a weight 60% higher than the average of the population and it was found that juveniles gained more weight than any other age classes, even though they were in the lowest rank of the hierarchy, due to the growing stage they are in. Contrary to expectations the individuals at highest ranks, who were heavier, gained less weight, but alpha male was not included in this analysis.

Keywords: Behavior · Body weight · Dominant individuals · Subordinate individuals · Scarcity · Abundance

INTRODUCTION

Colombia is considered as the third country with the highest primate species richness in America (Caro, 2015). However, much of this biodiversity is currently threatened mainly by the degradation or transformation of their habitats and it has been demonstrated that the destruction of the vegetation has been involved in the decline of many primate populations (Strier, 2000). For instance, 60% of primate taxa in the world are already threatened with extinction, and 75% of populations are experiencing dangerous declines (Estrada et al., 2017).

One of the most relevant factors affecting wild populations of Neotropical primates is fruit productivity, because community biomass is highly dependent on the production of fleshy fruit species (Stevenson, 2001). In addition, there are seasonal changes in the availability of tropical forest resources, generating changes in primate behavior (McConkey et al., 2003, Stevenson et al. 2000), and affecting patterns of social interactions, diet and habitat use (Hemingway & Bynum, 2005). Meanwhile, some species do not show adaptive behavior when their environment changes quickly. This limitation may become an important aspect of future primate studies, since tropical habitats around the world are increasingly influenced by human activities (Janson, 2000).

Because of the increasingly intrusive human activities, primates have had to adapt for their survival and there have been some cases in which certain species have modified behaviors. For instance, when fruit is scarce, the diets of all species change to include other foods items (Tutin, 1997) and even some species have included crops as part of their diet (Strier, 2000). Diet specialists are the most affected since they face lack of resources when their habitats are disturbed. Therefore, it is important to have a better understanding of the way in which populations interact with their habitat and what ecological factors determine the occurrence of primate populations (Flórez, 2011). In addition, it is important to know the response of primates to different changes in their habitats either anthropogenic (Strier, 2000) or natural, considering that the availability of almost all plant foods fluctuates between abundance and scarcity (Tutin, 1997). In this way, researchers can generate contributions in the conservation of primates and identify the risks that represent habitat alterations in primate populations (Strier, 2000).

The Tufted or Brown Capuchin monkeys (*Sapajus apella)* represent an ideal study model to investigate this topic for two main reasons. First, that capuchin monkeys are an opportunistic species (Tiddi et al., 2018) and particularly this is one of the species with greater adaptations to disturbed ecosystems, which means that an affectation in this species due to changes in forest productivity either by natural effects or by human intervention, implies that any other primate species could be the same or even more affected. In addition, this species has a social behavior characterized by strong hierarchy, where there is an alpha male with a very differentiated behavior (Janson, 1984) which shows the highest feeding rates, achieving a diet that is 20% higher in energy, compared to subordinate individuals (Janson, 1985).

Variation in primate behavior is related to habitat-wide abundance of ripe fruit, among other ecological factors (Snodderly et al. 2019). Therefore it is expected that decreased food production will change behavioral patterns, such as increasing time foraging or attacking other individuals, due to competition for the limited resource of ripe fruit (Snodderly et al. 2019). It is also likely to decrease individuals' weight, mainly of low ranking individuals. For this reason, we expect higher body weight variability in low than high ranking monkeys. Besides, weight gain is expected to be related with the hierarchical status, because highest ranks will gain more weight due to the possibility that they have of monopolizing resources. Some attempts have been made to predict the effect of fruit scarcity on different aspects of primates populations. For instance, it was found that most primate species changed their diets during periods when their major food class (e.g. ripe fruit) was in short supply (Stevenson et al., 2000; Tutin, 1997). On the other hand, Janson (1985) proved that capuchin monkeys social organization determines food intake rates, therefore weight as well, because dominant individuals feed more than subordinates.

In this context, this study aims to establish how the behavioral patterns and the body weight of individuals fluctuate depending on the food availability (i.e. community wide forest fruit productivity), and at the same time how can the hierarchy affect directly the possibility of monopolizing food and gain weight. Sullivan et al. (2006) established that the availability of food as well as the intake does not have a great influence on individuals (in terms of body weight), since there are other factors that determine to a greater extent the increase or decrease in weight, such as the level of physical activity or the hierarchical order of the population. However, it is clear that in many primate species, individuals of high social statues can monopolize resources, such as in capuchin monkeys (Janson 1985, Vogel & Janson 2007).

METHODS

Study Site

The biological reserve "Tomo Grande" is located in Santa Rosalía one of the municipalities of Vichada's department in Colombia (4º 51'45 " N, 70º 14'0"W). It is in the area between the 'Tomo' and 'Caño Grande' rivers (Correa-Gómez & Stevenson, 2010). The landscape is characterized by extensive natural savannahs and wooded vegetation in non-connected gallery forests. It shows a regime of monomodal precipitation, with a maximum of rainfall in the middle of the year, and the dry season is characterized by being very strong (Correa-Gómez and Stevenson, 2010).

Data collection

Study duration. The fieldwork lasted from September to December, 2018 and the second period occurred in April 2019 (since this month is associated to the period of the highest fruit productivity), ending with over 300 hours of behavioral observations.

Fruit production collection. To estimate forest fruit productivity 60 fruit traps were distributed along a linear transect inside the forest. The space between the traps was approx. 20 m, located randomly both to the right and to the left and at a distance of between 0 and 10 meters from the trail (Stevenson et al., 2004). The traps were checked, selected and cleaned each 15 days during the 5 months that the study lasted, collecting all the fruits and seeds of each trap. Afterwards, fruit and fruit pieces were weighed, dried for approximately 15 hours and weighed again (Stevenson et al., 2004)., and the plant species were determined to the lowest taxonomic level.

Identification of individuals. The animals in this study were not marked in any way, they were identified by individual differences in size, facial fur color patterns, and other distinctive features (e.g. stains, scars, etc.) (Janson, 1985) allowing the observer to recognize all individuals in the group. The study group was conformed by 17 individuals including a 'satellite female' (Atalía) that was part of the time isolated from the rest of the group. The Alpha male (Marco) had a very strong differentiated behavior and special treatments from the other individuals. He was large and it was impossible to weight during the scarcity period (when we were using the platform scale, since he was able take food while being supported in other substrates).

Behavioral sampling. The behavioral observations were conducted in natural contexts and additional observations were made during food provisioning (only five times during the study, just for obtaining body weight), data on this study was collected through three types of sampling: focal animal (i.e. activity patterns), scan (distance and behavior of neighbors) and ad libitum (social interactions) (Martin & Bateson 2007). Sampling was done by following the group from 6 am to 6 pm from Monday to Saturday, with focal lengths of either 20 minutes (Abondano et al. 2012) or several hours (Stevenson et al., 2000). Activities were classified in 1. Displacement, 2. Resting, 3. Feeding & Foraging, 4.Social Play, 5. Grooming, and 6. Aggression. Within sampling bouts, the activity was recorded every 2 or 5 minutes respectively, also it was important to record all behaviors of submission and aggression (Martin & Bateson 2007), recording the actors and receivers in order to determine the hierarchy through social behavior matrices and the index of dominance viz, CBI as described in Clutton-Brock et al. (1979).

Body weight data. To obtain the body weight of the individuals, *Inga edulis* fruits were used as bait. Monkeys were invited to move into a platform covered by leaves, or fruit pieces were attached to a liana which was tied to a small weight located on a rope between two trees (Ohaus balances, +/- 0.2g). Every time an individual got on the platform or the liana to take the bait the body weight data was collected, using a remote control or long cable to tare the balance from some distance. The identity of all adults, subadults and juveniles that were feeding were scored with their respective weights and the observations ended when all food items had been eaten (Tiddi et al., 2018).

Data analysis

All the data collected in the fruit traps was analyzed, only endozoochoric species were taken into account and in order to estimate fruit production the dry weight of the fruits per trap was converted to Kg/ha using the area of each trap. Then the average productivity per month was obtained taking each trap as replicate (mostly N = 58, due to fallen traps that were not included in the analyses).

For the behavior analysis, all the focal data registered in either 2 or 5 minutes was turned into frequencies to estimate monthly percentages (Marin, 2010), and paired t-tests were used to determine temporal differences in behavioral (Martin & Melfi, 2016). However, to be certain about the variation within months, contingency tables and Pearson correlation coefficients between the forest fruit productivity ($w=0.814$, $p>0.1$) and the average proportion of time per behavior were carried out as well ($p>0.05$ in all behaviors; Shapiro-Wilk). This was made to determine the level of association between the variables and taking into account normality in data distribution.

In addition, the social organization of this species is quite evident and does not change very frequently (Janson, 1984). Accordingly, the hierarchy patterns of the population were determined only once by three matrices of affiliative, agonistic and social play behaviors between group members, to stablish two categories: submissive and aggressive individuals. In addition, a viz Clutton-Brock et al.'s index (CBI) was calculated for each individual following the formula: $CBI = (B + b + 1) / (L + l + 1)$, where B = number of individuals whom the subject dominates, b = number of individuals whom those dominated by the subject in turn dominate, L = number of individuals who dominate the subject, l = number of individuals who dominate those dominating the subject (Bang et al., 2010).

To analyze body weight changes per individual month by month and due to normality in data distribution($p>0.05$ in all cases; Shapiro-Wilk). First, paired t-tests were carried out to determine significant difference among weights per individual within months, then Pearson correlation coefficients (r) between the forest fruit productivity and each individuals' weight calculated. In addition, variation coefficients of the scarcity time (September – December) were determined and contrasted with hierarchical ranks through a Mann-Whitney test (not parametric data), and finally a maximum change in weight, including the abundance period (April) was calculated as well as Relative Growth Rates (RGR) of both seasons in order to compare them among hierarchical levels. All statistical tests were produced in 'R' software, except for the variation coefficients, maximum changes and RGRs which were calculated in Microsoft Excel spreadsheets.

RESULTS

Fruit trap estimates

Forest fruit productivity showed a decreasing tendency from September to December, this last month as the one with the lowest productivity within all months, and then April was the highest and presumably the most productive month of the year (Table 1).

Table 1. Estimation of production of fleshy fruits in Reserva TomoGrande (Vichada, Colombia), during the study months.

Forest Fruit Productivity (Kg/ha)				
Sept	**Oct**	**Nov**	**Dec**	**Apr**
49.391	24.493	18.371	13.738	106.225

Variation in behavioral patterns

Overall, most of the time monkeys were engaged in displacement (30%) and feeding and foraging (20%), and besides 16% of the time were resting, 12% grooming or being groomed, 13% in aggressions and played 9% of their time (activity that was carried out mainly by juveniles and infants). But the behavioral variation within months was slight, with no statistically significant differences between any of the months ($p>0,05$ in all cases) (Figure 2).

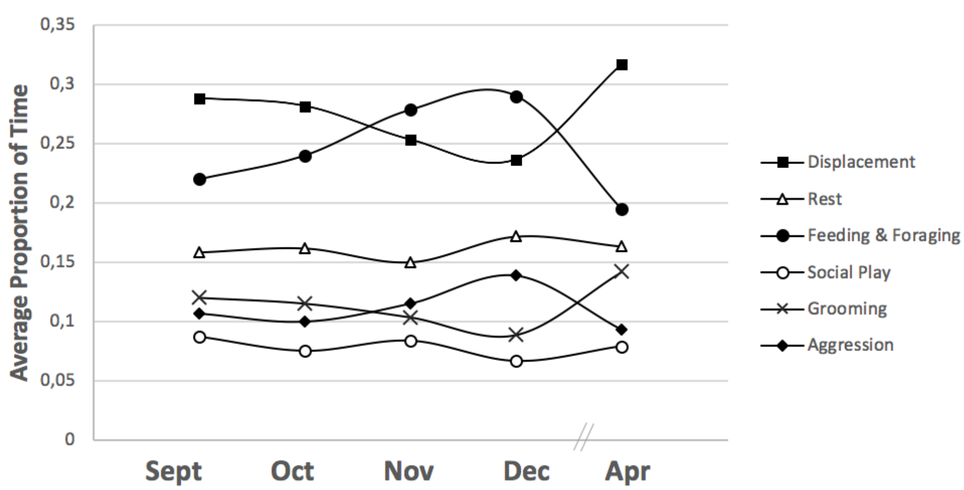


Figure 1. Fluctuation of the average proportion of time spent by the population on each activity per month.

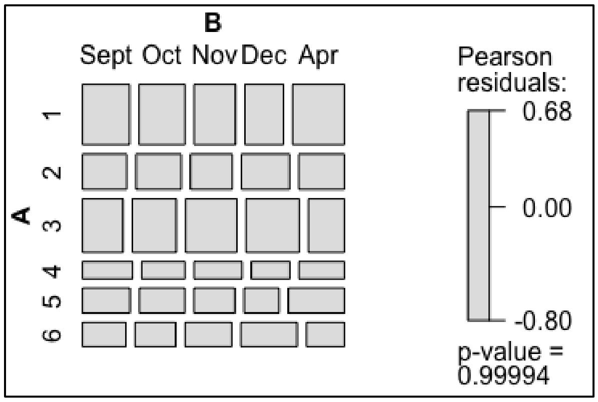


Figure 2. Mosaic Plot from contingency tables of behaviors per month for brown capuchin monkeys in Reverva TomoGrande (Vichada, Colombia). Behaviors as classified on methods

It is important to mention as well that 80% of aggressive interactions were seeing in feeding trees, and this could explain why on December there were more aggressions than the rest of the months and more time spent on feeding and foraging (Figure 1), taking into account that it is a period of fruit scarcity due to low fruit productivity (Table 1). Conversely, April had the highest forest fruit productivity and the least amount of aggressions, as well as the highest amount of time spent on grooming (Figure 1).

Relationship between Fruit Productivity and Behavior

Forest fruit productivity had a high positive correlation to displacement ($r = 0.89$, $p < 0.04$) and grooming ($r = 0.91$, $p < 0.02$) and it was highly negatively correlated to feeding and foraging ($r = -0.88$, $p < 0.04$). However, it was not correlated to resting ($r = 0.06$, $p > 0.9$), nor other social interactions (playing: $r = 0.3$, $p = 0.6$; aggression: $r = -0.69$, $p > 0.1$).

Body weight variation and relationship with Fruit productivity

There was some variation in the pattern of body weight for each monkey (Figure 3a). The ones that gained more weight from the beginning to the end of the investigation and in between months were the three juveniles (Meelo, Dana and Mike), All individuals and the population in general showed an increasing body weight tendency, though in some specific cases some individuals suffer from weight loss (specially between November and December).

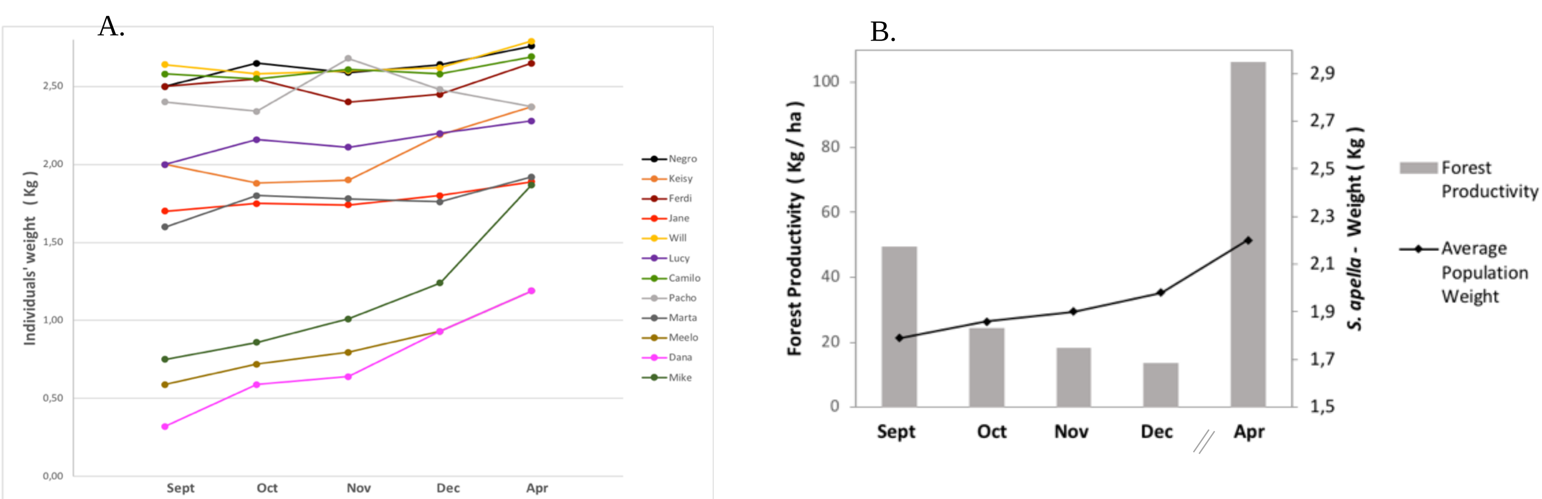


*Figure 3. Body weight variation of each of brown capuchin (*Sapajus apella*), studied in reserve TomoGrande (Vichada, Colombia), during 5 months. A. individual variation and B. Average and monthly Fruit production.*

Changes in body weight were relatively gradual. In fact, it was found that consecutive months were not significantly different, but any pair of months that have at least one month in between are significantly different (Table 2). On the other hand, data shows a pattern of stability and for some individuals decreasing points on the scarcity months (November and December). Overall, the population average weight does not correlate with the fruit productivity ($r = 0.69$, $p > 0.18$), in spite of the increasing tendency (Figure 3b). This may be due to the high variation in body weight between individuals, since, at least for some individuals (e.g. Will), its weight does correlate well to fruit production ($r = 0.95$, $p < 0.01$). Because of this, variation coefficients, maximum changes and relative growth rates of both periods were calculated for each individual and was found a tendency of higher gain weight in abundance season (Table 5).

Table 2. Paired t tests comparing body weight between consecutive and non-consecutive months

	t	p-value
Sept - Oct	-2,052	p > 0.06
Oct - Nov	-1,004	p > 0.33
Nov - Dic	-1,960	p > 0.07
Sept - Nov	-2,530	p < 0.02
Oct - Dic	-2,540	p < 0.02
Dic - Apr	-4,896	p < 0.0004
Nov - Apr	-4,130	p < 0.001
Sept - Apr	-4,890	p < 0.0004

Hierarchy

Based on social behavior (Figure 4), the group was divided into dominants (35%) and subordinates (65%). In the subordinate group most individuals were juveniles and infants (6) , 2 sub-adults, 2 female adults with dependent babies and 1 adult.

Relationship between Hierarchical Level and Behavior

The hierarchical level defines the behavior of an individual, for instance dominant individuals got more grooming and did less (Figure 4d), also the alpha male (Marco) did almost three times more aggressive behaviors than the next dominant (Negro) and received less aggressions than any other. Nevertheless, subordinates did not receive much aggressions and in fact other dominants besides Marco received more than most subordinates. Regarding subordinates, it is important to mention that juveniles and infants, are the only ones that play, they are not usually involved in aggressions and they were seen very frequently next or close to the dominants, especially next to Marco. This may show that even though some of them are in low ranks they have a very good treatment from the dominants (most of them), better than the one they give to adult subordinates. In addition, there can be behavioral variations whether an individual is dominant or subordinate. For instance, when the dominants are more aggressive the subordinates do not groom them as much, but when grooming increases aggressive behaviors decrease, this was what happened on April (Figure 1).

Furthermore, as this species is generalist (Janson, 1985), fruit scarcity does not affect them severely but they did have a change in their diet during the least productive months, for instance there is only one record of an individual (subordinate female) hunting and feeding on a bird. It was on December and despite the multiple aggressions she had to take from the dominant individuals she was able to escape with her meal. This could happen due to the differentiation among dominants and subordinates in regards to the access to food resources, because for instance they were seeing eating twice as often and stayed in the feeding trees longer, specially Marco who got even more aggressive than usual during foraging and feeding, expelling all the individuals from the feeding trees and staying with all the food for himself most of the time.

a

Affiliate Behavior

Actor \ Receptor	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17
1. Atalía		0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
2. Camilo	0		0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
3. Dana	0	0		0	8	0	10	0	0	2	0	0	0	0	8	0	0
4. Eva	0	1	2		0	0	3	0	0	0	0	0	14	0	0	5	0
5. Ferdi	0	0	0	0		0	0	4	0	0	0	0	5	0	0	0	0
6. Jane	0	0	0	0	0		0	0	0	25	0	0	0	0	5	0	0
7. Keisy	0	0	8	0	0	0		0	0	6	0	0	0	0	2	0	0
8. Lucy	0	0	0	0	0	0	0		25	0	0	0	0	0	0	2	0
9. Lucho	0	0	4	5	0	0	0	6		0	0	0	0	0	0	0	0
10. Marco	0	0	0	0	0	0	0	0	0		0	0	0	0	0	0	0
11. Marta	0	0	0	0	0	0	0	0	0	0		11	0	0	0	0	0
12. Mateo	0	0	12	0	0	0	0	0	0	0	7		0	0	0	0	0
13. Meelo	0	0	0	0	0	0	8	0	0	14	0	0		0	8	0	7
14. Mike	0	10	0	0	0	9	0	0	0	23	0	0	0		12	0	0
15. Negro	0	0	0	0	0	3	6	0	0	0	0	0	0	0		0	0
16. Pacho	0	0	0	0	0	16	10	0	0	0	0	0	0	0	0		0
17. Will	0	0	0	0	0	3	0	5	0	0	0	0	0	4	0	0	

b

Agonistic Behavior

Actor \ Receptor	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17
1. Atalía		0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
2. Camilo	0		0	0	5	0	0	0	0	0	0	0	7	3	0	8	0
3. Dana	0	0		0	0	0	0	0	0	0	0	0	0	0	0	0	0
4. Eva	0	0	0		0	0	0	0	0	0	0	0	0	0	0	0	0
5. Ferdi	0	9	0	0		0	0	4	0	0	0	0	0	0	0	0	4
6. Jane	0	0	0	0	0		0	0	0	0	0	0	0	0	0	0	0
7. Keisy	0	0	5	0	0	0		0	0	0	2	0	0	0	0	0	0
8. Lucy	0	0	0	0	0	0	0		0	0	0	0	0	0	0	0	0
9. Lucho	0	0	0	0	0	0	0	0		0	0	0	0	0	0	0	0
10. Marco	0	12	0	0	27	11	13	4	0		4	0	5	11	19	23	14
11. Marta	0	0	0	0	0	0	0	0	0	0		0	0	0	0	0	0
12. Mateo	0	0	0	0	0	0	0	0	0	0	0		0	0	0	0	0
13. Meelo	0	0	2	0	0	0	0	0	0	0	0	0		0	0	0	0
14. Mike	0	0	0	0	0	0	0	0	3	0	0	0	0		0	0	0
15. Negro	0	3	0	0	0	3	9	0	0	15	0	0	0	0		6	15
16. Pacho	0	0	0	0	0	0	0	0	0	0	0	0	0	2	0		0
17. Will	0	0	0	0	0	0	0	0	0	0	0	0	0	0	8	0	

c

Social Play

Actor \ Receptor	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17
1. Atalía		0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
2. Camilo	0		0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
3. Dana	0	0		0	0	0	0	0	11	0	0	0	12	15	0	0	0
4. Eva	0	0	0		0	0	0	0	0	0	0	0	7	0	0	0	0
5. Ferdi	0	0	0	0		0	0	0	0	0	0	0	0	0	0	0	0
6. Jane	0	0	0	0	0		0	0	0	0	0	0	0	0	0	0	0
7. Keisy	0	0	0	0	0	0		0	0	0	0	0	0	0	0	0	0
8. Lucy	0	0	0	0	0	0	0		0	0	0	0	0	0	0	0	0
9. Lucho	0	0	6	3	0	0	0	0		0	0	0	8	14	0	0	0
10. Marco	0	0	0	0	0	0	0	0	0		0	0	0	0	0	0	0
11. Marta	0	0	0	0	0	0	0	0	0	0		0	0	0	0	0	0
12. Mateo	0	0	0	0	0	0	0	0	0	0	0		0	0	0	0	0
13. Meelo	0	0	17	0	0	0	0	0	8	0	0	0		21	0	0	0
14. Mike	0	0	19	0	0	0	0	0	7	0	0	0	6		0	0	0
15. Negro	0	0	0	0	0	0	0	0	0	0	0	0	0	0		0	0
16. Pacho	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0		0
17. Will	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	

d

	Affiliate Behavior		Agonistic Behavior		Social Play			
	Actor	Receptor	Actor	Receptor	Actor	Receptor	Total	CBI index
Marco	0	70	143	15	0	0	228	3.28
Negro	10	35	51	27	0	0	123	2.0
Ferdi	4	13	17	32	0	0	66	1.28
Camilo	0	11	23	24	0	0	58	1.22
Will	12	7	8	33	0	0	60	1.11
Keisy	16	40	7	22	0	0	85	1.0
Pacho	26	7	2	29	0	0	64	0.3
Meelo	37	19	2	12	46	33	149	0.28
Mike	54	4	3	16	32	50	159	0.2
Lucho	15	25	0	0	31	26	97	0.18
Lucy	25	18	0	8	2	2	55	0.16
Jane	30	36	0	14	1	1	82	0.16
Marta	11	9	0	6	1	1	28	0.16
Dana	28	26	0	7	38	42	141	0.14
Eva	26	5	0	0	7	3	41	0.1
Mateo	19	11	0	0	2	2	34	0.1
Atalía	0	0	0	0	0	0	0	1

Figure 4. a. Submissive Matrix (Grooming behaviors) . b. Aggressive Matrix (direct aggressions, threats and persecutions). c. Social Play Matrix. d. Population in the hierarchical order, divided into dominants and subordinates with their respective values and dominance viz Clutton – Brock et al.'s index (CBI), Atalías' index is 1 due to no interaction with any individual.

Relationship between Hierarchical Level and Body Weight

Subordinates fear dominants, aggression is part of the reason but also is because they are older, larger and usually (but not in all cases) heavier. Marco for example is the biggest and heaviest individual within the population with a weight 60% higher than the average of the population. However, high ranked individuals did not gained more weight than the rest of the population, juveniles and infants did (Table 3) although they always had the lowest weights, they gained more weight overall and within months, because of the growing stage they are in. For this reason, if juveniles were contrasted to adults given their high variation coefficient it would show the difference in weight gain due to a growing stage in comparison to adults that already have a more stabilized body size.

Therefore, the juveniles that were weighed (Meelo, Dana and Mike) were compared to adults, in two periods: scarcity (September – December) with significant difference ($w=0$, $p < 0.009$) and abundance (September – April) with significant difference as well ($w=0$, $p < 0.01$). In addition, between dominants and subordinates there are significant differences in the scarcity period ($w=6$, $p < 0.04$) as well as in the entire study (including the abundance month) ($z=22.5$, $p < 0.04$).

Finally, it was found a tendency of stability and a slight decrease in the scarcity period and an increase in the abundance season for all individuals regardless their hierarchical rank, for instance the relative growth rate of each individual increases when the abundance month was included.

Table 3. Individuals' weight per month divided in hierarchical ranks, including indices per individual in scarcity (Sept – Dec) and abundance (Sept – Apr) seasons.

		Individuals' Weight (Kg)					*Sept-Dec*	*Sept - Apr*	*Sept-Dec*	*Sept - Apr*
		Sept	Oct	Nov	Dec	Apr	Variation Coefficient	Max. Change	Relative Growth Rate	Relative Growth Rate
Dominants	Negro	2,50	2,65	2,59	2,64$_{+/-0.2}$	2,76$_{+/-0.2}$	3%	0,26	2,51	2,56
	Camilo	2,58	2,55	2,61	2,58$_{+/-0.3}$	2,69	1%	0,11	2,44	2,49
	Will	2,64	2,58	2,60	2,62	2,79	1%	0,15	2,54	2,59
	Ferdi	2,50	2,55	2,40	2,45	2,65	3%	0,15	2,40	2,45
	Keisy	2,00	1,88	1,90	2,19	2,37$_{+/-0.2}$	7%	0,37	2,12	2,17
Subordinates	Marta	1,60	1,80	1,78	1,76	1,92	5%	0,32	1,67	1,72
	Lucy	2,00	2,16	2,11	2,2$_{+/-0.1}$	2,28$_{+/-0.3}$	4%	0,28	2,03	2,08
	Jane	1,70	1,75	1,74	1,80$_{+/-0.08}$	1,89	2%	0,19	1,64	1,69
	Pacho	2,40	2,34	2,68	2,48	2,37$_{+/-0.5}$	6%	0,29	2,44	2,49
	Meelo	0,59	0,72	0,80	0,93$_{+/-0.5}$	1,19$_{+/-0.4}$	19%	0,69	1,03	1,08
	Dana	0,32	0,59	0,64	0,93$_{+/-0.2}$	1,19$_{+/-0.2}$	39%	0,87	0,94	0,99
	Mike	0,75	0,86	1,01	1,24$_{+/-0.6}$	1,87$_{+/-0.4}$	22%	1,12	1,62	1,67

Discussion

Primate behavior varies, it can change from site to site, within species, in time, for environmental pressures, among other reasons, but perhaps the most characteristic aspects of primates are the adaptations that exist entirely in their behavior (Jolly, 1985). Besides, several studies have proven the range of flexible behavioral patterns that primates exhibit in response to local, ecological and demographic conditions (Strier, 2018). The results in this study showed relatively constant behavioral patterns in a wild Brown Capuchins' population during 5 months. However, there was evidence of correlations of some activities with forest fruit production (displacement: $r= 0.89$, $p < 0.04$, grooming $r= 0.91$, $p < 0.02$, feeding and foraging $r=0.88$, $p < 0.04$). It was expected that the proportion of time individuals spent on activities such as feeding and forging was influenced by fruit production due to the higher amount of time they spent foraging to obtain food in a scarcity season. It is possible that feeding on the seeds of palms (such as *Atalea maripa*) during scarcity may have allowed the monkeys to find enough resources and do not travel more to get nutrients. In addtion, it was expected that aggression was correlated as well, due to the increase in competition for ripe fruit, but this was not found, perhaps for the same reason. In other *Sapajus apella* studies, it was found that rates of aggression per feeding time differed significantly between season and, as found in this study, most aggressive interactions occurred at food trees (Janson, 1985).

However, previous research also has stressed that behavioral changes are not due mainly by food availability but for populations' social organizations, meaning that there could be more aggressions but not necessarily for a lack of food but for a lack of tolerance between individuals (Izawa, 1980). This is mentioned to happen because the levels of hierarchical order among group members, categorizing the alpha male as the highest rank who is part of the dominant group members, and within the subordinates individuals there can be tolerated and un-tolerated individuals (Janson, 1985). As expected dominant and subordinates individuals have differentiated behavioral patterns and it was found that the alpha male really differs from the rest, even from the other dominants. For example, he was groomed 3 times more than the average of the other dominants, and did as well 3 times more aggressions than the others. This behavior supports the description made by Janson (1985) about how dominance ranks significantly differ in behavior within individuals, for instance in food consumption he found that food intake of the alpha male of this species was 70-485% greater than that of subordinate juveniles and 31- 347% greater than that of subordinates adult males. He mentioned that the difference in food intake among individuals is due exclusively to differences in dominance. This would explain why Marco (alpha male) is 60% heavier than the average of the population, and is 3 times heavier than some subordinate individuals. According to Janson (1985) dominants' greater food intake might be for either their large size and strength, that allows them to open tough foods more easily, or for their aggressiveness which gives them an advantage over subordinates who have to either eat what is left or go to the peripherals.

Furthermore, contrary to expectations some dominants received more aggressions than some subordinate group members (Table 2.), which Janson mentions that is because high-ranking males are the ones that receive the biggest amounts of aggression from the alpha male, and some juveniles of low dominance rank enjoyed being around the alpha because of his protection against other group members (Janson, 1985). This patterns was also seen in this study.

Finally, body weight was expected to relied on hierarchy, and indeed the alpha male is by far the heaviest individual of the population, also as expected there is a body weight variation influenced by the season. It was found a pattern in most individuals in which there is a stability period and in some cases a decrease during the scarcity season, and then during abundance all the individuals weights increased. Some studies show that body weight fluctuation can depend on seasonality but no matter the food intake of an individual the dominance rank would most likely define or predict body weight variation, specially taking into account that dominants feed more than subordinates over entire periods of fruit scarcity (Janson, 1985).

Acknowledgments

I want to thank 'Proyecto Primates' as well as the 'Primatology and Tropical Forests Ecology Lab' of the Los Andes University for the opportunity of working with them and for all the helped provided for the fieldwork necessary for this study. Thanks to the welcoming people in the 'Reserve Tomo Grande' for the immense help provided during the 5 months. I am immensely grateful to Pablo R. Stevenson for sharing important information along with valuable comments, and suggestions throughout the realization of the study. Also I am grateful with the Ecology program (PUJ) for giving me all the knowledge necessary to fulfil this investigation and thanks as well to the R Project for providing useful open tools for handling and analyzing data for this project. Lastly, I am very grateful with Nelson Galvis who funded this study throughout COLCIENCIAS due to their fellowships for doctoral studies.

References

Abondano, L. A., & Link, A. (2012). *The social behavior of brown spider monkeys (Ateles hybridus) in a fragmented forest in Colombia.* International Journal of Primatology, 33(4), 769-783.

Bang et al. (2010). *Choosing an appropriate index to construct dominance hierarchies in animal societies: a comparison of three indices.* Animal Behavior 79 (2010) 631–636 MS. No. 09-00002R

Caro, D. (2015). *Una riqueza amenazada.* Asociación Primatologica Colombiana.

Clutton-Brock, T., et al., (1979). *The logical stag: adaptive aspects of fighting in red deer.* Animal Behaviour, 27, 211–225, doi:10.1016/0003-3472(79)90141-6.

Correa-Gómez, D. *& Stevenson, P. R. (2010). Estructura y diversidad de bosques de galería en una sabana estacional de los Llanos Orientales colombianos (Reserva Tomo Grande,Vichada).* Orinoquia, 14(2), 31-48.

Estrada et al. (2017). *Impending extinction crisis of the world's primates: Why primates matter*. Science Advances, Vol. 3, no. 1, e1600946

Flórez (2011*). Métodos de Estudio: Fenología de Plantas*. Asociación primatológica Colombiana.

Hemingway, C. A., & Bynum, N. (2005). *The influence of seasonality on primate diet and ranging.* Seasonality in primates: Studies of living and extinct human and non-human primates, 44, 57.

Janson, C.H. (1984). *Female choice and matting system of the brown capuchin (Cebus apella).* Zeitschrift fur Tierpsychologie 85:177-200.

Janson C.H (1985). *The matting system as a determinant of social evolution in capuchin monkeys (Cebus).* In: J.Else & P. Lee (ed.), Proceeding of the XIIth International Congress of Primatology. Cambridge University Press.

Janson, C. H. (2000). *Primate socio‐ecology: the end of a golden age.* Evolutionary Anthropology: Issues, News, and Reviews: Issues, News, and Reviews, 9(2), 73-86.

Marin, J.M. (2010). *Guía para el análisis de datos.* SPSS10. Disertación Doctoral.

Martin P. &. Bateson P. (2007). *Measuring Behaviour. An introductory guide.* Cambridge University Press.

Martin, R. & Melfi, M. (2016): *A Comparison of Zoo Animal Behavior in the Presence of Familiar and Unfamiliar People*. Journal of Applied Animal Welfare Science.

McConkey, K. R, et al. (2003*). Influence of forest seasonality on gibbon food choice in the rain forests of Barito Ulu, Central Kalimantan*. International Journal of Primatology, 24(1), 19-32.

Snodderly, D. M, et al.,(2019*). Initiation of feeding by four sympatric Neotropical primates (Ateles belzebuth, Lagothrix lagotricha poeppigii, Plecturocebus (Callicebus) discolor, and Pithecia aequatorialis) in Amazonian Ecuador: Relationships to photic and ecological factors*. *PloS one*, *14*(1), e0210494

Stevenson P.R, et al. (2000). *Influence of Fruit Availability on Ecological Overlap among Four Neotropical Primates at Tiniga National Park, Colombia 1.* Biotropica, 32(3), 533-544.

Stevenson, P. R. (2001). *The relationship between fruit production and primate abundance in Neotropical communities*. Biological Journal of the Linnean Society, *72*(1), 161-178.

Stevenson, P.R et al. (2004). *Phenological patterns of woody vegetation at Tinigua Park Colombia: Methodological comparisons with emphasis on fruit production.* Departamento de Ciencias Biológicas, Universidad de Los Andes. Bogotá, Colombia. Caldasia 26(1) 2004: 125-150

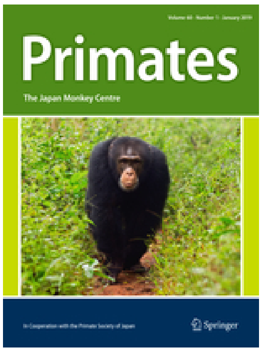
Strier (2000). *Primate behavioral ecology*. University of Wisconsin – Madison., ISBN 0 205-20019-2.

Sullivan et al. (2006). *Individual differences in physical activity are closely associated with changes in body weight in adult female rhesus monkeys (Macaca mulatta*). US National Library of Medicine. National Institute of Health. doi: 10.1152/ajpregu.00069.2006

Tiddi et al. (2019). *The impact of food provisioning on parasite infection in wild black capuchin monkeys: a network approach*. Primates, 1-10.

Tutin et al. (1997). *The primate community of the Lopé reserve, Gabon: Diets, responses to fruit scarcity, and effects on biomass*. American Journal of Primatology, 42(1), 1–24.

Vogel, E. R., & Janson, C. H. (2007). *Predicting the frequency of food‐related agonism in white‐faced capuchin monkeys (Cebus capucinus), using a novel focal‐tree method.* American Journal of Primatology: Official Journal of the American Society of Primatologists, 69(5), 533-550.



Primates

Editor-in-Chief: Tetsuro **Matasuzawa**

ISSN: 0032-8332 (print version)
ISSN: 1610-7365 (electronic version)

Journal no. 10329

Instructions for Authors

EDITORIAL POLICY

Primates publishes original and review articles, news and perspectives, book reviews, and other information on all aspects of primatology. Anyone involved in primate research may contribute.

The purpose of news and perspectives is the publication of (1) research reports with high news value that stimulate further research, and (2) papers that view known topics from different perspectives and/or with new theoretical considerations. In either case, authors are requested to submit short papers with high scientific/news value.

Case studies will be accepted for News and Perspectives only if (1) their observational data are excellent and (2) the resulting theoretical implications are important and clearly presented.

All manuscripts are subject to peer review and accepted papers will be copy edited. Manuscripts must be written in English and typed in 12-pt Times in double-line spacing with 3-cm margins and about 24 lines per page; lines should be numbered consecutively from the title through the references. Authors whose first language is not English are urged to have their manuscript read by a colleague who is a native English speaker and is familiar with their field of work before submitting the paper.

Page limits. Contributors are requested to write as concisely as possible and the paper should not normally exceed 10 printed pages (about 30 manuscript pages) in total, including the title page, tables, figures, figure legends, and reference list. Papers for news and perspectives should not exceed six printed pages (18 manuscript pages) in total.

During the submission process, authors may also submit the names and e-mail addresses of potential reviewers. The suggested reviewers should not have recent connections with the authors, such as being co-authors of other papers or collaborators on projects in the last three years.

When you submit a revised manuscript, please underline or highlight the revised places.

MANUSCRIPT SUBMISSION

Manuscript Submission

Submission of a manuscript implies: that the work described has not been published before; that it is not under consideration for publication anywhere else; that its publication has been approved by all co-authors, if any, as well as by the responsible authorities – tacitly or explicitly – at the institute where the work has been carried out. The publisher will not be held legally responsible should there be any claims for compensation.

Permissions

Authors wishing to include figures, tables, or text passages that have already been published elsewhere are required to obtain permission from the copyright owner(s) for both the print and online format and to include evidence that such permission has been granted when submitting their papers. Any material received without such evidence will be assumed to originate from the authors.

Online Submission

Please follow the hyperlink “Submit online” on the right and upload all of your manuscript files following the instructions given on the screen.

TITLE PAGE

Title Page

The title page should include:

- The name(s) of the author(s)
- A concise and informative title
- The affiliation(s) and address(es) of the author(s)
- The e-mail address, and telephone number(s) of the corresponding author
- If available, the 16-digit ORCID of the author(s)

Abstract

Please provide an abstract of 150 to 250 words. The abstract should not contain any undefined abbreviations or unspecified references.

Keywords

Please provide 4 to 6 keywords which can be used for indexing purposes.

TEXT

Text Formatting

Manuscripts should be submitted in Word.

- Use a normal, plain font (e.g., 10-point Times Roman) for text.
- Use italics for emphasis.
- Use the automatic page numbering function to number the pages.
- Do not use field functions.
- Use tab stops or other commands for indents, not the space bar.

- Use the table function, not spreadsheets, to make tables.
- Use the equation editor or MathType for equations.
- Save your file in docx format (Word 2007 or higher) or doc format (older Word versions).

Manuscripts with mathematical content can also be submitted in LaTeX.

LaTeX macro package (zip, 182 kB)

Headings

Please use no more than three levels of displayed headings.

Abbreviations

Abbreviations should be defined at first mention and used consistently thereafter.

Footnotes

Footnotes can be used to give additional information, which may include the citation of a reference included in the reference list. They should not consist solely of a reference citation, and they should never include the bibliographic details of a reference. They should also not contain any figures or tables.

Footnotes to the text are numbered consecutively; those to tables should be indicated by superscript lower-case letters (or asterisks for significance values and other statistical data). Footnotes to the title or the authors of the article are not given reference symbols.

Always use footnotes instead of endnotes.

Acknowledgments

Acknowledgments of people, grants, funds, etc. should be placed in a separate section on the title page. The names of funding organizations should be written in full.

When animals are used for experimentation, authors will be required to state at the end of the acknowledgments that they have complied with the ethical standards in the treatment of their animals with the guidelines laid down by the Primate Society of Japan, NIH (US), EC Guide for animal experiments or other equivalent guidelines; as well as with specific national laws where applicable.

Nucleotide sequence data

New nucleotide sequence data must be submitted and deposited in the DDBJ/EMBL/ GenBank databases and an accession number obtained before the paper can be accepted for publication. Submission to any one of the three collaborating databanks is sufficient to ensure data entry in all. The accession number should be included in the manuscript, e.g., as a footnote on the title page: “Nucleotide sequence data reported are available in the DDBJ/EMBL/GenBank databases under the accession number(s) –”. If requested the database will withhold release of data until publication. No data are to be withdrawn following publication.

SCIENTIFIC STYLE

Please always use internationally accepted signs and symbols for units (SI units).

Genus and species names should be in italics. The common names of animals should not be capitalized.

REFERENCES

Citation

Cite references in the text by name and year in parentheses. Some examples:

Negotiation research spans many disciplines (Thompson 1990).
This result was later contradicted by Becker and Seligman (1996).
This effect has been widely studied (Abbott 1991; Barakat et al. 1995a, b; Kelso and Smith 1998; Medvec et al. 1999, 2000).

Reference list

The list of references should only include works that are cited in the text and that have been published or accepted for publication. Personal communications and unpublished works should only be mentioned in the text. Do not use footnotes or endnotes as a substitute for a reference list.

Reference list entries should be alphabetized by the last names of the first author of each work. Order multi-author publications of the same first author alphabetically with respect to second, third, etc. author. Publications of exactly the same author(s) must be ordered chronologically.

- Journal article

  Gamelin FX, Baquet G, Berthoin S, Thevenet D, Nourry C, Nottin S, Bosquet L (2009) Effect of high intensity intermittent training on heart rate variability in prepubescent children. Eur J Appl Physiol 105:731-738. https://doi.org/10.1007/s00421-008-0955-8

  Ideally, the names of all authors should be provided, but the usage of "et al" in long author lists will also be accepted:

  Smith J, Jones M Jr, Houghton L et al (1999) Future of health insurance. N Engl J Med 965:325–329
- Article by DOI

  Slifka MK, Whitton JL (2000) Clinical implications of dysregulated cytokine production. J Mol Med. https://doi.org/10.1007/s001090000086
- Book

  South J, Blass B (2001) The future of modern genomics. Blackwell, London
- Book chapter

  Brown B, Aaron M (2001) The politics of nature. In: Smith J (ed) The rise of modern genomics, 3rd edn. Wiley, New York, pp 230-257
- Online document

  Cartwright J (2007) Big stars have weather too. IOP Publishing PhysicsWeb. http://physicsweb.org/articles/news/11/6/16/1. Accessed 26 June 2007
- Dissertation

  Trent JW (1975) Experimental acute renal failure. Dissertation, University of California

Always use the standard abbreviation of a journal's name according to the ISSN List of Title Word Abbreviations, see

ISSN LTWA

If you are unsure, please use the full journal title.

For authors using EndNote, Springer provides an output style that supports the formatting of in-text citations and reference list.

EndNote style (zip, 2 kB)

TABLES

- All tables are to be numbered using Arabic numerals.
- Tables should always be cited in text in consecutive numerical order.

- For each table, please supply a table caption (title) explaining the components of the table.
- Identify any previously published material by giving the original source in the form of a reference at the end of the table caption.
- Footnotes to tables should be indicated by superscript lower-case letters (or asterisks for significance values and other statistical data) and included beneath the table body.

ELECTRONIC FIGURE SUBMISSION

- Supply all figures electronically.
- Indicate what graphics program was used to create the artwork.
- For vector graphics, the preferred format is EPS; for halftones, please use TIFF format. MS Office files are also acceptable.
- Vector graphics containing fonts must have the fonts embedded in the files.
- Name your figure files with "Fig" and the figure number, e.g., Fig1.eps.

Line Art

- Definition: Black and white graphic with no shading.
- Do not use faint lines and/or lettering and check that all lines and lettering within the figures are legible at final size.
- All lines should be at least 0.1 mm (0.3 pt) wide.
- Scanned line drawings and line drawings in bitmap format should have a minimum resolution of 1200 dpi.
- Vector graphics containing fonts must have the fonts embedded in the files.

Halftone Art

Definition: Photographs, drawings, or paintings with fine shading, etc.
If any magnification is used in the photographs, indicate this by using scale bars within the figures themselves.
Halftones should have a minimum resolution of 300 dpi.

Combination Art

Definition: a combination of halftone and line art, e.g., halftones containing line drawing, extensive lettering, color diagrams, etc.
Combination artwork should have a minimum resolution of 600 dpi.

Color Art

Color art is free of charge for print and online publication.
Color illustrations should be submitted as RGB (8 bits per channel).

Figure Lettering

- To add lettering, it is best to use Helvetica or Arial (sans serif fonts).
- Keep lettering consistently sized throughout your final-sized artwork, usually about 2–3 mm (8–12 pt).
- Variance of type size within an illustration should be minimal, e.g., do not use 8-pt type on an axis and 20-pt type for the axis label.
- Avoid effects such as shading, outline letters, etc.
- Do not include titles or captions into your illustrations.

Figure Numbering

All figures are to be numbered using Arabic numerals.
Figures should always be cited in the text in consecutive numerical order.
Figure parts should be denoted by lowercase letters (a, b, c, etc.). If illustrations are supplied with uppercase labeling, lowercase letters will still be used in the figure captions and citations.
If an appendix appears in your article/chapter and it contains one or more figures, continue the consecutive numbering of the main text. Do not number the appendix figures, "A1, A2, A3, etc." Figures in online appendices (Electronic supplementary Material) should, however, be numbered separately.

Figure Captions

- Each figure should have a concise caption describing accurately what the figure depicts. Include the captions in the text file of the manuscript, not in the figure file.
- Figure captions begin with the term Fig. in bold type, followed by the figure number, also in bold type.
- No punctuation is to be included after the number, nor is any punctuation to be placed at the end of the caption.
- Identify all elements found in the figure in the figure caption; and use boxes, circles, etc., as coordinate points in graphs.
- Identify previously published material by giving the original source in the form of a reference citation at the end of the figure caption.

Figure Placement and Size

Figures should be submitted separately from the text, if possible.
When preparing your figures, size figures to fit in the column width.
Figures should be 39 mm, 84 mm, 129 mm, or 174 mm wide and not higher than 234 mm.
The publisher reserves the right to reduce or enlarge figures.

Permissions

If you include figures that have already been published elsewhere, you must obtain permission from the copyright owner(s) for both the print and online format. Please be aware that some publishers do not grant electronic rights for free and that Springer will not be able to refund any costs that may have occurred to receive these permissions. In such cases, material from other sources should be used.

Accessibility

In order to give people of all abilities and disabilities access to the content of your figures, please make sure that

All figures have descriptive captions (blind users could then use a text-to-speech software or a text-to-Braille hardware)
Patterns are used instead or in addition to colors for conveying information (color-blind users would then be able to distinguish the visual elements)
Any figure lettering has a contrast ratio of at least 4.5:1.

ELECTRONIC SUPPLEMENTARY MATERIAL

Springer accepts electronic multimedia files (animations, movies, audio, etc.) and other supplementary files to be published online along with an article or a book chapter. This feature can add dimension to the author's article, as certain information cannot be printed or is more convenient in electronic form.

Before submitting research datasets as electronic supplementary material, authors should read the journal’s Research data policy. We encourage research data to be archived in data repositories wherever possible.

Submission

Supply all supplementary material in standard file formats.
Please include in each file the following information: article title, journal name, author names; affiliation and e-mail address of the corresponding author.
To accommodate user downloads, please keep in mind that larger-sized files may require very long download times and that some users may experience other problems during downloading.

Audio, Video, and Animations

Aspect ratio: 16:9 or 4:3
Maximum file size: 25 GB
Minimum video duration: 1 sec
Supported file formats: avi, wmv, mp4, mov, m2p, mp2, mpg, mpeg, flv, mxf, mts, m4v, 3gp

Text and Presentations

Submit your material in PDF format; .doc or .ppt files are not suitable for long-term viability.
A collection of figures may also be combined in a PDF file.

Spreadsheets

Spreadsheets should be submitted as .csv or .xlsx files (MS Excel).

Specialized Formats

Specialized format such as .pdb (chemical), .wrl (VRML), .nb (Mathematica notebook), and .tex can also be supplied.

Collecting Multiple Files

It is possible to collect multiple files in a .zip or .gz file.

Numbering

If supplying any supplementary material, the text must make specific mention of the material as a citation, similar to that of figures and tables.
Refer to the supplementary files as “Online Resource”, e.g., "... as shown in the animation (Online Resource 3)", “... additional data are given in Online Resource 4”.
Name the files consecutively, e.g. “ESM_3.mpg”, “ESM_4.pdf”.

Captions

For each supplementary material, please supply a concise caption describing the content of the file.

Processing of supplementary files

Electronic supplementary material will be published as received from the author without any conversion, editing, or reformatting.

Accessibility

In order to give people of all abilities and disabilities access to the content of your supplementary files, please make sure that

The manuscript contains a descriptive caption for each supplementary material
Video files do not contain anything that flashes more than three times per second (so that users prone to seizures caused by such effects are not put at risk)

ETHICAL RESPONSIBILITIES OF AUTHORS

This journal is committed to upholding the integrity of the scientific record. As a member of the Committee on Publication Ethics (COPE) the journal will follow the COPE guidelines on how to deal with potential acts of misconduct.

Authors should refrain from misrepresenting research results which could damage the trust in the journal, the professionalism of scientific authorship, and ultimately the entire scientific endeavour. Maintaining integrity of the research and its presentation can be achieved by following the rules of good scientific practice, which include:

- The manuscript has not been submitted to more than one journal for simultaneous consideration.
- The manuscript has not been published previously (partly or in full), unless the new work concerns an expansion of previous work (please provide transparency on the re-use of material to avoid the hint of text-recycling (“self-plagiarism”)).
- A single study is not split up into several parts to increase the quantity of submissions and submitted to various journals or to one journal over time (e.g. “salami-publishing”).
- No data have been fabricated or manipulated (including images) to support your conclusions
- No data, text, or theories by others are presented as if they were the author’s own (“plagiarism”). Proper acknowledgements to other works must be given (this includes material that is closely copied (near verbatim), summarized and/or paraphrased), quotation marks are used for verbatim copying of material, and permissions are secured for material that is copyrighted.

  Important note: the journal may use software to screen for plagiarism.
- Consent to submit has been received explicitly from all co-authors, as well as from the responsible authorities - tacitly or explicitly - at the institute/organization where the work has been carried out, **before** the work is submitted.
- Authors whose names appear on the submission have contributed sufficiently to the scientific work and therefore share collective responsibility and accountability for the results.
- Authors are strongly advised to ensure the correct author group, corresponding author, and order of authors at submission. Changes of authorship or in the order of authors are **not** accepted **after** acceptance of a manuscript.
- Adding and/or deleting authors and/or changing the order of authors **at revision stage** may be justifiably warranted. A letter must accompany the revised manuscript to explain the reason for the change(s) and the contribution role(s) of the added and/or deleted author(s). Further documentation may be required to support your request.
- Requests for addition or removal of authors as a result of authorship disputes after acceptance are honored after formal notification by the institute or independent body and/or when there is agreement between all authors.
- Upon request authors should be prepared to send relevant documentation or data in order to verify the validity of the results. This could be in the form of raw data, samples, records, etc. Sensitive information in the form of confidential proprietary data is excluded.

If there is a suspicion of misconduct, the journal will carry out an investigation following the COPE guidelines. If, after investigation, the allegation seems to raise valid concerns, the accused author will be contacted and given an opportunity to address the issue. If misconduct has been established beyond reasonable doubt, this may result in the Editor-in-Chief’s implementation of the following measures, including, but not limited to:

If the article is still under consideration, it may be rejected and returned to the author.
If the article has already been published online, depending on the nature and severity of the infraction, either an erratum will be placed with the article or in severe

cases complete retraction of the article will occur. The reason must be given in the published erratum or retraction note. Please note that retraction means that the paper is **maintained on the platform**, watermarked "retracted" and explanation for the retraction is provided in a note linked to the watermarked article.
The author's institution may be informed.

COMPLIANCE WITH ETHICAL STANDARDS

To ensure objectivity and transparency in research and to ensure that accepted principles of ethical and professional conduct have been followed, authors should include information regarding sources of funding, potential conflicts of interest (financial or non-financial), informed consent if the research involved human participants, and a statement on welfare of animals if the research involved animals.

Authors should include the following statements (if applicable) in a separate section entitled "Compliance with Ethical Standards" when submitting a paper:

- Disclosure of potential conflicts of interest
- Research involving Human Participants and/or Animals
- Informed consent

Please note that standards could vary slightly per journal dependent on their peer review policies (i.e. single or double blind peer review) as well as per journal subject discipline. Before submitting your article check the instructions following this section carefully.

The corresponding author should be prepared to collect documentation of compliance with ethical standards and send if requested during peer review or after publication.

The Editors reserve the right to reject manuscripts that do not comply with the above-mentioned guidelines. The author will be held responsible for false statements or failure to fulfill the above-mentioned guidelines.

DISCLOSURE OF POTENTIAL CONFLICTS OF INTEREST

Authors must disclose all relationships or interests that could have direct or potential influence or impart bias on the work. Although an author may not feel there is any conflict, disclosure of relationships and interests provides a more complete and transparent process, leading to an accurate and objective assessment of the work. Awareness of a real or perceived conflicts of interest is a perspective to which the readers are entitled. This is not meant to imply that a financial relationship with an organization that sponsored the research or compensation received for consultancy work is inappropriate. Examples of potential conflicts of interests **that are directly or indirectly related to the research** may include but are not limited to the following:

- Research grants from funding agencies (please give the research funder and the grant number)
- Honoraria for speaking at symposia
- Financial support for attending symposia
- Financial support for educational programs
- Employment or consultation
- Support from a project sponsor
- Position on advisory board or board of directors or other type of management relationships
- Multiple affiliations
- Financial relationships, for example equity ownership or investment interest
- Intellectual property rights (e.g. patents, copyrights and royalties from such rights)
- Holdings of spouse and/or children that may have financial interest in the work

In addition, interests that go beyond financial interests and compensation (non-financial interests) that may be important to readers should be disclosed. These may include but are not limited to personal relationships or competing interests directly or indirectly tied to this research, or professional interests or personal beliefs that may influence your research.

The corresponding author collects the conflict of interest disclosure forms from all authors. In author collaborations where formal agreements for representation allow it, it is sufficient for the corresponding author to sign the disclosure form on behalf of all authors. Examples of forms can be found

here:

The corresponding author will include a summary statement in the text of the manuscript in a separate section before the reference list, that reflects what is recorded in the potential conflict of interest disclosure form(s).

See below examples of disclosures:

Funding: This study was funded by X (grant number X).

Conflict of Interest: Author A has received research grants from Company A. Author B has received a speaker honorarium from Company X and owns stock in Company Y. Author C is a member of committee Z.

If no conflict exists, the authors should state:

Conflict of Interest: The authors declare that they have no conflict of interest.

RESEARCH INVOLVING HUMAN PARTICIPANTS AND/OR ANIMALS

1) Statement of human rights

When reporting studies that involve human participants, authors should include a statement that the studies have been approved by the appropriate institutional and/or national research ethics committee and have been performed in accordance with the ethical standards as laid down in the 1964 Declaration of Helsinki and its later amendments or comparable ethical standards.

If doubt exists whether the research was conducted in accordance with the 1964 Helsinki Declaration or comparable standards, the authors must explain the reasons for their approach, and demonstrate that the independent ethics committee or institutional review board explicitly approved the doubtful aspects of the study.

The following statements should be included in the text before the References section:

Ethical approval: “All procedures performed in studies involving human participants were in accordance with the ethical standards of the institutional and/or national research committee and with the 1964 Helsinki declaration and its later amendments or comparable ethical standards.”

Ethical approval retrospective studies

Although retrospective studies are conducted on already available data or biological material (for which formal consent may not be needed or is difficult to obtain) ethical approval may be required dependent on the law and the national ethical guidelines of a country. Authors should check with their institution to make sure they are complying with the specific requirements of their country.

2) Statement on the welfare of animals

The welfare of animals used for research must be respected. When reporting experiments on animals, authors should indicate whether the international, national, and/or institutional guidelines for the care and use of animals have been followed, and that the studies have been approved by a research ethics committee at the institution or practice at which the studies were conducted (where such a committee exists).

For studies with animals, the following statement should be included in the text before the References section:

Ethical approval: “All applicable international, national, and/or institutional guidelines for the care and use of animals were followed.”

If applicable (where such a committee exists): “All procedures performed in studies involving animals were in accordance with the ethical standards of the institution or practice at which the studies were conducted.”

If articles do not contain studies with human participants or animals by any of the authors, please select one of the following statements:

“This article does not contain any studies with human participants performed by any of the authors.”

“This article does not contain any studies with animals performed by any of the authors.”

“This article does not contain any studies with human participants or animals performed by any of the authors.”

INFORMED CONSENT

All individuals have individual rights that are not to be infringed. Individual participants in studies have, for example, the right to decide what happens to the (identifiable) personal data gathered, to what they have said during a study or an interview, as well as to any photograph that was taken. Hence it is important that all participants gave their informed consent in writing prior to inclusion in the study. Identifying details (names, dates of birth, identity numbers and other information) of the participants that were studied should not be published in written descriptions, photographs, and genetic profiles unless the information is essential for scientific purposes and the participant (or parent or guardian if the participant is incapable) gave written informed consent for publication. Complete anonymity is difficult to achieve in some cases, and informed consent should be obtained if there is any doubt. For example, masking the eye region in photographs of participants is inadequate protection of anonymity. If identifying characteristics are altered to protect anonymity, such as in genetic profiles, authors should provide assurance that alterations do not distort scientific meaning.

The following statement should be included:

Informed consent: “Informed consent was obtained from all individual participants included in the study.”

If identifying information about participants is available in the article, the following statement should be included:

“Additional informed consent was obtained from all individual participants for whom identifying information is included in this article.”

RESEARCH DATA POLICY

The journal encourages authors, where possible and applicable, to deposit data that support the findings of their research in a public repository. Authors and editors who do not have a preferred repository should consult Springer Nature’s list of repositories and research data policy.

List of Repositories

Research Data Policy

General repositories - for all types of research data - such as figshare and Dryad may also be used.

Datasets that are assigned digital object identifiers (DOIs) by a data repository may be cited in the reference list. Data citations should include the minimum information recommended by DataCite: authors, title, publisher (repository name), identifier.

DataCite

Springer Nature provides a research data policy support service for authors and editors, which can be contacted at **researchdata@springernature.com**.

This service provides advice on research data policy compliance and on finding research data repositories. It is independent of journal, book and conference proceedings editorial offices and does not advise on specific manuscripts.

Helpdesk

AFTER ACCEPTANCE

Upon acceptance of your article you will receive a link to the special Author Query Application at Springer's web page where you can sign the Copyright Transfer Statement online and indicate whether you wish to order OpenChoice and offprints.

Once the Author Query Application has been completed, your article will be processed and you will receive the proofs.

Copyright transfer

Authors will be asked to transfer copyright of the article to the Publisher (or grant the Publisher exclusive publication and dissemination rights). This will ensure the widest possible protection and dissemination of information under copyright laws.

Offprints

Offprints can be ordered by the corresponding author.

Color illustrations

Publication of color illustrations is free of charge.

Proof reading

The purpose of the proof is to check for typesetting or conversion errors and the completeness and accuracy of the text, tables and figures. Substantial changes in content, e.g., new results, corrected values, title and authorship, are not allowed without the approval of the Editor.

After online publication, further changes can only be made in the form of an Erratum, which will be hyperlinked to the article.

Online First

The article will be published online after receipt of the corrected proofs. This is the official first publication citable with the DOI. After release of the printed version, the paper can also be cited by issue and page numbers.

Copyright transfer

Authors will be asked to transfer copyright of the article to the Japan Monkey Centre and the Publisher (or grant the Publisher exclusive publication and dissemination rights). This will ensure the widest possible protection and dissemination of information under copyright laws.

Editorial office

Dr. Tetsuro Matsuzawa

Editor-in-Chief, Primates

c/o Editorial Office

Japan Monkey Centre, Inuyama

Aichi 484-0081, Japan

Tel: +81-568-61-2327 Fax: +81-568-62-6823

e-mail: primates.jmc+gmail.com (replace "+" with "@" to use this e-mail address)

OPEN CHOICE

Open Choice allows you to publish open access in more than 1850 Springer Nature journals, making your research more visible and accessible immediately on publication.

Article processing charges (APCs) vary by journal – view the full list

Benefits:

- Increased researcher engagement: Open Choice enables access by anyone with an internet connection, immediately on publication.
- Higher visibility and impact: In Springer hybrid journals, OA articles are accessed 4 times more often on average, and cited 1.7 more times on average*.
- Easy compliance with funder and institutional mandates: Many funders require open access publishing, and some take compliance into account when assessing future grant applications.

It is easy to find funding to support open access – please see our funding and support pages for more information.

*) Within the first three years of publication. Springer Nature hybrid journal OA impact analysis, 2018.

Open Choice

Funding and Support pages

Copyright and license term – CC BY

Open Choice articles do not require transfer of copyright as the copyright remains with the author. In opting for open access, the author(s) agree to publish the article under the Creative Commons Attribution License.

Find more about the license agreement

READ THIS JOURNAL ON SPRINGERLINK

Online First Articles

All Volumes & Issues

♦ Primates Social Impact Award

Press Release: Sweet taste sensitivity o...

FOR AUTHORS AND EDITORS

2017 Impact Factor	**1.202**

Aims and Scope

Submit Online

Open Choice - Your Way to Open Access

Instructions for Authors

English Language Editing

SERVICES FOR THE JOURNAL

Contacts

Download Product Flyer

Shipping Dates

Order Back Issues

Article Reprints

Bulk Orders

ALERTS FOR THIS JOURNAL

Get the table of contents of every new issue published in Primates.

LOGIN

☐ Please send me information on new Springer publications in Zoology.

ADDITIONAL INFORMATION

Japan Monkey Centre

Primate Society of Japan

Online Submission

ANEXOS

1. MARCO REFERENCIAL

1.1. Marco teórico

Este trabajo se basa en 7 categorías teóricas; ecología de la conservación, ecología de poblaciones, ecología comportamental de primates o socio-ecología, comportamiento social en primates, *Sapajus apella* la cual tiene una subcategoría llamada “comportamiento social de *Sapajus apella*, fenología de bosques tropicales y productividad de bosques tropicales, todas estas son base fundamental para la elaboración de esta investigación. A continuación en la figura 1 serán presentadas las relaciones conceptuales entre los diferentes componentes y conceptos.

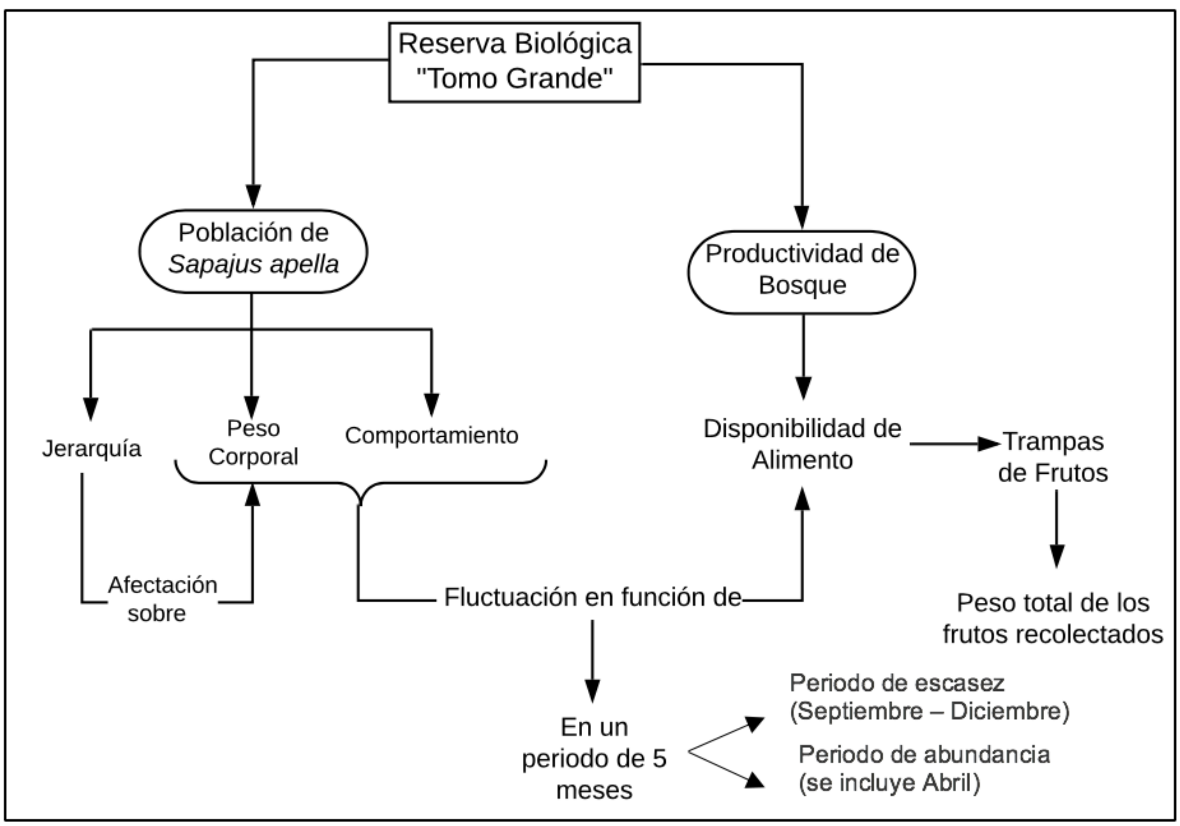


Figura 1. Diagrama conceptual de los conceptos y sus relaciones

1.1.1 Ecología de la Conservación

La Ecología de la Conservación es un paradigma relativamente reciente de la ecología, dando inicio en la década de los 80 *(Washitani 2001),* ya que a finales de 1970 fue cuando se empezó a tomar conciencia sobre la degradación que las actividades antrópicas estaban produciendo en el ambiente, así como sobre la pérdida de la biodiversidad y es por esto que tiene como objetivo mantener la biodiversidad biológica para garantizar la sostenibilidad intergeneracional a largo plazo *(Fonturbel, 2003).*

La conservación de la biodiversidad tiene dos enfoques, por un lado la conservación basada en especies y por otro la conservación de áreas protegidas*. (Sinclair & Byrom 2006).* Pese a que la mayor parte de los proyectos se centran en la conservación de especies puntuales bien sea por el valor económico y/o carismático que puedan tener *(Fonturbel, 2003)*, se han venido presentando enfoques de conservación más dirigidos hacia ecosistemas, que cómo las áreas protegidas permiten conservar no sólo las especies que se encuentren allí sino toda la biota, teniendo mejores resultados y permitiendo a su vez mitigar e incluso en algunos casos llegar a erradicar los efectos humanos en los diferentes ecosistemas *(Sinclair & Byrom 2006).*

Lo anterior, debido a que como lo establece el Convenio sobre la Diversidad Biológica (CBD) un área protegida es: "*un área geográficamente definida que esta designada o regulada y gestionada para lograr específicos objetivos de conservación*", y son esenciales para conservar la biodiversidad natural, cultural y bienes y servicios ambientales a través de actividades económicas, como el turismo (UICN & Dudley, 2008). Es por esto, que las áreas protegidas al restringir actividades que afecten la calidad del hábitat, cómo lo son la tala, la caza, entre otros, permiten tanto el establecimiento como la permanencia de una más alta diversidad de especies, por esta razón y siendo el área de estudio una reserva biológica se quiere dar un enfoque a esta investigación basado en la conservación.

1.1.2 Ecología de Poblaciones

El estudio de los grupos de individuos de una misma especie, es decir las poblaciones, en cuanto a las características estructurales y las dinámicas *(Morlans. 2014)* son abarcadas en la ecología de poblaciones. Se estableció hace varios años, que uno de los propósitos de la ecología de poblaciones es la identificación de las causas que determinan la abundancia de una o más especies en una localidad particular *(Franco, 1990).*

Es necesario al momento de realizar un estudio poblacional o tener que trabajar con poblaciones de una especie determinada conocer por una parte le estructura de esta, que abarca variables tales como el número de individuos, las abundancias y las densidades, el tamaño de los grupos, la proporción de edades, sexos, entre algunos otros (*(Morlans. 2014).* Por otra parte, se encuentran las dinámicas poblacionales, las cuales son sujetas al cambio o variación en el tiempo, y abarca conceptos cómo curvas o índices de crecimiento, tasas de natalidad y mortalidad, migraciones, etc *(Morlans. 2014).* Todas estas variables permiten conocer el comportamiento que está presentando una especie en un área particular.

Sin embargo, dependiendo del propósito del estudio debe haber un enfoque en ciertas variables específicas, en el caso de esta investigación queremos enfocarnos por una parte en aquellos patrones de comportamiento que se ven influenciados por la disponibilidad de alimentos haciendo énfasis en competencia intraespecifica y por otra parte en cambios jerárquicos de la población de *Sapajus apella.*

1.1.3 Ecología Comportamental de Primates (Socio-ecología)

La ecología comportamental, también conocida como socio-ecología, datándose los primeros estudios alrededor de 1930, y establecida formalmente cómo disciplinada en 1960 (Terborgh & Janson, 1986), se basa en el desarrollo de principios evolutivos para comprender las ventajas adaptativas del comportamiento en diferentes condiciones ecológicas (Krebs & Davis, 1993). Esta disciplina se basa por una parte en que el comportamiento está correlacionado con variables ambientales (Williamson, 1997) y por otra en cómo las estrategias a distintas condiciones ecológicas son utilizadas para la supervivencia y éxito reproductivo de los individuos de las distintas especies. (Steinmann, 2015).

De manera que para lograr comprender las diferentes estrategias que tienen las especies de primates se requieren muchos años para acumular observaciones suficientes de individuos suficientes (de distintas edades y sexos) para poder determinar patrones comportamentales generales por especie (Strier, 2000). No sin antes tener en consideración que debido a que los primates están sujetos a condiciones ecológicas complejas como por ejemplo a fluctuaciones anuales en la precipitación, las cuales generan diferentes temporadas de productividad y disponibilidad de recursos sus dietas, reproducción, rango y/o actividad se ven afectados (Strier, 2000), de manera tal que los patrones comportamentales pueden variar con mucha facilidad a nivel poblacional y de individuos.

Adicionalmente, se considera que uno de los hallazgos general más importante en la socioecología de primates ha sido el reconocimiento de distintos tipos de competencia alimentaria y sus efectos en las relaciones sociales, por ejemplo la competencia indirecta o “no agresiva” limita el tamaño del grupo pero tiene muy poca influencia sobre las relaciones sociales, mientras que la directa o también llamada “agresiva” promueve alianzas entre individuos (muchas veces basadas en parentesco). Además, otras investigaciones evidencian la fuerte influencia de las características del entorno sobre el comportamiento de los primates (Thierry, 2008), por ejemplo la distribución y abundancia de los recursos afectan los regímenes competitivos entre y dentro de los grupos, los cuales inducen diferentes patrones de relaciones sociales (Thierry, 2008), lo más frecuente es observar agresión y desplazamiento al competir por algún recurso lo que puede llegar a producir dominancia (Janson, 2000).

Por último, cabe resaltar que en un principio se suponía que la ecología era lo único que afectaba las relaciones sociales. Sin embargo, considerando que las sociedades son un sistema integrado hecho de múltiples relaciones que los individuos generan a través de procesos de interacción (Janson, 2000) se llegó a un consenso de varios autores acerca del vínculo entre el comportamiento de los primates y la ecología y que éste tenía mucho menos peso del que se creía, esto no implica que los factores ecológicos no sean importantes, sino que la organización social de los primates no está únicamente determinada por estos (Janson, 2000).

1.1.4 Comportamiento Social en Primates

La gran mayoría de los primates (con excepción de algunas especies) son gregarios, es decir que habitan en organizaciones o grupos sociales (Strier, 2000) y se considera que esto se debe a que los grupos tienen por una parte más éxito en la defensa y el acceso a los recursos (Wrangham, 1980), y por otro lado que son menos vulnerables a la depredación (Silk, 2001), y así como los humanos, casi todos los demás primates también viven en grupos caracterizados por patrones de comportamiento social tales como acicalamiento, forrajeo imitativo o cooperativo, relaciones de parentesco, cortejo ritualizado, comportamientos de apareamiento e interacciones competitivas estructuradas por la dominancia social (Smuts, et al. 1987).

De modo que el comportamiento de los primates y especialmente el social se ve influenciado por muchos factores que pueden llegar a generar fuertes cambios a nivel poblacional. Por ejemplo Janson (2000) establece que la competencia alimentaria así como el evitar la depredación son los que determinan el comportamiento de los primates. Chapais & Berman (2004) por su parte mencionan a las relaciones de parentesco como fuente motora del comportamiento social de la mayoría de especies, ya que muchas veces se tienden a formar relaciones de poder, dominanciada o alianzas basadas en parentesco, mientras que Strier (2000) establece que los comportamientos están más ligados a la supervivencia y el éxito reproductivo de los individuos.

Adicionalmente, los comportamientos sociales que una especie de primate puede tener pueden variar desde respuestas adaptativas para condiciones que caen en el rango dentro del cual evolucionaron las especies, hasta respuestas óptimas basadas en condiciones pasadas que ya no ocurren, hasta respuestas patológicas que caen fuera de los límites del alcance normal de reacción (Janson, 2000), hasta comportamientos altruistas que pueden poner en peligro a un individuo por salvar a otro (Strier, 2000).

Es debido a esto, y a los cambios que puede presentar tanto un individuo como una población en términos comportamentales que los expertos han tenido que considerar la posibilidad de que algunas poblaciones y especies de primates tengan comportamientos que en la actualidad pueden no interpretarse como adaptativos en las condiciones actuales, sino que pueden reflejar reacciones a cambios humanos masivos en el hábitat o presiones de selección pasadas muy diferentes de las de hoy (Janson, 2000).

1.1.5 *Sapajus apella*

Sapajus apella, antes *Cebus apella* (Linnaeus, 1758), más conocido como “Mico Maicero” es una especie de primate de la familia Cebidae, anteriormente del género Cebus, pero transferido a Sapajus en el 2012 (Lynch et al. 2012) se caracteriza por ser de colores castaños, de claros a oscuros, tener una cola prensil de hasta 50 cm, y un tamaño corporal de entre 35 y 49 cm, los machos pesan alrededor de 3.7 kg y 2.3 kg las hembras, tienen la cara oscura y bastante pelo a cada lado de la frente a manera de “cachos” (Defler, 2003).

Esta especie tiene la distribución geográfica más amplia de cualquier especie de primate neotropical y en Colombia se encuentra principalmente en el oriente del país, casi en toda la Amazonía, y en las tierras bajas del piedemonte amazónico de la cordillera oriental (Defler, 1985), y tiene en ciertas regiones una distribución parapatrica con *Cebus albifrons (*Defler, 2003). Adicionalmente, es un generalista en términos de uso de hábitats, se encuentra en una gran diversidad de ecosistemas, desde bosque caducifolio de galería en los Llanos Orientales hasta en bosque húmedo permanente e incluso en bosques de niebla y en manglares (Defler, 2003), sin embargo no forrajea ni se desplaza en bosque inundado, prefiriendo ambientes más secos y bosques más diversos o fértiles ya que utiliza con mayor frecuencia los estratos medio y bajo del bosque (Fleagle & Mittermeier, 1981).

Sapajus apella es considerado omnívoro, se alimenta principalmente de invertebrados pero también consume huevos de aves, frutos, hojas, vertebrados (ranas, lagartijas, aves y pequeños mamíferos) (Terborgh, 1983), e incluso ostras en manglares (Fernandez, 1991). Cabe resaltar que se alimenta también de una gran variedad de frutos, de unas 35 familias aproximadamente, y Terborgh (1983) resaltó la importancia de las palmas (*Arecaceae)* durante la época seca, cuando la oferta alimenticia se ve drásticamente reducida.

Debido a su amplia distribución geográfica, es una de las especies menos amenazadas de los primates Colombianos, y está considerada como “Least Concern” según la Lista Roja de la UICN. Sin embargo, puede haber algunas poblaciones en Colombia que estén siendo afectadas en Colombia por la fuerte presión de las actividades humanas (Defler, 2003).

1.1.5.1 Comportamiento Social de *Sapajus apella*

Anteriormente, en los Llanos Orientales el tamaño de grupos era en promedio de 8 a 9 individuos por grupo, compuesto generalmente por un macho adulto, varias hembras y juveniles (Defler, 1982), pero recientemente se han encontrado poblaciones de hasta 23 individuos, siendo 16 el tamaño promedio (Defler, 2003), las cuales pueden estar conformadas por machos de diferentes edades, varias hembras e individuos juveniles (Stevenson et al. 1992).

Esta especie tiene un comportamiento social caracterizado por fuertes jerarquías, en donde se encuentra un macho alfa quien hace prevaler su derecho a copular, inhibiendo a los otros para acceder a las hembras en el caso en el que haya otros machos reproductores (Janson, 1984). Adicionalmente, Janson (1985) investigó las interacciones sociales de la especie y encontró por una parte que los niveles de competencia intra-específica eran 10 veces mayores que la inter-específica y por otra parte evidenció una marcada diferenciación en las tasas de alimentación de acuerdo al status social dentro del grupo, teniendo los individuos dominantes una dieta energéticamente más alta en un 20% o más, en comparación con los individuos subordinados, quienes reciben más agresión.

1.1.6 Fenología de Bosques Tropicales

La fenología se define como el conocimiento de las relaciones existentes entre los fenómenos biológicos periódicos que suceden en las plantas y los cambios estacionales producidos en su hábitat *(Salazar, 2012).* Es decir la temporalidad de la floración y fructificación en un ciclo anual y Terborgh (1992) establece que estas manifestaciones pueden ser independientes de eventos climáticos. La fenología además, puede abarcarse a diferentes escalas, dado que por una parte la unidad de estudio puede varias desde una especie simple hasta un ecosistema complejo y por otra parte el área involucrada puede ser pequeña (para estudios intensivos de zonas de estudio específicas) o incluso muy grande (para estudios comparativos interregionales) (Lieth, 1974).

Dicho de otra manera, Flórez (2018) establece que se entiende como la ciencia que investiga los cambios que van mostrando los organismos a lo largo del tiempo, como puede ser los momentos en el que las plantas generan nuevas hojas, producen flores, frutos, o pierden su follaje. Los patrones fenológicos determinan la disponibilidad de alimento en el tiempo para numerosas especies de primates, lo que genera que el estudio de estos patrones permita conocer diversos aspectos de la ecología de estas especies *(Flórez, 2018).*

Debido a esto Lieth (1974) establece que se deben analizar las interacciones entre grupos de organismos y el ecosistema, debido a que en un entorno de oscilaciones estacionales los organismos pueden ya sea tener un ciclo de vida lo suficientemente corto como para completarse durante una determinada combinación de condiciones ambientales, o pueden (y este es el caso de los primates) generar diferentes estrategias que les permitan a los individuos adaptarse a cambios ambientales periódicos.

Es por esto que la fenología del bosque cumple un rol tan importante en la realización de investigaciones con primates, ya que cómo lo establece Flórez (2018) en una compilación de los métodos de estudio de la Asociación Primatológica Colombiana *" La integración de información fenológica a los estudios sobre aspectos de la ecología de los primates frugívoros es crucial para conocer, más allá de un plano descriptivo, sobre las adaptaciones y respuestas de estas especies a las dinámicas de su ecosistema".* Esto debido a que se considera que los patrones de crecimiento temporal y reproducción en plantas tienen una importante influencia en la estructura y dinámica de comunidades animales (Newstrom et al. 1994), así cómo también en su comportamiento.

1.1.7 Productividad de Bosques tropicales

La productividad de bosques se entiende como la producción de materia orgánica o biomasa acumulada en un área determinada por unidad de tiempo (Zelitch, 1971), se considera que es determinada por factores tales como radiación solar, dióxido de carbono, disponibilidad de agua, cantidad de follaje, temperatura ambiente, disponibilidad de nutrientes, composición y estructura de la vegetación, entre otros (Boisvenue & Runnings, 2006) y que varía dependiendo del área y el tiempo determinado.

Adicionalmente, es considerada base fundamental para los estudios con diversas especies de primates enfocados o relacionados con la dieta, debido a que los boques responden a las variaciones tanto a corto como a largo plazo del medio ambiente (Innes & Peterson, 2001), lo que genera que presenten cambios en la productividad a lo largo del tiempo ya sea por cambios en parámetros climáticos y del entorno (Williamson, 1997; Ryan et al. 1997), como también por la estacionalidad dada por el régimen de lluvias de un área determinada.

Actualmente, hay mucho debate sobre la productividad de los bosques tropicales y se ha encontrado que estos ya han experimentado cambios notables en la composición florística y en la estructura de los bosques a causa de presencia humana y del cambio climático (Clark, 2004). Slayback & Pinzon (2003) por ejemplo, evidenciaron una menor productividad en los ecosistemas tropicales en los años registrados como más cálidos y en las últimas décadas, estudios han demostrado un crecimiento en la mortalidad de los árboles, lo que implica que los bosques tropicales ya están siendo fuertemente afectados negativamente por los niveles actuales de temperatura y sequía (Clark, 2004).

No obstante, también se ha evidenciado que las plantas tienen una rápida adaptación a los cambios en las condiciones climáticas, y se han encontrado rasgos cambiantes de algunas especies bajo condiciones ambientales variables (Boisvenue & Runnings, 2006). Por lo que perturbaciones u otros fenómenos generan cambios en la composición de los bosques afectando de esta manera su productividad, teniendo en cuenta que los cambios como resultado del calentamiento global siguen sin estar claros (Maslin, 2005).

Por último, debido a que la productividad de bosque es clave para conocer el estado del ecosistema y ya que en la actualidad hay muchas preocupaciones sobre el mantenimiento de bosques en buen estado debido al declive que se ha presentado en los últimos años (Crow et al. 2006) es importante apostarle a su conservación aún más sabiendo que la productividad parece limitar tanto la biomasa de primates como la diversidad de especies, pero puede hacerlo de manera diferente para los folívoros y frugívoros (Janson, 2000), por lo que es de suma importancia comprender la influencia que tienen los cambios en la productividad sobre poblaciones de primates, especialmente en bosques tropicales.

1.2. Antecedentes

1.2.1 <u>Antecedentes Temáticos</u>

Actualmente existen algunos estudios acerca de cambios en patrones de comportamiento en primates debido a diferentes factores, Vogel & Janson (2010) encontraron que la abundancia y distribución de alimentos juegan un papel central en la teoría conceptual de la socioecología de primates y que la competencia alimentaria genera efectos en las relaciones sociales, por ejemplo la competencia indirecta limita el tamaño del grupo mientras que la directa afecta relaciones sociales promoviendo agresividad y alianzas basadas en parentesco *(Vogel & Janson, 2010)*.

Adicionalmente, McConkey et al. (2001) establecieron que debido a la reconocida irregularidad estacional de la disponibilidad de alimentos de los bosques tropicales, los animales están constantemente obligados a tomar decisiones complejas sobre qué recursos explotar, por esto muchas especies de primates neotropicales muestran cambios estacionales en el comportamiento de alimentación que están relacionados con la abundancia de alimentos específicos o factores climáticos *(McConkey et al. 2001).*

Finalmente, Hemingway & Bynum (2005) realizaron un estudio de las respuestas de los primates a la escasez de recursos con un enfoque en la flexibilidad del comportamiento, y encontraron que la baja disponibilidad de alimentos afecta el comportamiento social, la dieta, aumenta la distancia entre los individuos y se generan más conflictos por competencia y por territorio. *(Hemingway & Bynunm, 2005).*

1.2.2 Antecedentes de Contexto

Se han realizado varios proyectos de investigación tanto en flora como en fauna en la reserva biológica "Tomo Grande", la gran mayoría por parte del laboratorio de ecología de bosques tropicales y primatología (CIEM) de la Universidad de los Andes, uno de estos estudios se llevó a cabo en el 2010 por parte de Stevenson y Gómez quienes estudiaron la estructura y diversidad de tres hectáreas de bosques de galería, en el cual analizaron la diversidad y fisionomía vegetal. En este estudio se encontraron 120 especies y pese a que se encontró una similitud entre la flora llanera y amazónica, en esta área de estudio hay una diversidad baja en comparación con parcelas de la Amazonía *(Gómez & Stevenson, 2010).*

Adicionalmente, hay un estudio denominado "Avances en el diagnóstico de los servicios ecosistémicos de la Reserva Biológica y Productiva Tomo Grande Vichada (Colombia)" en el cual se establece que los bosques están dominados por Fabacea, Euphorbiacea, Salicaceae, Chrysobalancea y Lecythidaces. Adicionalmente, se encontró que los bosques de galería son más diversos que los planos de inundación pero acumulan menos biomasa *(Stevenson et al. 2012)* es decir tienen más especies pero menos individuos.

Finalmente, también existen diversas investigaciones acerca de la fauna de la región cómo la realizada por Bernal (2012) quien estudió la abundancia relativa de mamíferos y aves grandes de la reserva, y a si mismo en otro estudio se confirmó a partir de camaras trampa y transectos la presencia de una gran diversidad de fauna registrandose 19 mamiferos y aves tanto medianas como grandes. *(Stevenson et al. 2012)*

2. MATERIALES Y MÉTODOS

2.1 Diagrama de flujo: Procedimiento metodológico

A continuación en la figura 2 se presenta el diagrama metodológico, en el cual se pueden evidenciar las fases del proyecto, los procesos, los productos, insumos, y los métodos para la realización de la investigación.

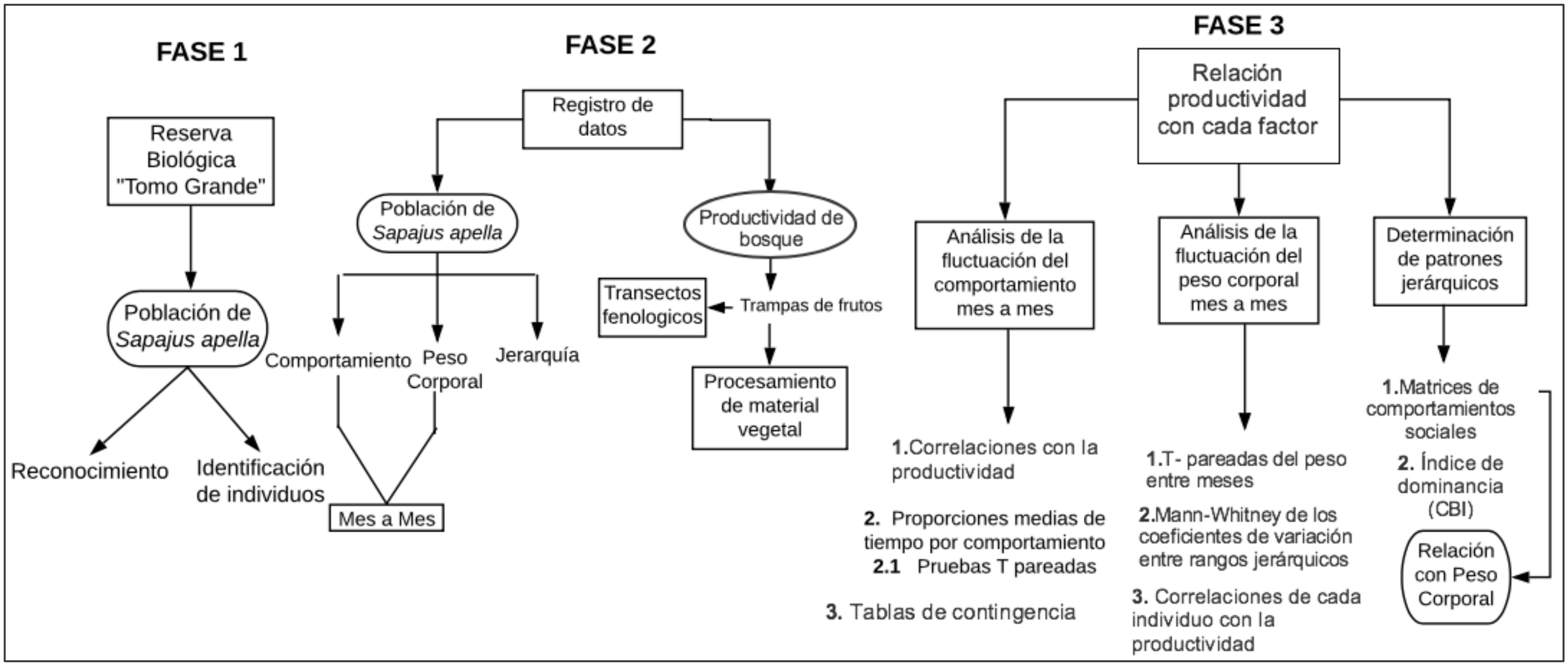


Figura 2. Diagrama del procedimiento metodológico del proyecto.

2.1.1 Fase 1 → Esta primera fase del proyecto se basa en la primera llegada a la zona de estudio, previo a la recolección de datos se debe por un lado reconocer el bosque, debido a que la reserva cuenta con sabanas extensas y parches de bosques de galería los cuales están nombrados de la siguiente manera: 1/2, 2/3, 3/4, 4/5 y 5/6, y el bosque en donde se encuentra la población de estudio es el llamado 5/6 por lo que es importante una correcta identificación de cuál es, cómo llegar, una familiarización en su interior y por último una revisión y limpieza de las trampas de frutos del bosque en cuestión para la posterior colecta de datos. Por otra parte, se requiere el reconocimiento de la población de *Sapajus apella,* esto implica lograr ubicar la población de la manera más rápida posible, así como también la correcta identificación de cada individuo previamente identificado, de lo contrario nombrar y fotografiar a todos los individuos considerados "nuevos".

2.1.2 Fase 2 → La segunda fase consiste en la toma de todos los datos necesarios. Por una parte se deben registrar los datos de la población de *Sapajus apella* los cuales son comportamiento; a través de focales registrando el comportamiento con base en unos códigos previamente establecidos cada 2 o 5 minutos dependiendo de la duración del focal, peso corporal; pesándolos en un balanza en la cual se les ubica un cebo para lograr que desciendan al piso, y por último jerarquía registrando comportamientos sociales, ya sean de sumisión o agresión que posteriormente a través de unas matrices de comportamientos sociales, junto con un índice de dominancia se determinará los patrones jerárquicos de la población.

Adicionalmente, se debe hacer una recolectar los datos necesarios para la determinación de la disponibilidad de alimento, lo cual se basa en la revisión y recolección de unas trampas de frutos ubicadas previamente en el bosque, para su posterior procesamiento.

2.1.3 <u>Fase 3 →</u> Una vez se tenga toda la información, tanto de la disponibilidad de alimento, cómo del comportamiento, peso corporal y jerarquía de la población, se procederá a realizar el análisis de datos el cual se basa en la fluctuación de cada factor en función de la disponibilidad de alimento (en términos de peso en gramos de los frutos con pulpa encontrados en las trampas). El análisis de cada factor será de manera independiente, comparando mes a mes los cambios que se presentan tanto en el comportamiento como en el peso corporal de los individuos, y la relación de cada uno con la productividad del bosque, en términos de influencia de la época de escasez o abundancia en cambios comportamentales y ganancia o pérdida del peso corporal, así como también la relación de los factores con la jerarquía con el fin de determinar si el nivel jerárquico de un individuo genera cambios comportamentales o si en época de escasez o de abundancia hay mayor ganancia o pérdida de peso entre dominantes y subordinados.

2.2 <u>Métodos de Recolección de Datos</u>

Durante el trabajo de campo se utilizaron diversas metodologías con el fin de recolectar todos los datos necesarios para la elaboración de la investigación, por una parte se encuentran los datos asociados a la productividad de bosque, y por otra parte los datos de *Sapajus apella* necesarios*,* es decir comportamiento, jerarquía y peso corporal.

En primer lugar, la metodología empleada en los estudios fenológicos asociados a las investigaciones en primatología puede variar dependiendo del objetivo de la investigación, las especies de estudio, y el ecosistema *(Flórez, 2018)*. Debido a que para esta investigación se pretende determinar la productividad de bosque, es importante mencionar que algunos estudios recientes han establecido que para efectos de cuantificar la producción total de alimento para especies frugívoras, la mejor metodología es la de trampas de frutos *(Flórez, 2018)*, la cual será la utilizada.

En el bosque en el que habita la población de *Sapajus apella* estudiada, se distribuyen 60 trampas de frutos en un transecto establecido para observaciones fenológicas, el espacio entre las trampas es de aproximadamente 20 metros, se encuentran ubicadas de manera aleatoria ya sea a la derecha o izquierda y la distancia a la que se encuentran del camino varia de 0 a 10 metros *(Stevenson et al. 2004)*. Las trampas se deben revisar, seleccionar y limpiar quincenalmente durante los 5 meses que duró el estudio, colectando todos los frutos y semillas de cada trampa.

Posteriormente, se debe realizar el procesamiento del material vegetal, el cual se realiza tomando todos los frutos y semillas recolectados, separados por número de trampa, los cuales deben ser pesados, luego secados durante 15 horas aproximadamente y pesados de nuevo. Se le debe asignar a cada fruto recolectado un morfotipo, o si se conoce: el nombre común, se debe registrar tanto el peso húmedo como el seco, e identificar hasta el menor nivel taxonómico posible (Stevenson et al. 2004).

Ahora bien, en cuanto a la medición de datos de comportamiento hay varios métodos importantes considerando dos niveles de observación. El primer nivel denominado reglas de muestreo específica qué sujetos hay que observar, existen tres tipos de muestreo: focal, de barrido y ad libitum, el primero registra la conducta de un individuo durante un periodo de tiempo determinado *(Martin & Bateson 2007),* el muestreo de barrido implica medir la actividad desarrollada por más de un individuo que se encuentre bajo observación, puede ser por ejemplo el número de individuos que están realizando un determinado comportamiento y el muestreo ad libitum involucra observaciones oportunistas, conocidas como comportamientos raros, ya sea por uno o varios individuos *(Martin & Bateson 2007)*.

El segundo nivel llamado reglas de registro específica cómo se va a registrar la conducta, es decir si será un registro continuo en el cual se miden duraciones reales de las conductas (hora inicio y hora fin), o si en cambio se realizará un registro temporal, en el que se registra sólo un punto en el tiempo *(Martin & Bateson 2007).* En cuanto a esta investigación se realizaron seguimientos por individuo de 6am a 6pm de lunes a sábado, con focales tanto de 20 minutos (Abondano et al. 2012) como por horas (Stevenson et al., 2000, registrando datos de comportamiento cada 2 o 5 minutos respectivamente. Se debe observar y registrar tanto el comportamiento del individuo focal como del vecino más cercano, prestando especial atención a comportamientos sociales tales como agresiones, acicalamientos, copulas o juegos entre individuos y en el caso en que alguna de estas se presentes se debe registrar el actor, el receptor, el contexto y las horas de inicio y fin (Martin & Bateson, 2007).

Adicionalmente, se registraron todos los comportamientos de sumisión y agresión, teniendo en cuenta los actores y receptores (Martin & Bateson, 2007) para junto con un índice de dominancia viz, Clutton – Brock et al.'s index (CBI), determinar la jerarquía (Clutton-Brock et al, 1979). Por último para obtener el peso corporal de los individuos, se optó por cebarlos y pesarlos, registrando los datos tanto del peso cómo del orden en que se alimentan los individuos. Para lograrlo se utilizaron dos balanzas (marca: OHaus, precisión +/- 2g) la primera balanza se ubicaba en un lugar un poco despejado y alejado de ramas o arboles en los que los individuos se pudieran colgar, se cubrió con hojas y se ubicó el cebo, el cual fue *Inga edulis* encima de la balanza de manera que los individuos tuvieran que bajar y pararse sobre la balanza, y así poder ser pesados, la otra balanza se colgaba de una cuerda amarrada a gran altura a dos arboles, se le amarraba una liana gruesa y a la liana le se amarraba el cebo lo más ajustado posible con el fin de que los individuos se colgaran en la liana y tuvieran dificultad para agarraran el cebo dando tiempo al observador de registrar el individuo y su peso exacto.

2.3 Métodos de Análisis de datos

En primer lugar, para estimar la productividad de bosque se analizaron todos los datos colectados en las trampas de frutos y sólo la especies endozoocoricas fueron tenidas en cuenta, de modo que para la estimación se tomaron los pesos secos de los frutos y junto al área de cada trampa, ya que cada una variaba se calcularon los Kg/ha de cada trampa registrada. Luego, el promedio de la productividad de cada mes fue obtenido tomando cada trampa como replica (en su mayoría N=58, debido a algunas trampas caídas que no fueron incluidas en el análisis).

En cuanto al análisis de datos se determinó el comportamiento de cada variable por métodos diferentes, en primer lugar para el comportamiento debido a ser una variable categórica se utilizaron por una parte una distribución de frecuencias, con el fin de determinar los porcentajes de los distintos comportamientos en la población en cada mes (Marin, 2010), y se calcularon las proporciones medias de tiempo por comportamiento por mes, con el fin de determinar con base en los comportamientos más relevantes si el tiempo promedio empleado fue significativamente diferente entre los meses, dada la normalidad de los datos (Pearson: $p > 0.28$, Shapiro Wilk: $p > 0.08$, Kolmogorov-Smirnov: $p > 0.26$) se realizaron pruebas t pareadas para comparar la proporción media del tiempo empleado en los comportamientos en los distintos meses (Martin & Melfi, 2016). Adicionalmente, se realizaron correlaciones de Pearson entre cada comportamiento y la productividad del bosque y por último se realizaron tablas de contingencia con el fin de determinar el nivel de asociación entre variables (siendo una cualitativa).

Por otra parte, debido al poco cambio que presentan las organizaciones sociales y ordenes jerárquicos en un periodo intra-anual en donde haya presencia de un macho dominante (Janson, 1984) (el cual es el caso de la población de estudio) no se analizó la fluctuación mes a mes sino se determinaron los patrones de jerarquía de la población del tiempo total por medio de tres matrices de comportamientos sociales, la primera era de comportamientos afiliativos es decir acicalamientos entre individuos, la segunda de comportamientos agonísticos, incluyendo tanto agresiones directas cómo amenazas o persecuciones, y la tercera era una matriz de juego entre individuos, comportamiento que era realizado exclusivamente por juveniles e infantes. Adicionalmente, se calculo el índice de dominancia viz, Clutton-Brock et al. para cada individuo siguiendo la fórmula: $CBI = (B + b + 1) / (L + l + 1)$, en dónde B =número de individuos a los que el sujeto dominó, b = número de individuos a quienes dominó el sujeto que a su vez dominaron a otros, L= número de individuos que dominaron al sujeto, l=número de individuos que dominaron a los que dominaron al sujeto (Bang et al., 2010).

Adicionalmente, la variación del peso corporal de los individuos mes a mes se analizó (debido a la normalidad en su distribución: $p > 0.05$ en todos los casos; Shapiro-Wilk) mediante por una parte pruebas t pareadas para evaluar las diferencias entre las pesos por individuo entre meses (Sullivan et al. 2006), adicionalmente se realizaron correlaciones de Pearson (r) entre la productividad del boque y el peso de cada individuo. Además, se calcularon los coeficientes de variación por individuo, del periodo de escasez (Septiembre – Diciembre) y se contrastaron con los rangos jerárquicos a través de una prueba de Mann-Whitney (datos no paramétricos), y finalmente se determinó el cambio máximo en peso de cada individuo incluyendo el periodo de abundancia (Abril) así como también las tasas de crecimiento relativo de la época de escasez y de abundancia, con el fin de comprarlas entre los niveles jerárquicos. Todas las pruebas estadísticas fueron realizadas en 'R', a excepción de los coeficientes de variación, cambios máximos y tasas de crecimiento relativo que fueron calculadas en hojas de cálculo de Microsoft Excel.

3. ÁREA DE ESTUDIO

3.1 Mapa de la Ubicación

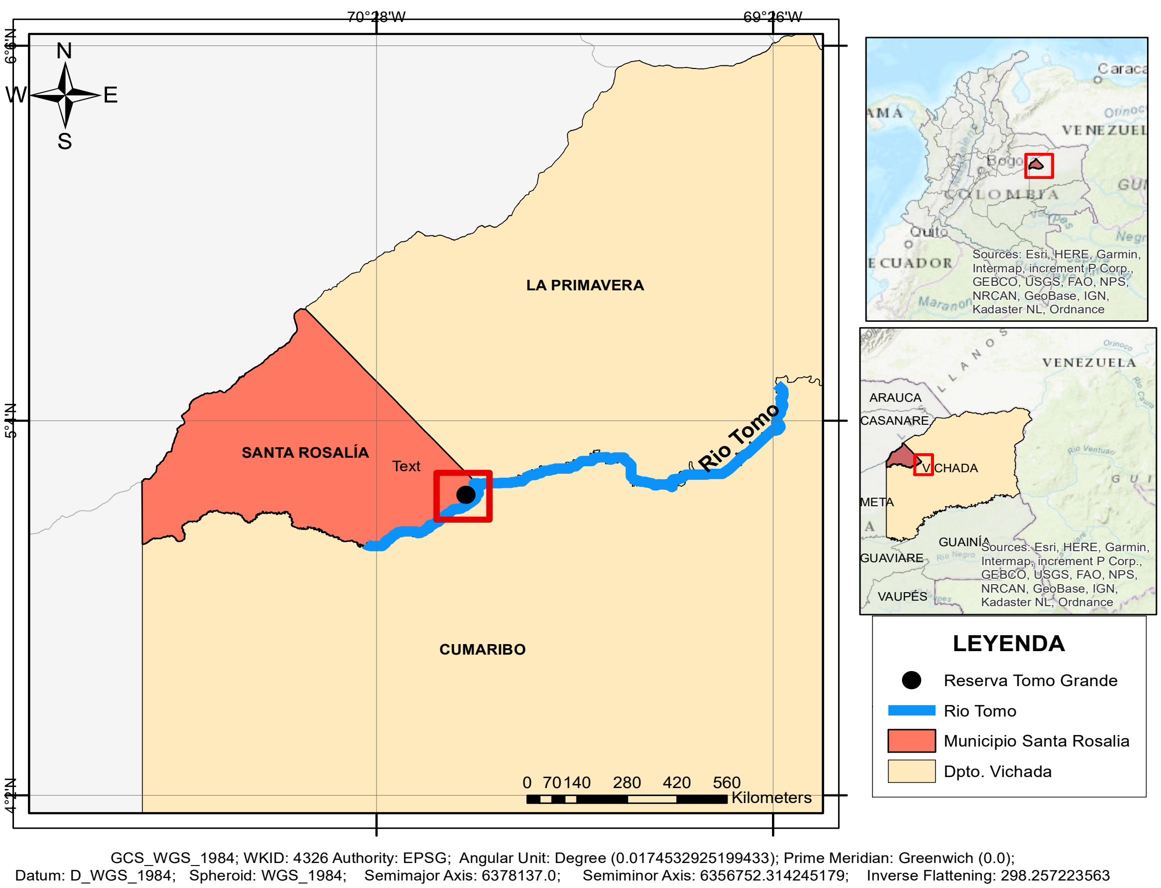


Figura 2. Localización del área de estudio

3.2 Contexto geográfico, biofísico y socio-económico

La reserva biológica “Tomo Grande” está ubicada en el municipio de Santa Rosalía, departamento del Vichada. Se encuentra en el área de desembocadura entre los ríos Tomo y Caño Grande, dentro de la vereda Nazareth *(Stevenson et al. 2010)*. La reserva hace parte de la zona de amortiguación del Parque Nacional Natural El Tuparro y forma parte de un esfuerzo privado de conservación denominado TomoVida, del cual hacen parte 9 predios los cuales pretenden complementar el esfuerzo de conservación del Tuparro *(Stevenson P.R, 2012).* Para poder llegar a la reserva desde la ciudad de Bogotá se debe llegar a Puerto Gaitan, de allí ir en Lancha hasta Santa Rosalía y posteriormente ya sea en moto o en camión se puede llegar, tras un recorrido total aproximado de 20 horas.

La cobertura de la zona consiste de sabanas extensas estacionales y vegetación boscosa en bosques riparios o de galería, con una temperatura promedio anual de entre 24 y 27ºC y precipitaciones mayores a 2000 mm *(Stevenson P.R 2012).* La zona registra un régimen de precipitación monomodal, con un máximo de lluvias hacia mediados del año, y la temporada seca se caracteriza por ser muy fuerte, ocurre entre los meses de diciembre y mayo y se presentan quemas periódicas *(Stevenson et al. 2010).* En cuanto a la vegetación se han colectado 250 especies de plantas y se registran pumas, jaguares, ocelotes, venados, zorros, saínos, ñeques, tapires, pavas, paujiles, anacondas, entre muchos otros. Adicionalmente cabe resaltar la presencia de 2 especies de primates: aulladores rojos (*Alouatta seniculus*) y micos maiceros (*Sapajus apella*) *(Stevenson et al. 2012).*

Por otra parte, con respecto al departamento del Vichada es el segundo más extenso del país pero el tercero menos poblado, el cual cuenta con 77,276 habitantes según el DANE (2018). Su capital es Puerto Carreño y cabe mencionar que a lo largo de los años ha sido uno de departamentos más afectados tanto por el narcotrafico como por el conflicto armado interno en Colombia. Sin embargo, tras más de dos años de la firma del acuerdo de Paz, la situación en el Vichada, y especialmente en el municipio de Santa Rosalía ha mejorado considerablemente. No obstante, se han presentado denuncias de varias autoridades indigenas de resguardos ubicados en las zonas rurales de la region. Adicionalmente, cabe resaltar que Santa Rosalía siempre ha sido un puerto estrategico de intercambio comercial de ganado y mercancia con los departamentos de Casanare, Meta y Arauca a través de los ríos Meta y Orinoco (Castro, 2015) y actualmente su economía gira en torno a la agricultura y a la ganadería, especialmente al cultivo de Soya y Maíz tradicional (DANE, 2014). Por último, es importante mencionar que el municipio cuenta con 8 veredas, una de ellas llamada “Nazareth” en donde se encuentra la reserva, esta vereda tiene aproximadamente 400 habitantes de los cuales más de la mitad son indígenas “Sikuani”, ellos habitan en resguardos alejados del resto de la comunidad y su lengua oficial es el Sikuani. Su principal sustento es la venta de “Mañoco” (alimento tradicional de comunidades indigenas), y la pesca, mientras que del resto de la comunidad es la ganadería y la porcicultura. Finalmente, la vereda cuenta con un escuela primaria con 20 niños aproximadamente y anualmente se gradúan de quinto en promedio 3.

4. CONCLUSIONES Y RECOMENDACIONES

Con el creciente impacto que ha tenido el desarrollo antropogénico en los bosques alrededor del mundo, 60% de especies de primates se han visto amenazadas, 75% han sufrido peligrosas disminuciones en sus poblaciones (Estrada et al. 2017) y otras tales como *Saguinus oedipus* ya se encuentran en peligro critico de extinción en este caso debido al tráfico de fauna y a la deforestación del bosque seco tropical colombiano (Guillen, 2017). Es por esto, que se debe ahondar en maneras de conservar los primates con el fin de prevenir la extinción de cualquier especie, para esto el entendimiento de las adaptaciones que puede presentar una especie frente a cambios ya sean naturales o generados por los humanos en su hábitat es fundamental para generar aportes en la conservación de la fauna silvestre y puede ayudar a prever el impacto que tendrán ciertos cambios en los ecosistemas a las especies que los habiten.

Es beneficioso también entender no sólo cómo los primates pueden adaptar sus comportamientos a cambios ecológicos en sus hábitats, sino qué otros factores pueden estar definiendo estas variaciones, es decir la determinación de los cambios tanto comportamentales como en el peso corporal que puede presentar una población de *Sapajus apella* frente a cambios en la disponibilidad de frutos en el bosque en el que habitan (debido a la temporalidad natural de los bosques neotropicales, en dónde hay épocas de escasez y épocas de abundancia) es fundamental para entender la respuesta de la población frente a una escasez de recursos. No obstante, es importante también determinar si las variaciones presentes en una población son dadas exclusivamente por el factor disponibilidad de alimento, o si se encuentran otros elementos que pueden estar influyendo en la flexibilidad comportamental y el cambio en el peso corporal de los individuos, debido a esto la determinación de la influencia de la jerarquía en estas variaciones, es importante para entender que el cambio en poblaciones ya sea en términos de comportamiento o peso corporal no se puede reducir a un solo elemento como la disponibilidad de alimento, sino que son distintos componentes los que generan influencia.

Los resultados en esta investigación muestran que en un periodo de tiempo relativamente corto no hay diferencias significativas en cuanto al comportamiento de la población. Sin embargo ciertos comportamientos, como por ejemplo comer y forrajear, acicalar o desplazarse están correlacionados con la productividad de bosque, lo que implica que por ejemplo la población tiene que gastar más tiempo que en otros meses buscando comida debido a la escasez de esta. Por otra parte, el peso registró una tendencia a estabilizarse y en algunos individuos hay disminuciones en los meses de mayor escasez, lo que indica que si existe cierta presión en la variación de peso corporal sobre la ganancia o pérdida de peso. Ahora bien, la jerarquía ejerce influencia sobre los comportamientos de los individuos, ya que se encontró que los dominantes suelen ser más acicalados y curiosamente más agredidos que los subordinados, esto se debe a la alta tasa de agresividad que presenta el macho alfa con respecto a los demás dominantes, así como también se encontró una diferenciación muy marcada del peso del macho alfa con respecto al resto de la población (60% mayor que el promedio) y pese a que los dominantes son más pesados que los subordinados, no tienen mayor ganancia de peso, mientras que los juveniles si, debido a la etapa de desarrollo en la que se encuentran.

Por último, para ampliar estos resultados, repetir este estudio durante un periodo de tiempo más prolongado ayudaría a solidificar la variación que tiene una población en términos comportamentales y de peso corporal, frente a la fluctuación anual de productividad de bosque, logrando comparar las dos temporadas (de escasez y abundancia) en su totalidad, así cómo también se recomendaría un análisis de las especies vegetales consumidas durante cada temporada con el fin de observar cambios en la dieta con base en la disponibilidad de frutos.

5. REFERENCIAS

Bang et al. (2010). *Choosing an appropriate index to construct dominance hierarchies in animal societies: a comparison of three indices.* Animal Behavior 79 (2010) 631–636 MS. No. 09-00002R

Bernal, L. S. A. (2012). *Abundancia relativa de mamíferos y aves grandes en la Reserva Tomo Grande (Vichada)* (Doctoral dissertation, Uniandes).

Bercovitch (1999). *Comparative Primate Socioecology.* Edited by P. C. LEE. Cambridge: Cambridge University Press. Pp.xii+412

Blanco (2013). Modelos ecológicos: descripción, explicación y predicción. ASOCIACIÓN ESPAÑOLA DE ECOLOGÍA TERRESTRE. Ecosistemas REVISTA CIENTÍFICA DE ECOLOGÍA Y MEDIO AMBIENTE ISSN 1697-2473

Boiscvenue C. & Running S. (2006). *Impacts of climate change on natural forest productivity - evidence since the middle of the 20th century. Global Change Biology, 12(5), 862–882.* doi:10.1111/j.1365-2486.2006.01134.x

Chapais & Berman (2004). *Kinship and behavior in primates.* Oxford University Press. ISBN: 0-19-514889-4

Chapman, C. A., & Pavelka, M. S. (2005). Group size in folivorous primates: ecological constraints and the possible influence of social factors. *Primates*, *46*(1), 1-9.

Chapman, C. (1985). The influence of habitat on behaviour in a group of St. Kitts green monkeys. *Journal of Zoology*, *206*(3), 311-320.

Clark, D (2004). *Sources or sinks? The responses of tropical forests to current and future climate and atmospheric composition*. Philosophical Transcripts of the Royal Society of London, Series B, 359, 477–491

Clutton & Harvey (1977). *Primate ecology and social organization.* School of Biological Sciences, University of Sussex. J. Zool. Lond (1977) 183, 1- 39

Clutton-Brock, T., et al., (1979). *The logical stag: adaptive aspects of fighting in red deer.* Animal Behaviour, 27, 211–225, doi:10.1016/0003-3472(79)90141-6.

Correa-Gómez, D. *& Stevenson, P. R. (2010). Estructura y diversidad de bosques de galería en una sabana estacional de los Llanos Orientales colombianos (Reserva Tomo Grande,Vichada).* Orinoquia, 14(2), 31-48*.*

Crow, T et al. (2006). *Forest Productivity: Producing Goods and Services for People.* NORTH CENTRAL RESEARCH STATION FOREST PRODUCTIVITY INTEGRATED RESEARCH AND DEVELOPMENT PROGRAM. Science Co-Leaders.

Defler T.R (1982). *A comparison of intergroup behavior in Cebus albifrons and Cebus apella.* Primates 23:385-392.

Defler T.R. (1985). *Contiguous distribution of two species of Cebus monkeys in El Tuparro National Park, Colombia.* American Journal Primatology 8:101-112.

Defler T.R (1985). *Those crafty, capricious, clever capuchins.* Animal Kingdom 89:16-21.

Defler, T.R. (2003). *Primates de Colombia.* Conservación Internacional, Colombia. Serie de guías tropicales de Campo 4. Universidad Nacional de Colombia.

Estrada et al. (2017). *Impending extinction crisis of the world's primates: Why primates matter*. Science Advances*,* Vol. 3, no. 1, e1600946

Fernandez, M. (1991). *Tool use and predation of oysters (Crassostrea rhuzophorae) by the tufted capuchin, Cebus apella, in brackish water mangrove swamp.* Primates 32(4):529-531.

Fleagle, J.G & Mittermeier, A. (1981). *Differencital habitat use by Cebus apellaand Saimiri sciureus in Central Surinam.* Primates 22:361-367.

Flórez (2011*). Métodos de Estudio: Fenología de Plantas.* Asociación primatológica Colombiana.

Fontúrbel, R. (2003). *Conservación de ecosistemas: un nuevo paradigma en l conservación de la biodiversidad*. Ciencia Abierta, (23), 1-18.

Fragaszy, D., Izar, P., Visalberghi, E., Ottoni, E. B., & de Oliveira, M. G. (2004). Wild capuchin monkeys (Cebus libidinosus) use anvils and stone pounding tools. *American Journal of Primatology: Official Journal of the American Society of Primatologists*, *64*(4), 359-366.

Franco (1990). Ecología de poblaciones. CIENCIAS. Especial 4. Open access.

Hutchinson, G. E. 1978. An Introduction to Population Ecology. Yale University Press, New Haven.

Gómez & Stevenson (2010). Estructura y diversidad de bosques de galería en una sabana estacional de los Llanos Orientales colombianos (Reserva Tomo Grande, Vichada). *Orinoquia*, *14*(2), 31-48.

Guillen, R. (2017). *El tití cabeciblanco solo habita en Colombia y está en vía de extinción.* Fundación mono titi

Hemingway, C.A, & Bynum, N. (2005). *The influence of seasonality on primate diet and ranging.* Seasonality in primates: Studies of living and extinct human and non-human primates, 44, 57.

Janson, C.H. (1984). *Female choice and matting system of the brown capuchin (Cebus apella).* Zeitschrift fur Tierpsychologie 85:177-200.

Janson C. H (1985). *Ecological and social consequences of food competition in brown capuchin monkeys.* Unpublished Ph.D. thesis, university of Washington, seattle.

Janson C.H (1985). *The matting system as a determinant of social evolution in capuchin monkeys (Cebus).* In: J.Else & P. Lee (ed.), Proceeding of the XIIth International Congress of Primatology. Cambridge University Press.

Janson, C. H. (1988). Food competition in brown capuchin monkeys (Cebus apella): quantitative effects of group size and tree productivity. *Behaviour*, *105*(1), 53-76.

Janson, C. H. (2000). *Primate socio‐ecology: the end of a golden age.* Evolutionary Anthropology: Issues, News, and Reviews: Issues, News, and Reviews, 9(2), 73-86.

Kimmins et al. (2008) Complexity in modelling forest ecosystems. How much is enough?. Ecology and Management 256: 1646-1658

Krebs J.R & Davis N.B (1993). *An introduction to Behavioral Ecology.* Blackwell Scientific Publications, Oxford.

Leos-Barajas et al. (2017). *Multi-scale Modeling of Animal Movement and General Behavior Data Using Hidden Markov Models with Hierarchical Structures*. International. Biometric Society Journal of Agricultural, Biological, and Environmental Statistics, Volume 22, Number 3, Pages 232–248. DOI: 10.1007/s13253-017-0282-9

Lieth (1974). *Phenology and Seasonality Modeling.* Ecological Studies Vol. 8. Springer-Verlag Berlin Heidelberg

Linnaeus C. (1758). *Systema Naturae,* ed. 10, vol. I, Regnum Animale. Holmiae.

Lynch, A et al. (2012). *Sapajus apella.* UICN, Union Internacional para la Conservación de la Naturaleza.

Marin, J.M. (2010). *Guía para el análisis de datos.* SPSS10. Disertación Doctoral.

Martin P. &. Bateson P. (2007). *Measuring Behaviour. An introductory guide.* Cambridge University Press.

Martin, R. & Melfi, M. (2016): *A Comparison of Zoo Animal Behavior in the Presence of Familiar and Unfamiliar People*. Journal of Applied Animal Welfare Science.

Maslin, M (2005). *Ecological versus climatic thresholds*. Science, 306, 2197–2198.

McConkey, K.R, et al. (2003). *Influence of forest seasonality on gibbon food choice in the rain forests of Barito Ulu, Central Kalimantan.* International Journal of Primatology 24(1), 19-32.

Morlans (2014). INTRODUCCION A LA ECOLOGÍA DE POBLACIONES . Editorial Científica Universitaria - Universidad Nacional de Catamarca ISSN: 1852-3013

Newstron et al (1994). *A new classification for plant phenology based on flowering patterns in lowland tropical rain forest trees at La Selva. Costa Rica*. Biotropica. 26:141-159.

Riddick, N. (2009). *Factors that Affect Social Hierarchy and the Influence of Social Rank and Menstrual Cycle on Cocaine Self-administration in Female Cynomolgus Monkeys* (Doctoral dissertation, Wake Forest University).

Ryan et al. (1997). *Age-Related Decline in Forest Productivity: Pattern and Process. Advances in Ecological Research, 213–262.*doi:10.1016/s0065-2504(08)60009-4

Salazar (2012). *Recuperación ecologica en tres kilometros de la parte alta de la subcuenca San Pedro en el municipio de Curumaní- Cesar, Colombia.* Tesis Universidad Francisco de Paula Santander, Ocaña.

Schrauf, C., Huber, L., & Visalberghi, E. (2008). Do capuchin monkeys use weight to select hammer tools?. *Animal cognition*, *11*(3), 413-422.

Sinclair & Byrom (2006). Understanding ecosystem dynamics for conservation of biota. Journal of animal Ecology, 75: 64-79.

Silk,J.B (2001). *Primate socioecology.* N. J. Smelser and Paul B. Baltes (editors) 2001 International Encyclopedia of the Social & Behavioral Sciences. Pergamon, Oxford.

Slayback, D. & Pinzon, J. (2003) *Northern hemisphere photosynthetic trends 1982–99*. Global Change Biology, 9, 1–15.

Smuts et al. (1987), *Primate Societies*. University of Chicago Press.

Snodderly, D. M, et al.,(2019*). Initiation of feeding by four sympatric Neotropical primates (Ateles belzebuth, Lagothrix lagotricha poeppigii, Plecturocebus (Callicebus) discolor, and Pithecia aequatorialis) in Amazonian Ecuador: Relationships to photic and ecological factors*. *PloS one*, *14*(1), e0210494

Suarez, S. A. (2014). *Ecological factors predictive of wild spider monkey (Ateles belzebuth) foraging decisions in Yasuní, Ecuador*. American journal of primatology, 76(12), 1185-1195.

Sullivan et al. (2006). *Individual differences in physical activity are closely associated with changes in body weight in adult female rhesus monkeys (Macaca mulatta*). US National Library of Medicine. National Institute of Health. doi: 10.1152/ajpregu.00069.2006

Steinmann A. (2015). *Ecología Comportamental: una introducción al estudio del comportamiento animal*. 2da edición.Resarch Gate.

Stevenson, P.R et al. (1992). *Relación entre la abundancia de frutos y las estrategias alimenticias de cuatro especies de priamtes en La Macarena, Colombia.* Unpublished manuscript. Report to Banco de la República.

Stevenson P.R, et al. (2000). *Influence of Fruit Availability on Ecological Overlap among Four Neotropical Primates at Tiniga National Park, Colombia 1.* Biotropica, 32(3), 533-544.

Stevenson, P. R. (2001). *The relationship between fruit production and primate abundance in Neotropical communities*. Biological Journal of the Linnean Society, *72*(1), 161-178.

Stevenson, P.R et al. (2004). *Phenological patterns of woody vegetation at Tinigua Park Colombia: Methodological comparisons with emphasis on fruit production.* Departamento de Ciencias Biológicas, Universidad de Los Andes. Bogotá, Colombia. Caldasia 26(1) 2004: 125-150

Strier (2000). *Primate behavioral ecology*. University of Wisconsin – Madison., ISBN 0 205-20019-2.

Terborgh, J. (1983). *Five New World Primates: A Study in Comparative ecology.* Princeton University Press.

Terborgh, J. (1992). *Diversity and the tropical rain forest*. Scientific American Library, W. H. Freeman, New York. Xii + 242 pages. ISBN 140-3213-5026-0, (hardback).

Terborgh & Janson (1986). *The sociology of primate groups*. Annual Review of Ecology and Systematics, Vol. 17 (1986), pp. 111-136

Thierry (2008). *Primate Socioecology, the Lost Dream of Ecological Determinism.* Evolutionary Anthropology 17:93–96.

Tiddi et al. (2019). *The impact of food provisioning on parasite infection in wild black capuchin monkeys: a network approach*. Primates, 1-10.

Tutin et al. (1997). *The primate community of the Lopé reserve, Gabon: Diets, responses to fruit scarcity, and effects on biomass.* American Journal of Primatology*,* 42(1), 1–24.

Vargas, S. A., et al. (2014). Population density and ecological traits of highland woolly monkeys at Cueva de los Guácharos National Park, Colombia. In *High altitude primates* (pp. 85-102). Springer, New York, NY.

Visalberghi, E., Addessi, E., Truppa, V., Spagnoletti, N., Ottoni, E., Izar, P., & Fragaszy, D. (2009). Selection of effective stone tools by wild bearded capuchin monkeys. *Current Biology*, *19*(3), 213-217.

Vogel, E. R., & Janson, C. H. (2007). *Predicting the frequency of food‐related agonism in white‐faced capuchin monkeys (Cebus capucinus), using a novel focal‐tree method.* American Journal of Primatology: Official Journal of the American Society of Primatologists, 69(5), 533-550.

Vogel, E. R., & Janson, C. H. (2011). Quantifying primate food distribution and abundance for socioecological studies: an objective consumer-centered method. *International Journal of Primatology*, *32*(3), 737-754.

Williamson (1997). *Primate Socioecology. Development of a Conceptual Model for the Early Hominid.* Doctoral Dissertation. University College London, Gower Street, London, WC 1E 6BT

6. ANEXOS

Material Fotográfico de Soporte

Imagen 1. Hembra adulta con infante dependiente

Imagen 2. Macho alfa de la población (Marco)

Imagen 3. Juvenil (Mike) junto a macho dominante (Negro) tras acicalarlo

Imagen 4. Juvenil (Meelo) comiendo

Imagen 5. Adulto forrajeando en el suelo

Imagen 6. Hembra subordinada vigilante tras ser agredida por el macho alfa