FEEDING ECOLOGY AND HABITAT USE OF THE SENEGAL PARROT

AT FONGOLI: POSSIBLE IMPLICATIONS FOR

SYMPATRIC CHIMPANZEES

by

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DEDICATION

This Master's Thesis is dedicated to the wild chimpanzee community and the wild parrot community of Fongoli, located within Senegal, West Africa. Without your presence, this research would not be possible.

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ABSTRACT

Little is known about the feeding ecology of the West African Senegal parrot (Poicephalus senegalus), and there is no information regarding possible dietary overlap with sympatric chimpanzees (Pan troglodytes verus). Given that parrots and primates share advanced cognition (Emery and Clayton, 2004), larger brain size (Olkowicz 2016) and a complex social system (Harpøth 2013); dietary overlap was hypothesized to be extensive. This study was done from May 2018 to July 2018 at the Fongoli Savanna Chimpanzee Project site, Senegal, with the goals to 1) establish a dietary profile for Senegal parrots, and 2) assess the amount of dietary overlap with chimpanzees in terms of food species and food parts eaten. It was found that Senegal parrot food items do overlap with those of chimpanzees. For example, both species ate Ficus, Saba senegalensis, Lannea mircocarpa, Lannea velutina, and Sclerocarya birrea. Because no direct competition for shared foods was seen during the study, it would suggest competition between Senegal parrots and chimpanzees might primarily be scramble. This study is the first step in providing a more complete picture of dietary overlap and feeding competition between Senegal parrots and chimpanzees.

I. INTRODUCTION

This study explores the relationship between sympatric Senegal parrots and chimpanzees within the savanna mosaic environment of southeastern Senegal. Baseline feeding ecology and habitat data was gathered on the previously unstudied Senegal parrot (*Poicephalus senegalus*) at Fongoli in Senegal, West Africa. This data was compared to feeding ecology data of the Fongoli chimpanzees (*Pan troglodytes verus*), in order to address aspects of community ecology and possible dietary overlap between the two species. If Senegal parrots share sympatric home ranges, overlap in foraging areas, show dietary preference for fruits, and share ecological dietary resources with chimpanzees, then parrots may be possible dietary competitors for these frugivorous apes.

The Competitive Exclusion Principle (Hardin 1960), inspired by Gause's Law (1934), states that for two species that have shared ecological pressures, are limited by similar ecological resources, and exploit the same ecological niche, then competition for resources would arise. This competition would be so fierce that the result would be extinction (typically of the species with less evolutionary fitness), or an evolutionary shift where one species evolves to fulfill a different ecological niche within the shared habitat. In some cases, evolution to fulfill a different niche does not mean abandoning the need for the shared ecological resources, but instead allows for a successful shift in how those ecological resources are accessed to avoid or lessen competition. An example of such change can be seen in blue monkeys (*Cercopithecus mitis*), redtail monkeys (*Cercopithecus ascanius*), and gray-cheeked mangabeys (*Lophocebus albigena*) who evolved different digestive gut microbiomes as a response to the dietary competition with

sympatric chimpanzees (Wrangham and Hunt, 1998). Evolved microbiomes allow these monkey species to digest unripe fruits that chimpanzees are not able to digest, allowing monkeys to access fruits as a dietary resource before chimpanzees are able to. These monkey species that are sympatric with chimpanzees have not abandoned being frugivorous, but instead evolved to lessen competition for ripe fruit. If Senegal parrots and the Fongoli chimpanzees live in the same habitat, have similar dietary preferences, and share ecological dietary resources, then competition would ensue for these limited dietary resources as outlined by the competitive exclusion principle.

Previous documentation of wild African parrot feeding ecology on the Meyer's parrot (*Poicephalus meyeri*) (Boyes and Perrin, 2009), the Black-cheeked lovebird (*Agapornis nigrigenis*) (Warburton and Perrin, 2005), the Rüppell's parrot (*Poicephalus rueppellii*) (Selman, Perrin, Hunter, and Dean, 2002) and the Greyheaded parrot (*Poicephalus fuscicollis*) (Symes and Perrin, 2003) suggested a broad diet, with at least 39 separate food items from 25 species, and a foraging regime from terrestrial to completely arboreal. The majority of research on parrots comes from captive studies done in the last 20 years (Homberger et al., 2006), resulting in a lack of knowledge about wild parrots, with many species still left unstudied (Renton, 2001). The current literature focuses on African and South American parrots, with few publications on Asian species (Renton, 2001). The shallowness of the time depth of parrot research means we have little data on conservation, cognitive abilities, ecology, communication, diet, niche specialization and interspecies competition in the wild.

Of particular interest in this study is possibility for scramble competition between sympatric Senegal parrots and chimpanzees. These species share advanced cognition

(Emery and Clayton, 2004), larger brain size (Olkowicz, 2016) and a complex social system (Harpøth, 2013). Large brain size requires a high calorie diet containing fats and sugars (Emery and Clayton, 2004). Within a harsh environment, such as Fongoli, high calorie diets are only obtainable by eating animal protein (meat/insects) or the reproductive parts of plants (fruits). If frugivorous dietary overlap occurs between chimpanzees and Senegal parrots, then competition between these species may exist.

Senegalese chimpanzee diets, as is the case for these apes' diets elsewhere, is characterized by frugivory (Pruetz, 2006). Dietary studies have been conducted at many other chimpanzee study sites (Table 1), with a consensus that chimpanzees are frugivorous. The Fongoli chimpanzee's diet of 60% fruits is on the lower end of the spectrum for chimpanzees, with other sites having proportions up to 80% (Hunt, 2019). For this study, dietary overlap among Senegal parrots and chimpanzees was analyzed, along with habitat use.

Table 1: Data on Chimpanzee Diet (Hunt, 2019)

Site	Fruit pulp	pith	leaf	insects	meat	flowers	bark	seed
Kibale Chimpanzee	79.0	16.9	2.6	0.0	0.9	0.2	0.2	0.4
Gombe Chimpanzee	63.3	16.5	16.6	3.4	0.3	0.0	0.2	0.0
Mahale Chimpanzee	56.7	19.1	10.6	5.9	0.9	0.1	0.2	6.0
Budongo Chimpanzee	64.5	3.2	19.7	0.0	N/A	8.8	N/A	N/A
Ngogo Chimpanzee	70.7	2.5	19.0	0.0	2.0	2.6	0.0	3.6
Fongoli Chimpanzee	60.8	1.4	4.3	23.7	0.6	5.5	2.3	1.6
Chimpanzee Average	65.8	9.9	12.1	5.5	0.8	2.9	0.8	2.3

The goals of this research were to contribute to a better understanding of wild African parrot feeding ecology, contribute to the knowledge of feeding ecology within the Fongoli frugivore community, and record possible ecological interactions between parrots and primates. The robust beaks of parrots (Tokita, 2004) and preference for low secondary compound foods (Reyes, unpublished data) suggest their diets will overlap with chimpanzees. The secondary aim of this study is to inform discourse regarding whether parrots are possible dietary competitors with sympatric chimpanzees, and therefore could result in possible competitive exclusion. Research questions and hypotheses are found in Table 2.

Table 2: Research Questions

Question	Null hypothesis	Alternative hypothesis
What is the diet of the wild Senegal parrots?	Parrots have a broad diet.	Parrots have a narrow diet.
What parts of the fruit do parrots eat?	Senegal parrots eat only seeds of fruits.	Senegal parrots eat various parts of fruits.
Do chimpanzees eat the same foods as sympatric parrots?	Parrots do not eat the same foods as chimpanzees.	Chimpanzees eat foods that parrots also consume.
What areas of the habitat are parrots most often observed in?		Parrots prefer certain habitat types.
Do chimpanzees use areas that parrots also use?	Parrots and chimpanzees are regularly found in the same areas.	Parrots and chimpanzees are not frequently found in the same areas.
How do parrots react when they see or hear primates?	Parrots do not react to primates.	Parrots react to primates.

II. METHODS

Study Site

A detailed description of Fongoli study site is outlined in Pruetz (2006). Fongoli is located within the southeastern corner of Senegal, West Africa. Senegal is a semi-arid and an open environment, very different from the lush continuous forest where chimpanzees are commonly studied elsewhere in West, East, and Central Africa. The study site is about 10 km from the town and regional capital of Kedougou. The topography of Fongoli is comprised of valleys, plateaus, and hills. Rainfall averages are 900 - 1100 mm annually (Pruetz, 2006). The country experiences short rainy seasons and long dry seasons (Table 3). Southeastern Senegal averaged an annual temperature of 28.2°C / 82.4°F (Pruetz, 2006), from 1961-1990 and averages 33°C /91°F in the month of May (Pruetz, 2006).

The study area is characterized by six major habitat types that are discussed at length within this thesis. The different habitat types are farm field, gallery forest, grassland, woodland, bamboo, and plateau. Birds have been shown to prefer closed habitat types (Chettri et al., 2005). Closed habitat types are defined as having closed tree canopies (where tree crowns are connected) while open habitat types are defined as having discontinuous tree canopies (where tree crowns that are not connected) (Chettri et al., 2005). Habitat types at Fongoli that are characterized as closed includes gallery forest and arguably woodland areas during the rainy season. Conversely, habitat types at Fongoli that are characterized as open include plateau, field, and grasslands. Bamboo is difficult to define because while there is little to no tree coverage, the bamboo poles can grow thickly together and provide coverage. The field site, in the southeastern corner of

Senegal, is within the distribution of Senegal parrots (Figure 1). GPS Coordinates of the study site are 12.7033° N, 12.2548° W.

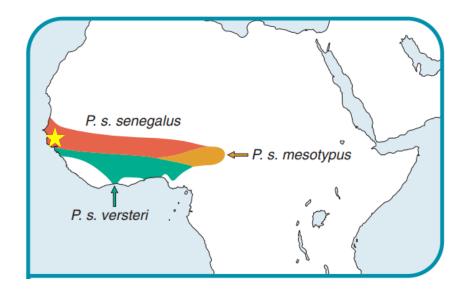


Figure 1: Map showing distribution of Senegal parrots (*P.s. senegalus*) (Forshaw, **2010**). Gold star indicates the location of the Fongoli field site.

Study Subjects

Study subjects included the Senegal parrots (*Poicephalus senegalus*) (Figure 2) and West African chimpanzees (*Pan troglodytes verus*) of Fongoli. Within Senegal, the entire parrot community includes the Senegal parrot (*Poicephalus senegalus*), the Roseringed parakeet (*Psittacula krameri*) and less commonly, the Brown-necked parrot (*Poicephalus robustus*) (Forshaw, 1989). This study exclusively focused on the Senegal parrot. Habitat use and feeding ecology of the other parrot species, which may be in the area during different times of the year, are not addressed within this study. Population densities of *Poicephalus senegalus* at this time are unknown and awaiting anaylses. Wild West African chimpanzees of Fongoli have been studied since April 2001 (Pruetz, 2006). Nest surveys yield a density of 0.09 individuals per square kilometer (Pruetz, 2002, 2006). The Fongoli Savanna Chimpanzee Project (FSCP) collects data by conducting

daily follows on adult male chimpanzees as focal subjects. The chimpanzee troop is comprised of 35 individuals, with 12 of those individuals being adult males.

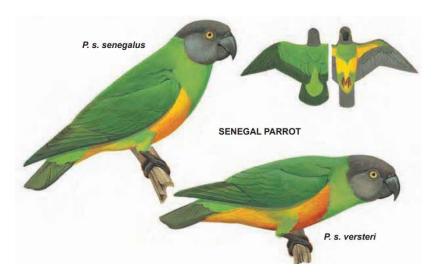


Figure 2: Illustration of a Senegal Parrot (Poicephalus senegalus) (Forshaw, 2010)

Data Collection

Senegal parrots feeding behavior was recorded from May 30 to July 16, 2018. Parrots had 766 individual feeding observations while chimpanzees had 989 individual feeding observations. The total hours of observation for parrots was 312 hours, and the total hours of observations for chimpanzees was 576 hours.

Chimpanzee observational data used in this study was collected by Dr. Pruetz during the same time as parrot observational data was recorded. Chimpanzee data collection was focused on adult male subjects (excluding injured or very ill individuals). All observations were conducted from a distance of at least 10 meters at all times and surgical masks were worn when chimpanzees moved closer, before moving away. Chimpanzees were followed continuously throughout the day, from night nest to night nest, with a data collection group comprised of no more than three observers. Phenology

data was recorded using the same phenology transect monthly, which contains over 900 trees. Diet data was collected during daily follows, with feeding data taken at five-minute intervals.

Parrot observations were completed by the author using tree vigils and, parrot follows when possible, along with reconnaissance transects (also known as "recce transects"). Boyes and Perrin's (2010) work on the Meyer's parrot (*Poicephalus meyeri*) provided methodology that was modified for the current study. The Meyer's parrot is a close genetic relative to the Senegal parrot (Athan and Deter, 1998). Therefore, it was expected that Senegal parrots' diet, foraging methods, and habitat use would be similar, given their similar morphology.

When choosing a tree for tree vigils, *Saba senegalensis* and *Ficus sycomorus* were fruiting at the time of this study and have been reported to be important food items of chimpanzees (Pruetz, 2006) and parrots (Boyes and Perrin, 2010; Forshaw, 1989). Therefore, the author chose them as reliable sources for observing parrot feeding, along with *Vitellaria* and *Lannea* trees. With these food sources, different tree species throughout the study area were surveyed randomly in order to ensure a representative sample of the habitat. Trees that have been reported to be nesting sites for parrots, such a *Saba senegalensis* and *Adansonia digitate* trees in Sakoto ravine (Figure 3), were also surveyed in tree vigils.

Tree vigil data was collected as follows: date, time, weather, tree/food species consumed, type of food consumed, parts of food consumed (fruit pulp, seed, bark, etc.), GPS location of the tree, parrot vocalizations, fecal droppings on trees that morphologically represented parrot droppings, dropped food items at the base of trees

with evidence of parrot chewing/parrot mandible bites, and observation of any primates in the area. Tree vigils were conducted Mondays, Wednesdays, and Fridays, while transect data was collected Tuesdays, Thursdays, and Saturdays. Tree vigils started at 600 hours, breaking for their resting period (between 1100 hours – 1600 hours) (pers. obs.) then continued in the evenings to watch their evening feed and attempted to locate the chosen sleeping tree.

Transect data recording utilized the existing trail system in Fongoli that is currently being used for collecting *Galago* surveys, as well as a separate, existing phenology transect. Six transects were used in total and were labeled as Transect 1, Transect 2, and so on. Each transect was four kilometers in length and included each of the different habitat types of Fongoli (grassland, bamboo, farm fields, woodland, gallery forest, plateau). The author walked one transect per day, at a rate of one kilometer per hour.

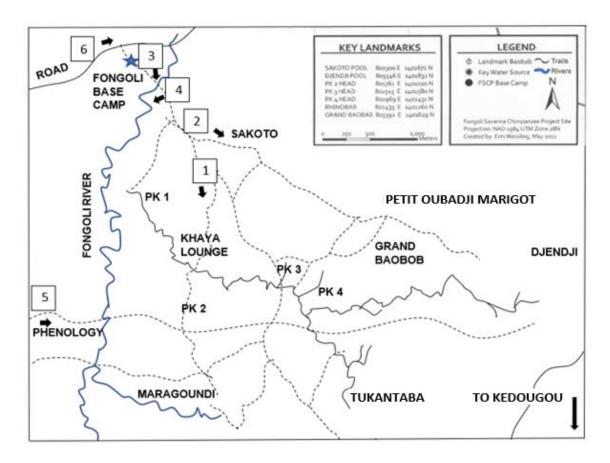


Figure 3: Map of Fongoli Transects. Transect 1: Start in Sakoto and went towards Maragoundi. Transect 2: Start in Sakoto and went towards Tukantaba. Transect 3: Start outside of camp and went out through Sakoto towards the Grand Baobab/Petit Oubadji Marigot. Transect 4: Start outside of camp and went along the Fongoli River. Transect 5: Phenology. Transect 6: Road from camp Fongoli leading towards next village, Bontonkalin (spelling of village may be incorrect).

Transect surveys began at 600 hours and ended at 1100 hours. This time frame for data collection was ideal because Senegal parrots typically feed in the morning after waking from the nest (around 630 hours), settled down throughout the morning for social interaction (pers. obs.). At approximately 1100 hours a small group of parrots would usually rest in one selected tree, while other subgroups of the flock would break off into surrounding individual trees. Resting periods occurred from 1100 hours to approximately 1600 hours (pers. obs.), after which the parrots become active again for feeding. Parrots

fed, moved around, and socially interacted before perching in an evening sleeping tree. Parrots perched in the tree they will sleep in before the sun goes down (at the latest, at 1900 hours) (pers. obs.).

Data recorded for transects included: observer, date, time, length of transect, transect name, weather, time of encounter, habitat parrot was sighted in, detection method, loud or soft call, observed perched or flying, number of parrots observed in a group and the tree name. If the parrot was foraging/feeding, the following data was collected: name of food source, type of food (leaves, pith, seeds, fruit, etc.), parts of food (skin, seed, flesh, etc.), vocalizations of primates, and distance from the transect that parrots were observed (in meters).

When multiple parrots were observed flying, the group size was recorded.

Previous studies found Senegal parrots traveled in small groups (less than 10 typically)

(Forshaw, 1989), and this was found to be the case with the parrots at Fongoli as well.

The only non-human primates observed during parrot observations throughout the course of this study were two monkey species, the patas monkey (*Erythrocebus patas*) and the vervet monkey (*Chlorocebus pygerythrus*). Parrots typically alarm called when monkeys were nearby. Once hearing the parrots' alarm call, monkeys typically left the area. Monkeys may have fled as a result of parrot alarm calls, but they also may have fled from the human observer. Senegal parrots were not personally observed by the author to be in the exact same area as chimpanzees, although this has been observed in the past (Pruetz, pers. comm.). This was surprising since chimpanzees traveled throughout the different habitat types of the Fongoli study site (Pruetz, 2006), and the author observed parrots doing the same.

Due to the openness of the Fongoli landscape and tree canopies, parrot follows were possible during tree vigils. When conducting parrot follows, parrots would exit one tree, their direction of flight would be recorded, and flight was visually observed as they landed in the next feeding tree, typically only a few meters away. The author would then follow to this next tree and continue recording feeding data. If parrots exited one tree and their direction of flight could not be seen to the next tree, the author walked in the direction of flight and used the sound of movement and parrot vocalizations to try and locate parrots. If the parrots were assumed to be in a tree based on auditory observations of parrot calls, the author waited for ten minutes near the tree. After ten minutes, if no visual observations had occurred, the author walked directly towards the tree. If parrots were in the tree, they moved once the author reached the tree trunk. When the author lost a parrot group, a new tree vigil was performed in another location.

To record feeding data, each time a parrot consumed a food item it was counted as a single observation of feeding, also known as one feeding bout. If parrots, for example, ate a fig in one part of the tree, and then flew to a different part of the tree where it consumed a different fig, this was counted as two observations of feedings. Part of the reason for this is parrots are not banded/tagged and therefore the author could not identify individual parrots. The Fongoli Savanna Chimpanzee Project collected chimpanzee feeding data differently, adhering to the Project's standard operating procedures.

Chimpanzee individuals were individually identified, and chimpanzee adult male subjects were followed throughout the day, from night nest to night nest. Feeding bouts are defined as a chimpanzee feeding without interruption of greater than five minutes.

Percentage of feeding observations for each species was used to account for the differences in the data collection methods (Table 5, Table 6).

Data Analyses

A chi square non-parametric test were preformed using BMI SPSS (version 25) under two main assumptions; parrots had the opportunity to select any area of the habitat that was deemed available, and observations were collected in an unbiased manner ensuring that data were randomly distributed. Chi square analysis was performed to determine if parrots utilize each habitat type (bamboo, field, gallery forest, grassland, plateau, and woodland) for foraging in the exact proportion to the habitat type's occurrence within Fongoli. The observed occurrence of parrot feeding bouts were compared with the expected occurrence of parrot feeding bouts for each habitat type. Any expected observations less than five and any category that did not have at least one expected observation was removed from analysis (Dixon and Massey, 1969).

After the chi square analysis was preformed to determine if parrots' used habitat types in exact proportions to which the habitat type occurred within Fongoli, a post hoc test was used to conclude whether Senegal parrots show preference, or avoidance, for certain habitat types (Figure 6).

Research Limitations

This research was limited because parrots were not habituated. However, habituation was not the goal of this project because Senegal parrots are wild caught for the pet trade or the entertainment industry (Evans, 2001). It is for the benefit of conservation efforts that wild parrot populations be unhabituated, and therefore all non-

invasive observations used in this project were made at a distance using a spotting scope or binoculars. The length of study is another major limitation. From May to July is not long enough to truly understand the variation in wild Senegal parrot diets, however this study was only able to be collected during the summer between school sessions. An annual study is needed to fully understand wild parrot diets in this area of Senegal.

IACUC approval (IACUC approval number 20182109177) was obtained for this study prior to data collection. Visibility was not a limitation in this study due to the openness of the study site.

III. RESULTS

The following tables outline the data gathered in order to calculate the percentages of food type categories consumed by Senegal parrots (*Poicephalus senegalus*) and chimpanzees (*Pan troglodytes verus*) at Fongoli. Chimpanzee data was collected by Dr. Pruetz and/or the Fongoli Savanna Chimpanzees Project during the same field season that parrot data was collected (Table 3). Table 3 shows fruit as the highest proportion of food type consumed by both Senegal parrots (77%) and chimpanzees (62%). Within this study, Senegal parrots were frugivorous (Table 3). Chimpanzees across African research field sites are known to be frugivorous (Table 1).

Table 3: Chimpanzee and Parrot Diet Summer 2018. Proportions of food type categories consumed by Fongoli chimpanzees and Senegal parrots during the months of May, June, and July 2018.

Food type	Chimpanzees*	Parrots
Fruit	62%	77.42%
Leaves	20%	0%
Piths/stems/roots	10%	0%
Insects	5%	0%
Meat	3%	0%
Flowers	0%	1.04%
Seeds/other	0%	21.54%
Total	100%	100%

^{*} Fongoli Savanna Chimpanzee Project unpublished data

In order to address preference to fruiting resources for parrots (chimpanzees are known to be frugivorous), phenology data would be needed in order to demonstrate that a majority of fruit is being consumed during a time of low, high, or average fruit availability within the environment. Calculating how much fruit on average is available

within the environment from May 30 to July 16, 2018 (the time period data was collected for this study), comes from the Fongoli Savanna Chimpanzee Project phenology transect. Phenology data is available in the form of monthly averages (Table 4).

Table 4: Monthly fruit availability in Fongoli, shown as a percentage of feeding trees bearing fruit. The number of years per month in this sample is reported in parentheses (Pruetz, unpublished).

Month	Season*	Average & +/- SE	Average rainfall mm +/- SE
January (5)	Dry	9.66 +/- 1.09	0 +/- 0
February (5)	Dry	11.84 +/- 1.38	0 +/- 0
March (4)	Dry	14.84 +/- 3.75	0 +/- 0
April (3)	Dry	18.83 +/- 3.83	8.1 +/- 1.98
May (5)	Transitional	19.38 +/- 1.84	59.5 +/- 4.73
June (3)	Wet	9.20 +/- 2.55	164.4 +/- 4.97
July (4)	Wet	9.54 +/- 2.49	231.7 +/- 9.84
August (4)	Wet	12.99 +/- 13.79	214.2 +/- 13.79
September (5)	Wet	12.02 +/- 2.93	283.2 +/- 20.52
October (5)	Transitional	8.85 +/- 2.58	99.9 +/- 10.72
November (5)	Dry	8.28 +/- 1.95	1.3 +/- 0.41
December (4)	Dry	10.61 +/- 2.85	0 +/- 0
Annual Monthly Average		12.17 +/- 1.08	88.5

^{*} Monthly precipitation and temperature records from Pruetz and Bertolani (2009), Bogart and Pruetz (2011) and Pruetz et al. (under review).

In Table 4, the month of May was a transitional time between the wet and dry season, with an above annual monthly average fruit availability (avg. 19.38, SE +/- 1.8). Parrot feeding data was only collected at the end of May, beginning on May 30. Data was collected throughout the entire month of June, which was categorized as wet and as time

of below average fruit availability (avg. 9.20, SE +/- 2.55). Data for this study was collected for half of July, until July 16, which was also a wet month, as well as a month of below average fruit availability (avg. 9.54, SE +/- 2.49).

During transects, encounter rates of parrots were higher within certain habitat types, however Senegal parrots were observed throughout the study site, across the different habitat types (farm fields, gallery forest, grassland, woodland, bamboo, and plateau). Encounters were often, with an average encounter rate of once every 20 minutes. Within the total 312 hours of parrot observations, 766 individual observations of parrot feedings were recorded. Total hours observed for chimpanzees was 576 hours, and chimpanzees were recorded feeding 989 time.

Senegal parrots consumed 15 different food species (Table 5). Parrots ate fruit pulp from eleven food species, seeds from three species, and flowers from one species. No consumption of piths or leaves were recorded. Out of the total 766 individual observations of parrot feedings, 593 times they fed on fruit pulp, 165 times they fed on seeds, and eight times they fed on flowers.

Table 5: Parrot food list May to July 2018 from Transects

Parrot Foods (15 total) Scientific name	Types of Food Consumed	Parts of Food Consumed	Number of Total Observations	%
1. Agneissus	S	W	68	8.88%
2. Adansonia digitate	F	W	48	6.27%
3. Bombox costatum	F	FP	12	1.57%
4. Cola cordifolia	F	S	6	0.78%
5. Combretum lecardi	F	W	3	0.39%
6. Ficus	F	W	119	15.54%
7. Lannea microcarpa	F	W	135	17.62%

8. Lannea Velutina	F	W	25	3.26%
9. Parkia biglobosa	F	S	4	0.52%
10. Pterocarpus erinaceus	S	S	89	11.62%
11. Pterocarus Lucnas	FL	W	8	1.04%
12. Saba senegalensis	F	FP	56	7.31%
13. Sclerocarya bierrea	F	FP	24	3.13%
14. Terminalia macroptera	S	S	8	1.04%
15. Vitellaria paradoxa	F	FP	161	21.02%

Food Type Key: F - fruit (u - unripe, r - ripe), L - leaves/shoots (n - new), C - bark/cambium, fl - flower/inflorescence, P - pith/stem, M - leaves swallowed whole, possibly for medicinal purposes, S - seed.

Food Parts Key: W – whole food, FP -Fruit pulp, FS – seed of fruit, S – seed, L – leaves, FL – flower.

In comparison, chimpanzees fed from 27 different food species, including six mammalian species (Table 6). Chimpanzees ate fruit pulp from 15 food species, leaves from five food species, and piths from one food species. Chimpanzees ate meat from six different mammalian species. Chimpanzees were recorded feeding 989 individual times with 609 times they fed on fruit, 103 times they fed on piths, 224 times they fed on leaves, and 62 times they fed on meat.

Table 6: Chimpanzee food list May to July 2018

rusic or chimpunzer	2004 225 21269 40	J 441,		
(27 total)	Types of Food Consumed	Parts of Food Consumed	Number of Observations	%
Scientific name				
1. Adansonia digitata	F (u,r) fl, L, C	W	43	4.36%
2. Baissea Multiflora	L	L	119	12.06%
3. Bombax costatum	F (u), fl	W	13	1.32%
4. Cisscus populnea	F.P	W	13	1.32%
5. Cola cordifolia	F (u,r)	FP	31	3.14%
6. Cordyla pinnata	F	W	52	5.27%

7. Ficus	F,M, L, P, C	W	85	8.61%
ingens/sur/umbellata		***	10	1.010/
8. Hexalobus monopetalus	F (u r), L	W	10	1.01%
9. Hymenocardia	L (n), fl	L, FL	25	2.53%
acida	_ (/,	_,		_,,,
10. Lannea	F	W	43	4.36%
microcarpa				
11. Lannea velutina	F	W	29	2.94%
12. Oxytenanthera	P. L (n)	L	103	10.44%
abbysinicia	1 · L (II)	L	103	10.1170
13. Parkia biglobosa	F	W	23	2.33%
14. Pterocarpus	L (n, m),C, fl	L, FL	64	6.48%
erinaceus	L (II, III),C, II	L, I L	0-1	0.4070
15. Saba senegalensis	F (r. 11). P	W	260	26.34%
15. Buba benegatensis				
16. Sclerocarya	F	W	1	0.10%
bierrea				
17. Smilax anceps	L	L	12	1.22%
18. Vitellaria	F(r)	W	1	0.10%
paradoxa				
19. Ximenia	F	W	2	0.20%
americana				
20. Zizyphus	F	W	3	0.30%
mauritania &				
mucronata				
21. Zehneria	L(n)	L	4	0.41%
thwaitesii				
Mammalian Prey				
List				
22. Galago	Meat	M	11	1.11%
senegalensis				
23. Tragelaphus	Meat	M	3	0.30%
scriptus				
24. Papio papio	Meat	M	1	0.10%
25. Apis mellifera	Meat	M	8	0.81%
26. Spodoptera	Insect	M	1	0.10%
exempta				
27. Oecophylia	Insect	M	29	2.94%
longindoa				

Types of Foods Key: F - fruit (u - unripe, r - ripe), L - leaves/shoots (n - new), C - bark/cambium, fl - flower/inflorescence, P - pith/stem, M - leaves swallowed whole, possibly for medicinal purposes, S - seed.

Food Parts Key: W – whole food, FP -Fruit pulp, FS – seed of fruit, S – seed, L – leaves, FL – flower. Animal flesh - M

When comparing dietary overlap parrots and chimpanzees shared 11 food species (Table 7). Of these 11 shared items, all are fruit resources. These fruits also have higher proportions out of total observations which may be interpreted to mean that parrots and chimpanzees not only overlap in dietary fruiting resources, but those fruiting resources (such as saba and fig) may also be preferred dietary items for both chimpanzees and Senegal parrots (Table 7).

Table 7: List of overlap food items between Senegal parrots and West African chimpanzees during May to July 2018. % indicates proportion out of total observation hours.

Dietary Overlap Items	Parrots %	Chimpanzees %
1. Adansonia digitate	6.27%	4.36%
2. Bombax costatum	1.57%	1.32%
3. Cola cordifolia	0.78%	3.14%
4.Ficus ingens/sur/umbellate	15.54%	8.61%
5. Lannea microcarpa	17.62%	4.36%
6. Lannea velutina	3.26%	2.94%
7. Parkia biglobosa	0.52%	2.33%
8. Pterocarpus erinaceus	11.62%	6.48%
9. Saba senegalensis	7.31%	26.34%
10. Sclerocarya birrea	3.13%	0.10%
11. Vitellaria paradoxa	21.02%	0.10%

The two different data collection methods for parrot feeding, transects and tree vigils, produced similar results. *Vitellaria paradoxa* shows a higher value for transect

(orange bar, Figure 4) data than for tree vigil (blue bar, Figure 4) data even though tree vigils were conducted at *Vitellaria paradoxa* trees, demonstrating how data collection results were not skewed towards tree vigils (Figure 4). In terms of which method is the most comparable to the chimpanzee diet data results, with the exception of *Lannea* tree vigil data, it seems the transect data is more comparable. This may be because of the systematic method in which transects are conducted. Transects also survey a larger sample of trees, while tree vigils focus on a limited number of tree species.

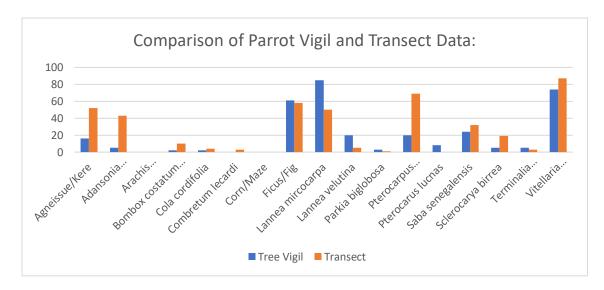


Figure 4: Comparison of parrot vigil and transect data. The graph displays parrot feeding data of different food item through the two different methods used to observe parrots; tree vigil and transects. The graph illustrates the differences in the amount of observations of different foods in regard to the method used to observe parrots.

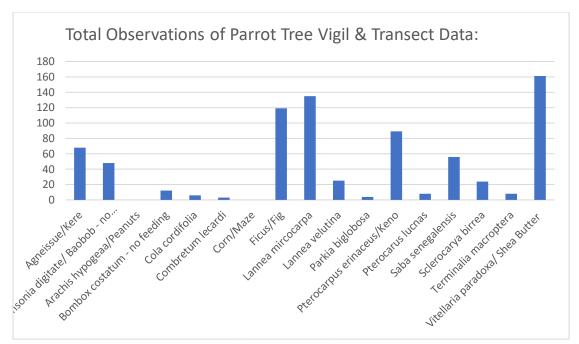


Figure 5: Combined total data of food sources from both tree vigil and transect data for parrots. Bars show which foods were observed being consumed the most frequently.

Below are the calculated habitat proportions for each of the four kilometer transects (Table 8). These values were used as the expected values for a chi square analysis for habitat use. For transects, a total of 24,000 meters of the Fongoli landscape was surveyed. Of this, 16.5% was bamboo habitat, 4.1% regenerating farm fields, 8% gallery forest, 3.7% grassland habitat, 20.2% plateau, and the largest proportion 46.8% is woodland (Table 8). The gallery forests were broken into small patches spread throughout the Fongoli landscape. The landscape of Fongoli is often described as a mosaic (Pruetz, 2006).

Table 8: Habitat Proportions. Total proportions were calculated by each transect being 4,000 meters, multiplied by six transects, gives a total of 24,000 meters surveyed.

Habitats	Bamboo		Gallery Forest	Grassland	Plateau	Woodland
Transect 1	0%	8.3%	0%	0%	41.7%	50.1%
Transect 2	36.3%	0%	10.5%	22%	18%	13.3%

Transect 3	63%	0%	38%	0%	0%	0%
Transect 4	2.3%	0%	1.8%	0%	46%	50%
Transect 5	0.5%	4%	0%	0%	4.1%	78.2%
Transect 6	0%	12.5%	0%	0%	0%	87.5%
Total meters surveyed:	4059m	990m	1990m	880m	4842m	11239m
Proportion of out 24,000 meters	16.5%	4.1%	8%	3.7%	20.2%	46.8%

A chi square test was conducted on the habitat use of Senegal parrots relative to the proportion of each habitat type along transects surveyed (Table 9). This chi square test revealed a significance in that parrots do not utilize each habitat type for foraging in the exact proportion of each habitat types occurrence within the study area. Instead of using habitat types proportionately, parrots show preference and avoidance for certain habitat types. In short, the parrots avoided bamboo, grasslands, and plateau, but preferred farm fields and gallery forests (Table 10).

Table 9: Habitat use proportions of Senegal parrots

Habitat Types	Total meters surveyed	Proportions (%) of total habitat	# of parrots observed (n) in each habitat	# of parrots expected in each habitat	Proportions (%) observed in each habitat type
Bamboo	4,059m	16.9%	17	27.2	10.5%
Field	990m	4.1%	26	6.6	16.1%
Gallery Forest	1,990m	8.3%	24	13.4	14.8%
Grassland	880m	3.7%	10	6.0	6.2%

Plateau	4,842m	20.2%	10	32.7	6.2%
Woodland	11,239m	46.8%	75	75.8	46.30%
Total:	24,000m	100%	162	161.9	100%

Table 10: Overall Chi Square Test.

TT 114 AT			(O T) 2	C1 101
Habitat Types	Observed	Expected	$\frac{(O-E)^2}{E}$	Significance
*Bamboo	17	27.2	3.825	Significant = avoidance
*Field	26	6.6	57.02424	Significant = preference
*Gallery Forest	24	13.4	8.385075	Significant = preference
*Grassland	10	6	2.666667	Significant = avoidance
*Plateau	10	32.7	15.7581	Significant = avoidance
Woodland	75	75.8	0.008443	Not Significant
Total:	162	161.9	6.18E.05	

^{*} indicates significant difference between observed and expected. **Overall chi square value = 87.667, p-value = 9.2389, df = 5

To conduct analyses of habitat type use, the observed number of parrots was divided by the expected number of parrots per habitat type based on the proportion of habitat type available along transect surveyed at Fongoli (Table 11).

Table 11: Observed versus expected calculations

Habitat Types	Observed	Expected	Observed/Expected
Bamboo	17	27.3	0.65
Field	26	6.6	3.94
Gallery Forest	24	13.4	1.79
Grassland	10	6.0	1.67
Plateau	10	32.8	0.31
Woodland	75	75.9	0.99
Total:	162		

Next, parrot use of each habitat type (Figure 6) shows preference via the ratio of observed parrots divided by expected parrots (Table 11) in relation to habitat type by increasing preference.

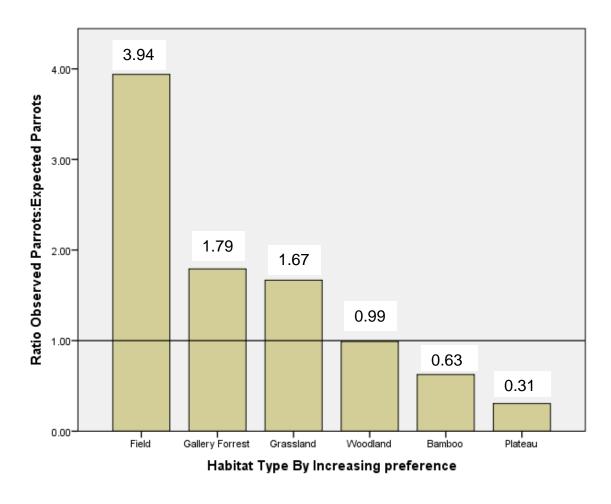


Figure 6: Habitat type by increasing preference. Observed/Expected ratios are listed above bars.

The woodland habitat type were used by parrots in the same proportion that woodland habitat occurs within Fongoli, indicating a lack of preference or avoidance (Figure 6). Bamboo habitat type were observed being used by parrots less than expected, indicating avoidance. Plateau habitat type were also observed being used by parrots much less than expected, indicating avoidance. The field habitat type was observed being used by parrots much more than expected, indicating preference. The gallery forest habitat type was observed being used by parrots more than expected, indicating preference. A post hoc was preformed to determine which individual habitat types were shown preference or avoidance by parrots (Table 12).

Table 12: Post Hoc Test Results.

Habitat Types	Observed	Expected	(O-E) ² E	Post hoc Values	Significance: Preference/ Avoidance
Bamboo	17	27.2	3.825	-	Not Significant
*Field	26	6.6	57.02424	P < .005	Preference
Gallery Forest	24	13.4	8.385075	P < .15	Trending toward Preference
Grassland	10	6	2.666667	-	Not Significant
*Plateau	10	32.7	15.7581	P < .01	Avoidance
Woodland	75	75.8	0.008443	-	Not Significant
Total:	162	161.9	6.18E.05		
				87.667	chi square statistic
				9.2389	p value
				5	degrees of freedom

^{*} indicates significant difference between observed and expected. **Overall chi square value = = 87.667, p-value = 9.2389, df = 5

When reviewing the initial chi square test results, all habitat types were important for parrots except for the woodland habitat type. However, using a post hoc test (Table 12), only two habitat types were significant, with field being significantly preferred (p < .005) and plateau being significantly avoided (p < .01), and gallery forest trending towards preference (p < .15), but was not significant.

IV. DISCUSSION

There were several major goals in this study of Senegal parrots (*Poicephalus senegalus*) and chimpanzees (*Pan troglodytes verus*) at the Fongoli study site in Senegal. I aimed to describe the diet of Senegal parrots, to estimate any dietary overlap with sympatric chimpanzees, and if dietary overlap was confirmed, to see how parrots and chimpanzees coexisted at the Fongoli.

Senegalese Parrot Diet

There is a notable lack of Senegal parrot literature. There seems to be only two published articles where the sole research subject was the Senegal parrot (Demery et al., 2011; Brooks et al., 1983). Research has been conducted where Senegal parrots, along with other different parrot species, are the study subjects of captive research (McDonald et al., 2015; Evans, 2011; Athan et al., 1998; Straub et al., 2002). Wild Senegal parrot habitat use, diet or feeding ecology remains vastly under studied. Forshaw's (1989) book seems to be the best source for information on wild Senegal parrots, but contains only one and a half pages devoted to information on distribution, breeding season, and personality characteristics of the Senegal parrot, underscoring how little is known about the species.

In this study, Senegal parrot flock numbers (individuals within a flying group) remained constant throughout the time frame observations were recorded. There was no difference in Senegal parrot diet from May to July 2018; they ate the same food items throughout the duration of this study. The research presented in this study show Senegal parrots within Fongoli mainly consumed fruits. Fruits may be a preferred food item given the phenology data (Table 4). For some fruits with larger seeds, such as *Sclerocarya*

birrea and Vitellaria paradoxa, parrots only consumed the fruit pulp then discarded the seed once finished (pers. obs.). For seed items that are consumed (Pterocarpus erinaceus and Terminalia macroptera), the seed is directly consumed, and all fruit pulp is chewed away and discarded (pers. obs.).

In comparison, the Senegal parrot's close relative the Meyer's Parrot (*Poicephalus meyeri*) has been studied in some depth by South African researchers (Boyes and Perrin, 2010; 2009). where they attempted to gather feeding ecology data and habitat usage data. The authors found for Meyer's parrots that the highest proportion of their diet consisted of 62% seed predation. The authors concluded seeds were the preferred food type of the Meyer's parrot and that fruit pulp only consumed as a byproduct of seed predation (Boyes and Perrin, 2010). It may be that the closely related Meyer's parrot and Senegal parrot differ in their dietary preferences because of the ecological differences between the South African Botswana environment of the Meyer's parrot and the West African Senegal environment of the Senegal parrot. Senegal climate contrasts with Botswana, in that Senegal tends to have hotter temperatures on average (Thiam and Singh 2002; Kruger and Shongwe 2004).

In this study, parrots preferred field and gallery forest habitat types at Fongoli, while bamboo and plateau were avoided habitat types. Parrots may prefer field habitat types as they tend to be a reliable food source (Forshaw, 1989) for parrots, and local Senegalese people reported parrots raiding their crops, especially in August as maize and peanuts are being grown at that time (D. Kante, pers. comm.). Fields that are in the process of regrowth after a planting season have low growing trees. Senegal parrots in this study were observed perching in field trees and appeared to be camouflaged due to

the thick, new foliage cover. Gallery forest is a habitat type that typically contains parrot food resources (Renton, 2001). In this study, Senegal parrots ate mostly fruit food sources, and most fruiting trees were found within patches of gallery forest in the Fongoli study area. This results in gallery forest being a preferred habitat type, likely for its increased food availability in comparison to other habitat types. Bamboo habitats likely contain little food for parrots, while open plateau habitat types likely contain no food for parrots as they are categorized by having no tree cover. Parrots' preference and avoidance of certain habitat types may be a result of how much food resources and tree coverage are available within each habitat type.

Parrots face different ecological circumstances in dry forests habitats such as Fongoli, then parrots who may live within a lush continuous canopy of a rain forest. A few dry habitat parrot species have been studied in terms of diet and habitat use, mainly within South American species (Renton, 2001; Gilardi, 1997; Gilardi and Munn, 1998; Ragusa-Netto, 2007; Masello et al., 2006).

Within the lowland Atlantic forest of Brazil, Galetti studied six sympatric parrots and parakeet species (Gilardi, 1997). Galetti reported body mass and fruit hardness as being correlated, suggesting large parrots can access hard and soft fruits, while smaller parrots focus on soft fruits. Galetti described the six species living within a dry forest to be frugivorous along with consuming seeds, suggesting it may be a trend of dry habitat parrots living within a hot, resource patchy landscape. Temperatures of Brazil in this region reached on average 26.8°C (Gilardi, 1997) during the dry seasons, similar to Fongoli temperatures. Parrots typically migrate, following patterns of food abundance (Gilardi, 1997), however *Psittacidae* in this area were reported to be at the study site

year-round, similar to the reports in this study of the Senegal parrots remaining in Fongoli year-round. *Psittacidae* were reported by Galetti (1997) to raid orchards to consume seeds of oranges, similar to how Fongoli Senegal parrots have been reported to raid farmer's crops. Galetti (1997) reported *Psittacidaes* to prefer to feed on the understory of trees and at forest edges.

Masello (2006) studied the burrowing parrots of north eastern Patagonia,
Argentina, which is a dry forest. In this environment, burrowing parrots (*Cyanoliseus patagonus*) form large flocks up to 263 members. Masello (2006) describes a daily activity pattern similar to this study's observations of Senegal parrots, where parrots alternate throughout the day between periods of resting and foraging/feeding. Masello (2006) reported burrowing parrots to preform long daily movements due to the distance between patches of food resources. The patchiness is a consequence of human activity (Masello, 2006), a similar threat Senegal parrots face in Fongoli.

Gilardi and Munn (1998) studied multiple species of the Peruvian Amazon parrots and reported similar habitat use as in this study, in that Peruvian Amazons used all habitat types throughout the study area, showing preference for areas with increased tree cover. They reported parrots to make long day ranges for foraging because the dry landscape of Manu National Park is a mosaic were resources are distributed in a patchy manner (Gilardi and Munn, 1998). Fongoli is a mosaic landscape with resources occurring also in a patchy nature (Pruetz, 2006) therefore it can be predicted that Senegal parrots may have long day ranges for foraging, such as Peruvian Amazon parrots (Gilardi and Munn, 1998).

Renton (2001) studied habitat and diet of Lilac-crowned parrots (*Amazona finschi*) of Western Mexico, a dry forest with patchy resources. Food sources were reported to be in abundance during the rainy season. Renton (2001) reports Lilac-crowned parrots to be seed predators as their main diet, however diet flexibility is reported. Seasonality is reported to greatly affect dietary choices (Renton, 2001). Lilac-crowned parrots use all available habitat types and seemed to demonstrate spatial memory of seasonal food resources (Renton, 2001). Renton (2001) states parrots exhibit a narrow food niche during the late dry season, for food availability decreases in the dry season. Lilac-crowned parrots were not reported to migrate and instead stay within the study area year-round (Renton, 2001). Senegal parrot have also been observed within the study area year-round (Pruetz, per. comm.) and therefore are also assumed to not migrate. Seasonality can be assumed to play a large role in Senegal parrot annual diet, just as it was reported to affect Mexican Lilac-crowned parrot diet annual diet (Renton, 2001).

Ragusa-Netto (2007) studied the Green-cheeked parakeet (*Pyrrhura molinae*) in the dry habitat of Western Brazil. The Green-cheeked parakeet is a small bodied bird, much like the Senegal parrot. Seasonality plays a large part in dietary choices and food availability of this species (Ragusa-Netto, 2007). Parakeets consumed a frugivorous diet, along with seeds. Figs are a preferred food item of Green-cheeked parakeets making up 70% of the diet (Ragusa-Netto, 2007). Parakeets were reported to move throughout the entire study site, occupying all habitat types in order to forage for fruits which are a distributed across the landscape in a patchy nature, but they did not migrate (Ragusa-Netto, 2007). Senegal parrots were also reported to move throughout the entire study area

of Fongoli like the Green-cheeked parakeet, this may provide more evidence that dry forest parrots, including Senegal parrots, have increased day ranges.

From the literature, it seems parrots follow certain patterns when living in hot, dry forest landscapes. Literature reports parrots living in a variety of flock sizes (Forshaw, 1989; Masello, 2006), which proposes the idea that size of flock may not be directly controlled by living in a dry, hot forest. Across the globe, it seems dry hot forest landscapes are patchy in nature (Masello, 2006). Fruit is also a patchy source that is distributed across habitat types in clumps (Ragusa-Netto, 2007). This causes parrots to have a long day ranges for foraging. Parrots seem to be more frugivorous in dry, hot landscapes than wet rain forest landscapes. Senegal parrots, in this study, consumed a diet with the highest proportion being fruits, and the second highest proportion being seeds, which may be a similarity to parrots living in dry environments elsewhere.

Given the patchy nature of fruiting resources, dry habitat parrots seem to have an increased spatial memory in order to track locations of dietary resources, and track individual trees that fruit at different times of the year (Renton, 2001). Seasonality had an impact on the diets of all dry habitat parrots/parakeets in the studies reviewed (Renton, 2001; Gilardi, 1997; Gilardi and Munn, 1998; Ragusa-Netto, 2007; Masello et al., 2006). In the studies reviewed, none of the parrots migrated with all dry habitat landscape parrots being present in the study area year-round. Within this study, Fongoli Senegal parrots, within the time frame of this study, followed these trends and have similar habitat use and feeding ecology of parrots in dry, hot landscapes studied elsewhere (Renton, 2001; Gilardi, 1997; Gilardi and Munn, 1998; Ragusa-Netto, 2007; Masello et al., 2006).

Parrot and Chimpanzee Coexistence

A general survey of the habitat and estimations of chimpanzee population numbers have already been published (Morgan, et al., 2006; Plumptre et al., 2006; Pruetz, 2002; Blom et al., 2001; Sugiyama et al., 1988; Tutin and Fernandez, 1984) and the Fongoli chimpanzees has been studied for a little under two decades by Pruetz. Chimpanzees are the best studied of all the wild mammals due to long term study sites, such as Jane Goodall's Gombe Stream National Park in Tanzania, which has been researching chimpanzees for nearly 60 years (Goodall, 2013), as well as multiple, newer, long-term study sites (Wilson et al. 2012).

At Fongoli, chimpanzees are sympatric with parrots and both species have been observed traveling throughout the entire Fongoli study area (per. obs.). Although Senegal parrots (*Poicephalus senegalus*) and chimpanzees (*Pan troglodytes verus*) were never observed in any tree simultaneously during this study, they did show dietary overlap in fruit species. Chimpanzees and Senegal parrots were shown within this study to follow a frugivorous diet and all food times that overlapped between the two species' diets were fruiting resources (Table 7). Overlap items had relatively high proportions, meaning those fruiting dietary items may also be items of preference for both species, such as saba and figs (Table 7).

It is important to note that birds are not a prey item of Fongoli chimpanzees as they are at other field sites (Morris and Goodall, 1977). Therefore, predator avoidance cannot explain the lack of parrot-chimpanzee cofeeding.

Feeding competition, being the interest in this study, can take two main forms; contest and scramble. Contest competition is defined as limited resources being

monopolized by only one or a few individuals (Van Noordwijk and Van Schaik, 1988). In primates, contest competition typically takes form in the way of a dominate individual, or a dominate group (such as a macaque matriarchy), monopolizing limited food resources from other lower ranking group members (Isbell, 1991). This is different from scramble competition where resources are not monopolized by a single individual (or single small group) but instead all members of the group, or all members of the ecosystem, are able to gain access to the resource (Colegrave, 1994). How an individual gains access to a certain resource is often a product of evolutionary strategy (Colegrave, 1994), such as monkeys in Kibale, Uganda arriving to a tree first to consume unripe fruit while chimpanzees must wait to enter the tree at a later time to feed, once the fruit has ripened (Wrangham and Hunt, 1998).

Because of the amount of dietary overlap, it may be that parrots and chimpanzees likely experienced scramble competition during this study. Areas of use by parrots and chimpanzees within the Fongoli habitat do overlap, with the species accessing those shared spaces at different times. Observations revealed that parrots and chimpanzees eat from the same individual foraging trees but at different times (and/or on different days). In this study, chimpanzees and parrots feed on the same food species, same parts of the food species (fruit pulp), and are doing so roughly at the same time of year, therefore this study suggest they engage in scramble competition.

Alternately, the coexistence of parrots and chimpanzees at Fongoli could be explained as niche separation. It is of interest which parts of the tree are Senegal parrots and chimpanzees using. Given the difference in body weight between the species, with chimpanzee male body weight averaging 88–132 pounds (Uehara and Nishida, 1987)

and Senegal parrot male body weight averaging 120 to 170 grams (Prinzinger and Hänssler, 1980), one can hypothesize that they may forage in different sections of a single tree. Parrots can be presumed to be feeding on terminal branches while chimpanzees may be assumed to be feeding more center to the tree, given their heavier body weight. However, Pruetz has observed chimpanzees frequently pulling branches inward towards the trunk of the tree in order to feed off the terminal ends of branches (FSCP, unpublished data). If parrots and chimpanzees do use different parts of a single tree, niche separation is possible.

Personal observations of parrots when chimpanzees were vocalizing indicated chimpanzees and parrots may listen in to each other's vocalization when navigating around the landscape. This may be occurring in order for chimpanzees and parrots tell the location of where possible shared dietary resources may be found within the landscape. This could be evolutionary advantageous as it could act as an ecological strategy to increase foraging efficiently. By listening, an individual can lower its energy expenditure by traveling around the landscape less in search of food, another possible reason this could be evolutionary advantageous. Chimpanzees have been reported to listen to bird food calls in other areas of Africa. In Kibale Forest Uganda, Hauser and Wrangham (1990) reported frugivorous birds and chimpanzees responding to each other's food and predator calls. They concluded this may occur because chimpanzees may benefit in interspecific competition for frugivorous resources. The bird species reported to have such interactions with chimpanzees are often hornbills (Ceratogymna elata) (Rainey and Zuberbuhler, 2004). Given that parrots are often sympatric with chimpanzees across Africa and, as presented in this study, can follow a frugivorous diet, it can be

hypothesized parrots and chimpanzees may listen to one another calls for similar ecological benefits.

V. CONCLUSIONS

Previous literature states that Senegal parrots (*Poicephalus senegalus*) eat mostly seeds (Forshaw, 2013). However, within this study Senegal parrots were shown to be primarily frugivorous, along with consuming seeds. Phenology data (Table 4) showed that during the time observations were collected (May 30, 2018 – July 16, 2018) fruit availability was lower than other times of the year and was lower than the monthly annual average. With parrots eating up to 77% fruits (Table 3) during a time of low fruit availability, it can be concluded that Senegal parrots show preference to fruit as a dietary resource and therefore may be categorized as frugivorous. Further investigation of Senegal parrot feeding ecology in terms of a year-round study is needed to determine if Senegal parrots follow a frugivorous diet year-round.

This study was a first attempt to gather basic data of Senegal parrot feeding ecology in order to obtain a more holistic view of community ecology within Senegal. Primatologists tend to focus on nonhuman primates, to the exclusion of other species living in the same environment (Collins, 2003). Typical discourse includes chimpanzees living among, interacting and possibly being influenced by other primates, such as monkeys, but rarely do researchers consider other non-primate animals being possible ecological competitors. Primates live in habitats full of other animals, each playing their own part of the community ecology that dictates their individual ecology (Webb et al., 2002; Chapman, Wrangham, and Chapman, 1994). For this research chimpanzees (*Pan troglodytes verus*) were studied in conjunction with parrots, with each species competing for limited food availability in an environment where the conditions were extreme.

The main research questions proposed at the start of this study were successfully answered. Parrot and chimpanzee food sources within the study site did overlap. Both Senegal parrots and chimpanzees have sympatric home ranges and foraging areas, and the food source consumption choices were nearly identical, with a focus on frugivory. In reference to the competitive exclusion principle (Hardin 1960), Senegal parrots and chimpanzees may be competing through scramble competition over limited food availability during the transition from day to rainy seasons.

Monkeys have been known to compete with chimpanzees through scramble competition (Wrangham et al., 1998) with the theory being based in shared ecology, ancestry, and similar evolutionary pressures. Parrots and chimpanzees do not share a recent ancestry, unlike monkeys and chimpanzees who do. However, scramble competition still ensues between the two species, which may be related to their similarities of advanced cognition (Emery and Clayton, 2004), larger brain size (Olkowicz, 2016), complex social system (Harpøth, 2013), and a preference to avoid secondary chemical compounds in food resources (Reyes, unpublished). Fueling an advanced cognition due to the increased amount of neuron connections in the brain (Olkowicz 2016) requires a high calorie diet. In a habitat such as Fongoli, one of the ways to obtain a high calorie diet is to eat meat, insects, and/or eat fruits (Gebhardt, 1994; Bogart and Pruetz, 2011). Chimpanzees eat meat, fruits, and insects (Table 6), while parrots in this study were shown to be frugivorous (Table 3). These similarities can cause similar ecological and evolutionary pressures on the individual species, resulting in the possibility that parrots, and chimpanzees may have undergone convergent evolution (Emery and Clayton, 2004).

Scramble competition does not necessarily only occur between species of similar intellectual ability. For example, the red seed weevil (*Smicronyx fulvus*) damages seeds to the point where they can no longer be consumed. Female red seed weevils lay their eggs in seeds, then when the eggs catch, larvae eat most of the kernel before falling out of the seed (Lombardo, 2009). For animals who are primary seed predators, such as some bird species (Howe, 1990), the red seed weevil would be in scramble competition with those animals for access to the seed resource. Scramble competition inherently does not have to do directly with similar intellectual ability, however similar intellectual ability or simply being more highly cognitive may play a role in scramble competition between parrots and chimpanzees. Given their limitation of a high calorie diet due to intellect, this may contribute to a more selective nature of dietary resources and may make competition for those rare resources more intense.

This study of parrot and chimpanzee feeding ecology only covered the months of late May to early July and therefore is a limited representation of what parrot and chimpanzee feeding ecology may look like year-round. Seasonality is assumed to play a large part in diet selection in such an extreme environment as Fongoli. This seasonality factor would result in parrot diets differing throughout the year, as has been shown with chimpanzees (Conklin-Brittain et al., 1998; Wrangham et al., 1998; Yamagiwa and Basabose, 2006, Pruetz 2006, Bogart and Pruetz, 2011). In future directions, an annual study is desired to gain a more representative sample of chimpanzee and parrot feeding ecology and how it fluctuates throughout one calendar year.

APPENDIX SECTION

Photos of Senegal Parrot food items that were collected during fieldwork in Senegal, West Africa. All photos were taken by Kaleigh Reyes, 2019. Arrows will show where parrot bites have taken place on fruit(s).



Shea Butter (*Vitellaria* paradoxa) fruit. Top fruit with steam is parrot eaten fruit, bottom fruit was hand dissected by Kaleigh Reyes to examine parts of fruit.



Shea Butter (*Vitellaria* paradoxa) fruit. Top is parrot eaten fruit.

Bottom/Right is fruit cut open by Kaleigh Reyes, with seed removed to show size of seed and skin layer.



Shea Butter (*Vitellaria* paradoxa) fruit. Top fruit is parrot eaten, bottom is whole (uneaten/untouched) shea butter fruit.



Shea Butter (*Vitellaria paradoxa*) fruit eaten by parrot. Skin of fruit is eaten while seed is discarded.



Shea Butter (*Vitellaria paradoxa*) fruit eaten by parrot(s).





Cola cordifolia fruit. Top photo shows fruit being split open by Kaleigh Reyes, second picture shows fruit open with seeds displayed. Last photo shows fruit untouched/unopened in it's complete form.





The three photos on this page all display figs (*Ficus*). The first two photos show a single fig, green in color meaning it is unripe. Parrots prefer ripe figs which become more red in color and softer to the touch. Unripe figs, like these green ones, are very hard to the touch/harder to squeeze.







Both of these photos on this page show Keno (*Pterocarpus erinaceus*). Chimpanzees eat the leaves of keno while Parrots eat the fruit, pictured here. With a flaky outside and a spiky center, the center contains a seed. Parrots rip off the flakes (see bottom photo), reach the center, and pry it open with their powerful beaks to retrieve the seed inside.



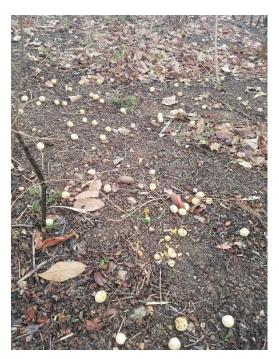


The three photos on this page show *Sclerocarya birrea* fruit. White in color and in a circle shape, the second photo shows the fruit as whole/untouched. The top and bottom photo show fruits I had picked up off the forest floor that parrots had dropped while eating. Clear parrot mandible bite marks can be seen (refer to arrows).













While eating *Sclerocarya* birrea fruit, parrots strip off the outer layer in small strips, taking bite after bite in a line until a whole strip can be removed. The photos on this page show *Sclerocarya birrea* fruit on the forest floor, photos taken after parrots had foraged in the tree. Layers of stripped outer skin can be seen in the photo to the left of this text box.

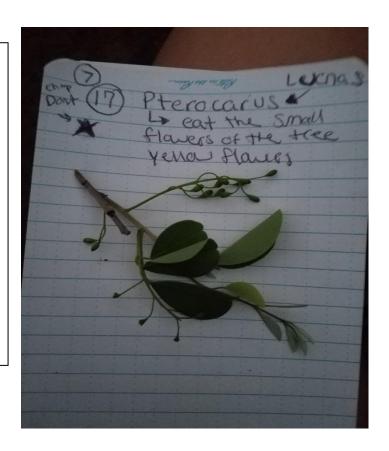
This photo shows another winged fruit, similar to Keno (Pterocarpus erinaceus), called Terminalia macroptera. It is eaten by parrots in the same method, where outer flakes are removed, center is accessed and cracked open, then inside seed is eaten while everything else is discarded.



This show shows a kind of *Lannea*. There are two kinds of *Lannea* with the main difference being size; *Lannea mircocarpa* and *Lannea velutina*. Parrots eat both kinds, with the smallest of the two varieties being shown here.



This photo shows *Pterocarus Luncas*, a plant where parrots eat the small green balls located at the end of branches.



This photo contains Kere (*Agneissue*), a plant that when whole has the shape of a flower, with the flower being made of tiny seeds that make up the pedals. Shown here are those seed "pedals", which parrots eat.



LITERATURE CITED

- Archabald, K., & Naughton-Treves, L. (2001). Tourism revenue-sharing around national parks in Western Uganda: early efforts to identify and reward local communities. *Environmental conservation*, 28(2), 135-149.
- Athan, M. S., & Deter, D. (1998). Guide to the Senegal parrot and its family. *Barron's Educational Series*.
- Bertolani, P., & Pruetz, J. D. (2011). Seed reingestion in savannah chimpanzees (Pan troglodytes verus) at Fongoli, Senegal. *International Journal of Primatology*, 32(5), 1123.
- Blom, A., Almaši, A., Heitkönig, I. M. A., Kpanou, J. B., & Prins, H. H. T. (2001). A survey of the apes in the Dzanga-Ndoki National Park, Central African Republic: a comparison between the census and survey methods of estimating the gorilla (Gorilla gorilla gorilla) and chimpanzee (Pan troglodytes) nest group density. *African Journal of Ecology*, 39(1), 98-105.
- Bogart, S. L., & Pruetz, J. D. (2011). Insectivory of savanna chimpanzees (Pan troglodytes verus) at Fongoli, Senegal. *American Journal of Physical Anthropology*, *145*(1), 11-20.
- Boyes, R. S., & Perrin, M. R. (2009). Generalists, specialists and opportunists: niche metrics of Poicephalu s parrots in southern Africa. *Ostrich*, 80(2), 93-97.
- Boyes, R. S., & Perrin, M. R. (2010). The feeding ecology of Meyer's Parrot *Poicephalus meyeri* in the Okavango Delta, Botswana. *Ostrich*, 80(3), 153-164.
- Brooks, D. E., Greiner, E. C., & Walsh, M. T. (1983). Conjunctivitis caused by Thelazia sp in a Senegal parrot. *Journal of the American Veterinary Medical Association*, 183(11), 1305.
- Chapman, C. A., Chapman, L. J., Wangham, R., Hunt, K., Gebo, D., & Gardner, L. (1992). Estimators of fruit abundance of tropical trees. *Biotropica*, 527-531.
- Chapman, Colin A., Richard Wrangham, and Lauren J. Chapman. "Indices of habitat-wide fruit abundance in tropical forest." *Biotropica* (1994): 160-171.
- Chapman, C. A., Chapman, L. J., & Lefebvre, L. (1989). Variability in parrot flock size: possible functions of communal roosts. *Condor*, 842-847.
- Chettri, N., Deb, D. C., Sharma, E., & Jackson, R. (2005). The relationship between bird communities and habitat. *Mountain Research and Development*, 25(3), 235-244.

- Colegrave, N. (1994). Game theory models of competition in closed systems: asymmetries in fighting and competitive ability. *Oikos*, 499-505.
- Collins, Anthony (2003). Health Guidelines for Visiting Researchers in Gombe National Park to Minimize Risk of Disease Transmission among Primates (Updated 8/01/03). *Pan Africa News*, 10(1).
- Conklin-Brittain, N. L., Wrangham, R. W., & Hunt, K. D. (1998). Dietary response of chimpanzees and cercopithecines to seasonal variation in fruit abundance. II. Macronutrients. *International Journal of Primatology*, 19(6), 971-998.
- Demery, Z. P., Chappell, J., & Martin, G. R. (2011). Vision, touch and object manipulation in Senegal parrots Poicephalus senegalus. *Proceedings of the Royal Society of London B: Biological Sciences*, rspb20110374.
- Dixon, Wiltred J., and F. J. Massey. "Introduction to Statistical Analysis McGraw-Hill." *New York* (1969): 342-343.
- Downs, C. (2005). Artificial nest boxes and wild Cape Parrots Poicephalus robustus: persistence pays off. *Ostrich-Journal of African Ornithology*, 76(3-4), 222-224.
- Emery, N. J., & Clayton, N. S. (2004). The mentality of crows: convergent evolution of intelligence in corvids and apes. *science*, 306(5703), 1903-1907.
- Emery, N. J., & Clayton, N. S. (2004). Comparing the complex cognition of birds and primates. *Comparative vertebrate cognition* (pp. 3-55). Springer, Boston, MA.
- Evans, M. (2001). Environmental enrichment for pet parrots. *Practice*, 23(10), 596.
- Forshaw, J. M., & Cooper, W. T. (1989). Parrots of the world. London: Blandford.
- Galetti, M. (1997). Seasonal abundance and feeding ecology of parrots and parakeets in a lowland Atlantic forest of Brazil. *Revista Brasileira de Ornitologia-Brazilian Journal of Ornitology*, 5(7), 12.
- Gilardi, J. D., & Munn, C. A. (1998). Patterns of activity, flocking, and habitat use in parrots of the Peruvian Amazon. *The Condor*, 100(4), 641-653.
- Gebhardt, S. E. (1994). Nutritive value of foods. *DIANE* Publishing.
- Goodall, J. (2013). Jane Goodall: 50 Years at Gombe. Abrams.
- Hardin, G. (1960). The competitive exclusion principle. science, 131(3409), 1292-1297.

- Harpøth, S. W. (2013). Vocal Modification Abilities and Brain Structures in Parrots—how do they Correlate? (*Doctoral dissertation, Department of Biology, Faculty of Science, University of Copenhagen*).
- Hauser, M. D., & Wrangham, R. W. (1990). Recognition of predator and competitor calls in nonhuman primates and birds: a preliminary report. *Ethology*, 86(2), 116-130.
- Head, J. S., Robbins, M. M., Mundry, R., Makaga, L., & Boesch, C. (2012). Remote video-camera traps measure habitat use and competitive exclusion among sympatric chimpanzee, gorilla and elephant in Loango National Park, Gabon. *Journal of Tropical Ecology*, 28(6), 571-583.
- Homberger, D. G., Enkerlin-Hoeflich, E. C., Snyder, N. F., Wiley, J. W., Munn, C. A., Graham, J., & Matson, K. D. (2006). *Manual of parrot behavior*.
- Howe, H. F. (1990). Seed dispersal by birds and mammals: implications for seedling demography. *Reproductive ecology of tropical forest plants*, 7, 191-218.
- Hunt, Kevin. (2019) Chapter 5 Scratching Out a Living in an Unforgiving World: Habitat and Diet. 2-22. *Unpublished*
- Iringa's, J. O., Downs, C. T., Symes, C. T., & Perrin, M. R. (2002). Diet of the cape parrot, Poicephalus robustus, in afromontane forests in Kwazulu-Natal, South Africa. *Ostrich-Journal of African Ornithology*, 73(1-2), 20-25.
- Isbell, L. A. (1991). Contest and scramble competition: patterns of female aggression and ranging behavior among primates. *Behavioral ecology*, 2(2), 143-155.
- Kruger, A. C., & Shongwe, S. (2004). Temperature trends in South Africa: 1960–2003. *International journal of Climatology*, 24(15), 1929-1945.
- Lambert, J. E. (1998) Primate digestion: interactions among anatomy, physiology, and feeding ecology. *Evolutionary Anthropology: Issues, News, and Reviews*, 7(1), 8-20.
- Lieberman, M., & Lieberman, D. (1986). An experimental study of seed ingestion and germination in a plant-animal assemblage in Ghana. *Journal of Tropical Ecology*, 2(2), 113-126.
- Lindsey, G. D., Arendt, W. J., Kalina, J., & Pendleton, G. W. (1991). Home range and movements of juvenile Puerto Rican parrots. *The Journal of wildlife management*, 318-322.
- Lombardo, J. A., & McCarthy, B. C. (2009). Seed germination and seedling vigor of weevil-damaged acorns of red oak. *Canadian journal of forest research*, 39(8), 1600-1605.

- Masello, J. F., Pagnossin, M. L., Sommer, C., & Quillfeldt, P. (2006). Population size, provisioning frequency, flock size and foraging range at the largest known colony of Psittaciformes: the Burrowing Parrots of the north-eastern Patagonian coastal cliffs. *Emu-Austral Ornithology*, 106(1), 69-79.
- McDonald Kinkaid, H. Y. (2015). Species-level determinants of stereotypic behaviour, reproductive success, and lifespan in captive parrots (Psittaciformes) *Doctoral dissertation*.
- Morgan, D., Sanz, C., Onononga, J. R., & Strindberg, S. (2006). Ape abundance and habitat use in the Goualougo Triangle, Republic of Congo. *International Journal of Primatology*, 27(1), 147-179.
- Morris, K., & Goodall, J. (1977). Competition for meat between chimpanzees and baboons of the Gombe National Park. *Folia primatologica*, 28(2), 109-121.
- Naughton-Treves, L., Treves, A., Chapman, C., & Wrangham, R. (1998). Temporal patterns of crop-raiding by primates: linking food availability in croplands and adjacent forest. *Journal of Applied Ecology*, 35(4), 596-606.
- Neu, C. W., Byers, C. R., & Peek, J. M. (1974). A technique for analysis of utilization-availability data. *The Journal of Wildlife Management*, 541-545.
- Olkowicz, S., Kocourek, M., Lučan, R. K., Porteš, M., Fitch, W. T., Herculano-Houzel, S., & Němec, P. (2016). Birds have primate-like numbers of neurons in the forebrain. *Proceedings of the National Academy of Sciences*, 113(26), 7255-7260.
- Plumptre, A. J., & Cox, D. (2006). Counting primates for conservation: primate surveys in Uganda. *Primates*, 47(1), 65-73.
- Prinzinger, R., & Hänssler, I. (1980). Metabolism-weight relationship in some small nonpasserine birds. *Experientia*, 36(11), 1299-1300.
- Pruetz, Jill D., P. Bertolani, K. Boyer Ontl, S. Lindshield, M. Shelley and E. G. Wessling. "New evidence on the tool-assisted hunting exhibited by chimpanzees (Pan troglodytes verus) in a savannah habitat at Fongoli, Sénégal." *Royal Society Open Science* 2.4 (2015): 140507.
- Pruetz, J. D., Marchant, L. F., Arno, J., & McGrew, W. C. (2002). Survey of savanna chimpanzees (Pan troglodytes verus) in southeastern Senegal. *American Journal of Primatology*, 58(1), 35-43.
- Pruetz, J. D. (2006). Feeding ecology of savanna chimpanzees (Pan troglodytes verus) at Fongoli, Senegal. *Feeding ecology in apes and other primates*, 326-364.

- Pruetz, J. D. (2017). Updated copy of Fongoli Protocol for Chimpanzee Follows. *Unpublished*.
- Ragusa-Netto, J. (2007). Feeding ecology of the Green-cheeked parakeet (Pyrrhura molinae) in dry forests in western Brazil. *Brazilian Journal of Biology*, 67(2), 243-249.
- Rainey, H. J., Zuberbühler, K., & Slater, P. J. (2004). Hornbills can distinguish between primate alarm calls. Proceedings of the Royal Society of London. *Series B: Biological Sciences*, 271(1540), 755-759.
- Renton, K. (2001). Lilac-crowned Parrot diet and food resource availability: resource tracking by a parrot seed predator. *The Condor*, 103(1), 62-69
- Renton, K., Salinas-Melgoza, A., De Labra-Hernández, M. Á., & de la Parra-Martínez, S. M. (2015). Resource requirements of parrots: nest site selectivity and dietary plasticity of Psittaciformes. *Journal of Ornithology*, 156(1), 73-90.
- Salinas-Melgoza, A., & Renton, K. (2005). Seasonal variation in activity patterns of juvenile Lilac-crowned Parrots in tropical dry forest. *The Wilson Bulletin*, 117(3), 291-295.
- Selman, R. G., Perrin, M. R., Hunter, M. L., & Dean, W. R. J. (2002). The feeding ecology of Rüppell's Parrot, Poicephalus rueppellii, in the Waterberg, Namibia. *Ostrich*, 73(3-4), 127-134.
- Silk, M. J., Croft, D. P., Tregenza, T., & Bearhop, S. (2014). The importance of fission—fusion social group dynamics in birds. *Ibis*, *156*(4), 701-715.
- Sugiyama, Y., & Soumah, A. G. (1988). Preliminary survey of the distribution and population of chimpanzees in the Republic of Guinea. *Primates*, 29(4), 569-574.
- Straub, J., Pees, M., & Krautwald-Junghanns, M. E. (2002). Measurement of the cardiac silhouette in psittacines. *Journal of the American Veterinary Medical Association*, 221(1), 76-79.
- Symes, C. T., & Perrin, M. R. (2003). Feeding biology of the greyheaded parrot, Poicephalus fuscicollis suahelicus (Reichenow), in northern province, South Africa. *Emu*, 103(1), 49-58.
- Thiam, E. H. I., & Singh, V. P. (2002). Space-time-frequency analysis of rainfall, runoff and temperature in the Casamance River basin, southern Senegal, West Africa. *Water SA*, 28(3), 259-270.

- Tokita, M. (2004). Morphogenesis of parrot jaw muscles: understanding the development of an evolutionary novelty. *Journal of morphology*, 259(1), 69-81.
- Tolsma, A. D., Menkhorst, P. W., & Stamation, K. A. (2014). A Habitat Monitoring Protocol for the Orange-bellied Parrot Neophema chrysogaster. Unpublished Client Report for Regional Services Division Barwon South West. *Arthur Rylah Institute for Environmental Research, Department of Environment and Primary Industries, Heidelberg, Victoria.*
- Tutin, C. E., & Fernandez, M. (1984). Nationwide census of gorilla (Gorilla g. gorilla) and chimpanzee (Pan t. troglodytes) populations in Gabon. *American Journal of Primatology*, 6(4), 313-336.
- Uehara, S., & Nishida, T. (1987). Body weights of wild chimpanzees (Pan troglodytes schweinfurthii) of the Mahale Mountains National Park, Tanzania. American *Journal of Physical Anthropology*, 72(3), 315-321.
- Van Noordwijk, M. A., & Van Schaik, C. P. (1988). Scramble and contest in feeding competition among female long-tailed macaques (*Macaca fascicularis*). *Behaviour*, 105(1-2), 77-98.
- Warburton, L. S., & Perrin, M. R. (2005). Foraging behaviour and feeding ecology of the Black-cheeked Lovebird Agapornis nigrigenis in Zambia. *Ostrich-Journal of African Ornithology*, 76(3-4), 118-129.
- Wrangham, R. W., Conklin-Brittain, N. L., & Hunt, K. D. (1998). Dietary response of chimpanzees and cercopithecines to seasonal variation in fruit abundance. I. Antifeedants. *International Journal of Primatology*, 19(6), 949-970
- Webb, C. O., Ackerly, D. D., McPeek, M. A., & Donoghue, M. J. (2002). Phylogenies and community ecology. *Annual review of ecology and systematics*, 33(1), 475-505.
- Wilson, M. L., Kahlenberg, S. M., Wells, M., & Wrangham, R. W. (2012). Ecological and social factors affect the occurrence and outcomes of intergroup encounters in chimpanzees. *Animal Behaviour*, 83(1), 277-291.
- Yamagiwa, J., & Basabose, A. K. (2006). Diet and seasonal changes in sympatric gorillas and chimpanzees at Kahuzi–Biega National Park. *Primates*, 47(1), 74-90.