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Dominance and Foraging in White-faced Capuchins

by

Carolyn L. Hall ©

A thesis submitted to the faculty of Graduate studies and Research in partial fulfillment of

the requirements for th ee of Master of Arts

Department of Anthropology

Edmonton, Alberta

Fall 1995

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Jan O Murie
Dr. J.O. Murie

Stan Boutin
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Date: August 24, 1995

DEDICATION

This thesis is dedicated to

my parents, who taught me to follow my dreams,

and to Murray Humphries, who taught me to believe in myself.

ABSTRACT

Group living entails both costs and benefits, and within social groups dominance-mediated competition for resources may skew cost/benefit ratios in favour of dominant animals. I examined rank-related differences in the use of spatial positions and dietary choices by white-faced capuchins (Cebus capucinus). Dominant animals were more likely to be found in central positions, where they likely experienced a lower predation risk, and within the center they were more likely to be found in forward positions, where prey depletion was lower. Capuchins also exhibited rank-related dietary differences, with dominants more likely to use foods that occurred in large clumps and subordinates more likely to use foods that occurred in small clumps. I argue that the observed spatial patterns and dietary differences resulted from the avoidance of dominant animals by subordinates, rather than the aggressive exclusion of subordinates by dominant animals.

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Chapter One. Introduction

The concept of social dominance appears in the behavioural literature for a variety of taxa, but is particularly prominent in the literature on birds and mammals. The concept has been used in a variety of contexts, and operationally defined in various ways (reviewed by Bernstein 1981). If a dominance relationship exists between two individuals, then the outcome of a competitive interaction between them will be predictable. Furthermore, the outcome will be based on the identities of the two individuals, and the outcome of previous interactions, rather than on factors such as territoriality or "trained" winners and losers (Bernstein 1981). The distinction between a dominance interaction and one based on "trained" winners or losers is that, in the latter, animals are conditioned to act consistently submissively or aggressively, regardless of the identity of their opponent, whereas in a dominance interaction, an individual may act either submissively or aggressively, depending on whether it perceives its opponent as dominant or subordinate (Bernstein 1981). As stressed by Rowell (1974), an important component of any dominance interaction is that one animal shows submissive behaviour. It is only if the subordinate recognizes the relationship, or "predicts" the outcome of an aggressive interaction by showing submission, that one can assume a dominance relationship exists (Bernstein 1980).

Thus, dominance is defined by the consistent direction of aggressive behaviour between individuals, but does not necessarily predict the rate at which aggression occurs (Walters and Seyfarth 1987; Fedigan 1992). High-ranking animals may only rarely engage in aggression towards other group members, while lower-ranking animals may frequently exhibit aggressive behaviors (Bernstein 1980, Fedigan 1992). However, in some species high ranking animals do perform the majority of the aggression (Cebus apella, Janson 1985; Cercopithecus aethiops, Horrocks & Hunte 1983).

Dominance in primates is not necessarily correlated with physical attributes such as size or strength, especially for female primates (Walters and Seyfarth 1987). In many cercopithecine species, female dominance rank is dependent on the rank of the female's mother, whereas male rank is dependent on the mother's rank while they are young, but switches to size, strength, and other determinants of fighting ability as the male gets older (Walters & Seyfarth 1987). Much less is known about the acquisition of dominance rank in non-cercopithecine species, but in some species dominance rank appears to have an age component; in mantled howlers (Alouatta palliatta) younger females are generally dominant to older females (Jones 1980) whereas in chimpanzees (Pan troglodytes) older females are generally dominant to younger ones (Nishida & Hiraiwa-Hasegawa 1987). In both howlers and chimpanzees, male-male coalitions seem to be important for contests that change an individual's dominance status (Walters & Seyfarth 1987; Nishida & Hiraiwa-Hasegawa 1987). In Cebus sp. dominance hierarchies exist, but the process by which individuals of either sex acquire their rank is unknown (Robinson & Janson 1987; Walters & Seyfarth 1987).

Once dominance hierarchies have been established, subordinates will not benefit from resource-based aggressive competition with dominant animals, since they will be unlikely to win an interaction, but will presumably receive a cost from the aggressive encounter (Popp and Devore 1979). Therefore, subordinate animals will be expected to actively avoid dominant individuals, and situations with the potential for conflict (Popp and Devore 1979). This type of avoidance occurs in red deer (Cervus elaphus, Thouless 1990), juncos (Junco hyemalis, Caraco et al. 1989) and oystercatchers (Haematopus ostralegus, Ens and Goss-Custard 1984), and may be an important component of many dominance-based social systems.

Group living entails both costs and benefits for animals, and dominant individuals may be able to use their rank to minimize the costs they receive and maximize the benefits. Within the space occupied by a group, costs and benefits may vary between spatial positions, and dominants may use their rank to gain access to preferred spatial positions (Robinson 1981; Janson 1990). Furthermore, any avoidance of dominant animals by subordinates will decrease the amount of direct competition for food between dominant and subordinate animals. However, the benefit of this decreased competition may be skewed toward dominant animals. If resources are clumped in space, and dominant animals are present in clumps of preferred resources, then subordinates will be forced to avoid those resources and shift their diets in favour of other resources. Hence, the avoidance of dominant animals may result in reduced access to certain food items for subordinate animals, and therefore represents a subtle form of contest competition (Janson and van Schaik 1988) Finally, if aggressive competition does occur over some food items, dominant animals will benefit, since they are more likely to obtain the contested food item, while subordinates will experience only the cost of interaction, and no compensatory benefit (Popp and Devore 1979).

Dominance influences the use of spatial positions by Cebus apella and Cebus nigrivittatus (Janson 1990; Robinson 1981). However, in both species aggression from the most dominant animals is not highly correlated with dominance rank, and is another factor regulating where an individual is found. Janson (1985) also examined the influence of aggressive competition on food consumption in C. apella. Dominant C. apella have a higher rate of intake at food sources where aggression is common, but the rate of aggression received is more important than dominance rank when animals feed on food sources over which fighting is uncommon. Overall, dominants have a significantly greater total food intake than subordinates. Thus, both dominance rank and tolerance by high ranking animals are important influences on the food consumption of individual C. apella.

In this thesis I examine the effects of dominance on spatial patterns and dietary choices in the white-faced capuchin (Cebus capucinus). Cebus capucinus exhibit a linear dominance hierarchy, with adult males generally dominant over adult females, except for the alpha female who is dominant over some of the lower ranking males (Fedigan 1993). Phillips (1995) concluded that contest competition over food is not important in C. capucinus, because rates of aggression are low. However, if subordinate animals are avoiding dominant animals, dominance may affect access to resources without high rates of aggression. Therefore, in this study I examine the differential use of spatial positions and foods by animals of different rank, to investigate directly the influence of dominance rank on these variables.

In Chapter Two I investigate rank-related spatial patterns within the group, and suggest a proximate mechanism responsible for these patterns. Chapter Three is an

investigation of rank-related dietary differences, and patterns of aggression and avoidance over different types of food items. Rank-related spatial patterns and dietary differences are discussed in terms of the costs and benefits of group living, and the processes by which dominance rank may affect the costs and benefits received by an animal.

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[1]Chapter Two. Spatial Benefits Afforded by High Rank in White-faced Capuchins

Living in a group both imposes costs and provides benefits for an animal. Potential benefits include decreased predation risk and the enhancement of foraging success, while one of the most prominent costs is increased competition for food (see Krebs and Davies 1981 for a review). Decreased predation risk may occur because of increased vigilance, since the total vigilance will increase with increased group size, even if individual vigilance is marginally reduced (Pulliam 1973; Bertram 1980). Additionally, animals in groups should experience a lower predation risk because of dilution; an individual antelope in a group of 100 has only one chance in one hundred of being the victim in a single successful attack (Krebs and Davies 1981). Foraging benefits of group living may include an increased likelihood of finding food (Ward and Zahavi 1973), an increased ability to defend clumped resources (Wrangham 1980; Bertram 1978), a lower variance in food intake (Mangel 1990; Miller In Press), and an increase in the amount of time available for foraging because of a decrease in the amount of time spent in vigilance (Powell 1974; Bertram 1980; Boinski 1988; Black et al. 1992; Carrascal and Moreno 1992). Increased costs may be imposed by increases in both scramble and contest competition (Janson and van Schaik 1988; van Schaik and van Noordwijk 1988; Isbell 1991). Any number of these costs and benefits may be relevant for a given population, and individuals are expected to minimize their cost/benefit ratio.

Within the physical boundaries of a group, different spatial positions may represent different costs and benefits. Central positions should represent a lower predation risk than edge positions (Hamilton 1971; Vine 1971). Animals on the edge will be the first

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[1] A version of this chapter has been submitted for publication. Hall and Fedigan. Animal Behaviour.

encountered by a predator, making them more likely to be the object of an attack than more central individuals (Vine 1971). Additionally, animals on the edge have fewer neighbours, so they will receive a lower benefit from both conspecific vigilance and the dilution effect. Several studies have shown that animals on the edge of a group spend more time being vigilant than their central counterparts (Murton et al. 1971; Inglis & Lazarus 1981; Underwood 1981; van Schaik and van Noordwijk 1988; Janson 1990b; Black et al. 1992). Thus, edge positions represent lower benefits in terms of both reduced predation risk and the trade off between vigilance and foraging. However, edge positions may also represent lower costs than central positions, since competition for food should be higher in the centre where the density of animals may be greatest (Robinson 1981).

Within a moving group, costs and benefits may also differ from front to back. Animals in the leading edge will have a higher predation risk, since they will be the first to encounter a predator, and therefore are more likely to be the object of an attack. Additionally, they are the first to enter new areas that have not been scanned for predators by other group members, and so they receive a lower group vigilance benefit. However, they will also be the first to search new areas for food, and therefore will not suffer from depletion by other group members (Robinson 1981; Janson 1990b). Finally, since other members of the group will be approaching from behind, they may be subject to intense contest competition (Murton et al. 1971; Robinson 1981; Janson 1990b). Animals immediately behind the leading edge can use the animals in the front of the group as a "predation buffer", but will still be close enough to the front so that depletion should not represent a significant cost. Additionally, they may be able to capitalize on food found by members of the leading edge through contest competition (Murton et al. 1971; Robinson 1981; Janson 1990b). Within the midsection and rear of the group the predation buffer is again larger, depletion effect greater, and the effect of contest competition smaller because there are fewer animals approaching from behind, although this may be confounded by the increased competition in central positions.

Individuals trying to minimize their cost/benefit ratio should show preferences for those spatial positions that have low costs relative to benefits. Therefore, within groups that are organized by a social dominance hierarchy, dominants may use their rank to gain access to preferred positions, and to exclude subordinates from those positions. A slight variation of this, with similar consequences, is that dominants may use preferred spatial positions, and subordinates may avoid competition from dominants by using less preferred positions. A variety of studies have shown that dominant birds within flocks use positions with lower predation risk than those used by subordinates (Ekman and Askenmo 1984; Hogstad 1986, 1987; Desrochers 1989; Suhonen et al. 1993), and that when dominants are removed, subordinates will forage in the positions previously used by dominants (Alatolo and Moreno 1987; Hogstad 1987; Desrochers 1989). Robinson (1981) found that dominance rank correlates with centralness in groups of wedge-capped capuchin monkeys (*Cebus nigrivittatus*). Rayor and Uetz (cited in Lima and Dill 1989) found that within colonies of web-building spiders (*Metepeira incrassata*), larger individuals actively seek the centre of the colony, where predation from wasps is lower, relegating smaller individuals to the edge. Hughes (1992) found that the dominance rank of arctic grayling (*Thymallus arcticus*) is perfectly correlated with the desirability of their feeding position.

Thus, dominant individuals in a variety of species use their rank to gain access to preferred spatial positions.

In this study I investigate the effect of dominance rank on the use of spatial positions within two social groups of white-faced capuchin monkeys (Cebus capucinus). Two previous studies on other species of capuchins (C. apella and C. nigrivittatus) have found correlations between social rank and the use of space within a group (Robinson 1981; Janson 1990a). Furthermore, they found correlations between an animal's behaviour and the tendency for it to be central, or forward, within the group (see also Boinski 1993, In Press). Here, I directly examine the behaviour of animals while they forage in different positions, and use this to investigate the relative costs and benefits offered by spatial positions within the group. Additionally I make use of a seasonal difference in foraging success to examine rank-related responses to foraging competition. Finally, I suggest a proximate mechanism that may be responsible for the spatial distribution observed.

METHODS

Study Site and Species

The study was conducted in the dry tropical forest of Santa Rosa National Park, Costa Rica. The climate is characterized by two distinct seasons; the dry season extends from mid-December to mid-May, and the wet season is from May through November (Chapman 1987).

The white-faced capuchin (Cebus capucinus) is a medium sized monkey in which females weigh about 70% of the average male weight of three kilograms (Glander et al. 1991). The species is primarily arboreal, but individuals will sometimes descend to the ground to forage. White-faced capuchins live in multi-male, multi-female groups (Oppenheimer 1968; Buckley 1983; Mitchell 1989; Perry 1995), and in Santa Rosa the average group size is 14 individuals (Fedigan 1986; Fedigan et al. in press). Within these groups it is possible to determine a linear dominance ranking among adults, with adult males individually dominant over females, except for the alpha female who usually ranks above one or more of the lower ranking males (Fedigan 1993). Cebus capucinus are omnivorous; the bulk of their diet is made up of fruit, and to a lesser extent insects (Chapman and Fedigan 1990; Freese and Oppenheimer 1981). In addition, they prey opportunistically on small vertebrates(Fedigan 1990; Perry and Rose 1994), and only rarely eat leaves and flowers (Oppenheimer 1968; Buckley 1983; Chapman and Fedigan 1990; Mitchell 1989).

Data Collection

Focal data were collected on the adult and subadult members of two groups. Group I consisted of three adult males, three adult females, five juveniles, and three infants. Group II consisted of three adult males, four adult females, two subadult males, ten juveniles, and four infants. Both groups were well habituated to observation, as they have been part of a long term study by Dr. L. M. Fedigan for the past 11 years.

Behaviour was sampled using the focal animal continuous sampling method (Altmann 1974), with a sample length of ten minutes. Sampling was performed daily, from dawn to dusk, throughout the periods of May 1994 to August 1994 (wet season), and January 1995 to March 1995 (dry season). Similar amounts of data were obtained in each field season (169 hours in the wet season and 151 hours in the dry season), resulting in a total of 320 hours of data. An average of 11.32 hours of data were taken for each animal during the wet season (totals for individuals ranged from 10.79 to 11.88 hours), and an average of 10.09 hours of data was taken for each animal in the dry season (totals ranged from 9.93 to 10.34 hours). At the beginning and end of each focal session I recorded the spatial position of the animal (Fig. 2-1), the identity of all animals within 10 metres of the focal animal, the identity of the nearest neighbour (excluding infants), and the distance to the nearest neighbour (recorded as less than 3 metres, 3 to 6 metres, or 6 to 10 metres). The two measures for nearest neighbour were not taken if no animals were within 10 metres of the focal animal. The spatial position of the focal animal was also recorded five minutes into the sample.

In addition to focal sampling, all supplantations, threats, fear grimaces, and retreats (Appendix A) were recorded *ad libitum* (Altmann 1974) and used to construct a dominance hierarchy. Once dominance hierarchies had been established for each group, a dominance rank score was computed for each animal so that data from both groups could be pooled. The score represents the proportion of animals in the hierarchy over which that animal ranks, and is calculated as $s / N-1$, where s = the number of animals in the

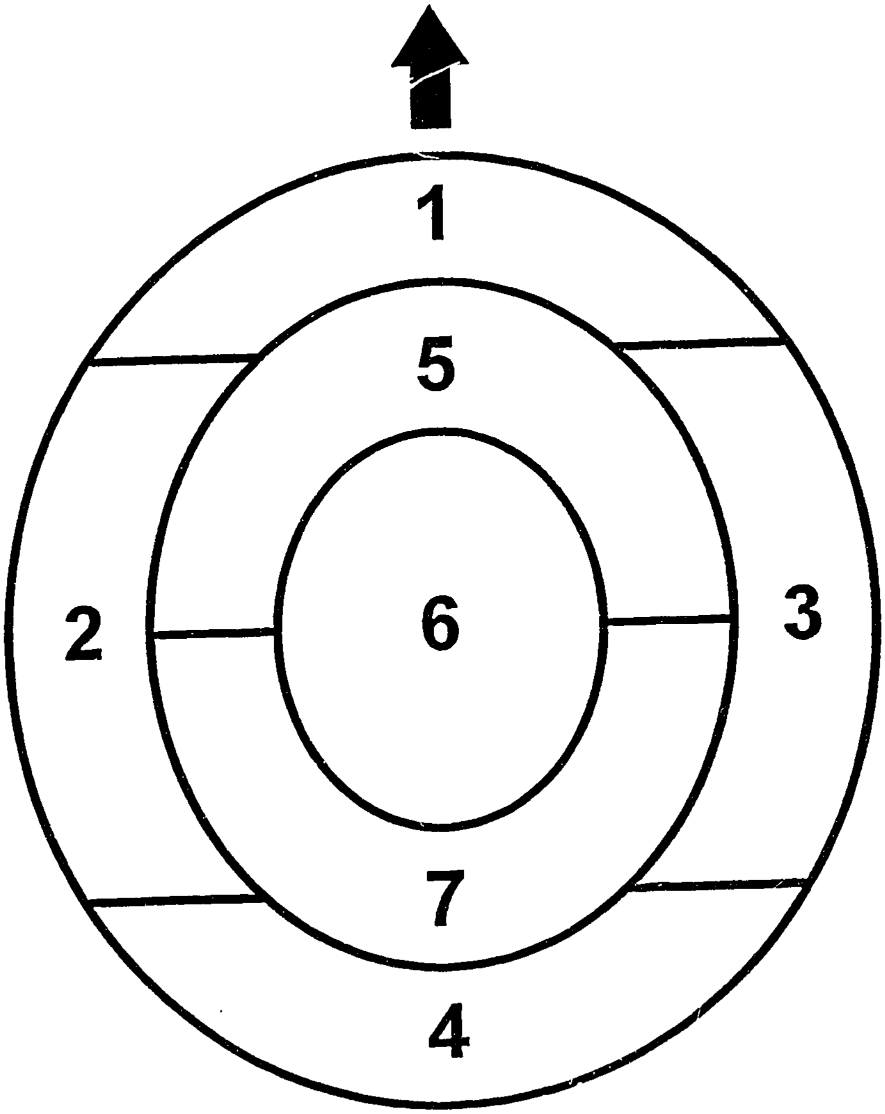


Figure 2-1: Spatial positions within the group. Arrow points in the direction of group movement (after Janson 1990a).

hierarchy that are subordinate to the animal, and N = the total number of animals in the hierarchy (Cheney & Seyfarth 1981).

Analyses

Spatial position

Janson (1984) found that samples of behaviour separated by only five minutes were not independent. Therefore, I tested consecutive spatial readings within samples for autocorrelation (cross-correlations procedure, Norusis 1993), and found them to be independent. All spatial readings (beginning, middle, and end of sample) were pooled in order to investigate where individuals spent their time. Positions one through four were designated as the edge, and five through seven as the centre (Fig. 2-1). Similarly, positions one and five were designated as the front of the group, while the rest of the positions were considered the back of the group. Edge ratios and front ratios were calculated for each animal as the proportion of readings during which that animal was recorded as being in edge or front positions, respectively. Data were tested for normality and if necessary, were log-transformed to achieve normality. I conducted regression analyses of spatial position versus dominance rank, for each sex in each season. One male was determined to be an outlier (Studentized deleted residual and Cooke's distance, Norusis 1993), and was therefore removed for the analyses. This male was a small subadult male, who throughout the analyses exhibited behaviour similar to that of the females, rather than the males. Since this may be a function of his age and size, he was removed from analyses whenever it was necessary to control for sex, and when tests were run separately by sex.

To investigate the spatial habits of the animals in more detail, the proportion of readings during which an individual was found in each spatial position was calculated for each animal. These proportions were tested for correlation with dominance rank, controlling for sex using partial correlations. Data for positions two and three were pooled, on the assumption that these positions would represent similar costs and benefits. Therefore six proportions were calculated, and will be referred to as proportion one, proportion two-three, proportion four, and so on.

Behaviour

To investigate the behaviour of individuals while located in different spatial positions, focal samples were divided into two five minute periods, the first period associated with the beginning spatial reading and the second period with the end spatial reading. Middle readings were discarded. Since focal data were not evenly distributed among animals all statistical tests were performed on rates, obtained by dividing the time engaged in the behaviour of interest by total time. To control for individual characteristics that may covary with the tendencies of individuals to be in certain spatial positions, I used Wilcoxon matched-pairs tests, pairing the behaviour of an individual in two different spatial positions. I used a non-parametric test because of the small sample size (n = 15). All analyses were run separately for each season because the two seasons may represent different ecological pressures.

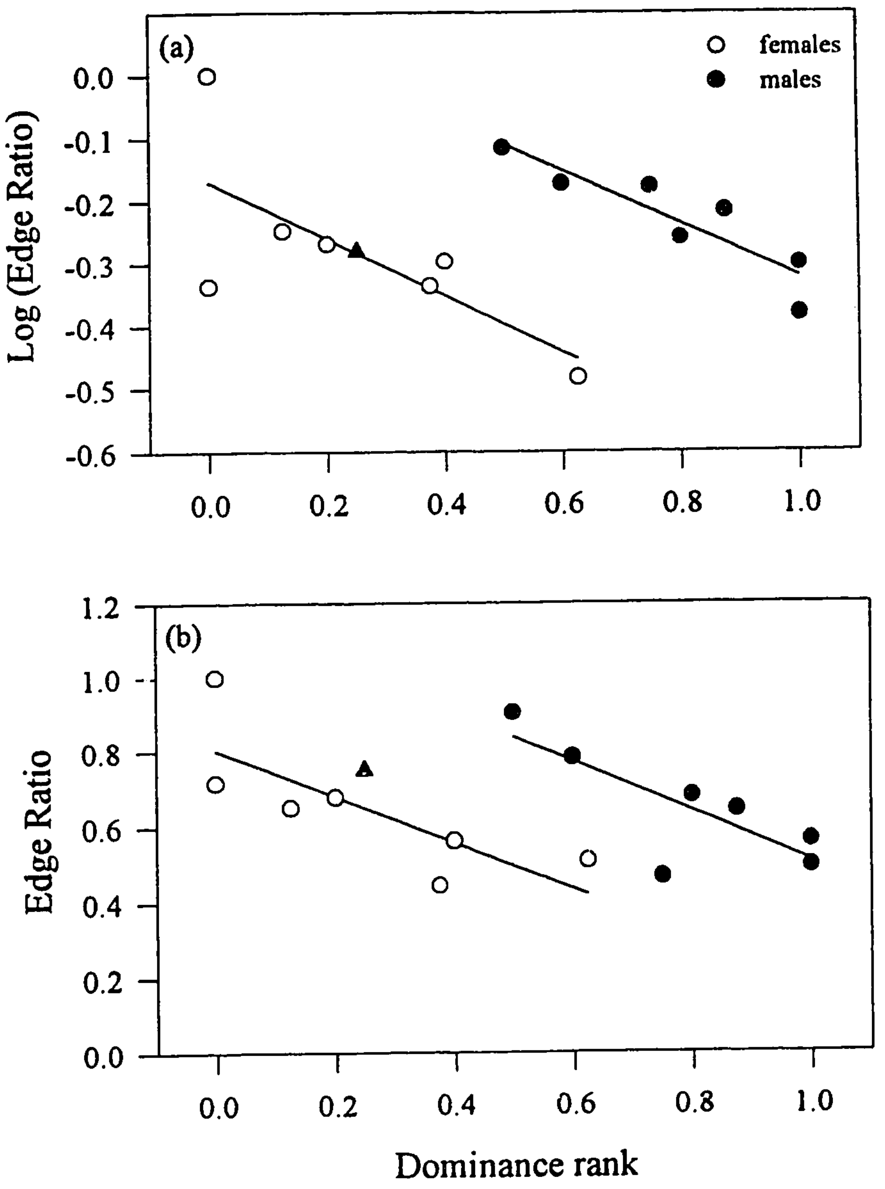
RESULTS

Spatial Position

Within the sexes, high rank was associated with low edge ratios (Fig. 2-2). All regressions of edge ratio versus dominance rank were significant, except females in the wet season, for which the P value was 0.066 and $r^2 = 0.52$. A similar analysis using front ratio showed no significant trends (wet season for females P = 0.73, $r^2 = 0.026$ and for males P = 0.34, $r^2 = 0.18$, dry season for females P = 0.34, $r^2 = 0.18$, and for males P = 0.21, $r^2 = 0.29$).

Based on the prior analyses of edge ratios, I predicted that, controlling for sex, proportions one, two-three and four (edge positions) should be negatively correlated with dominance rank, and proportions five, six and seven (centre positions) should be positively correlated with dominance rank. In both seasons, all correlations were in the direction predicted (Table 2-1). In the wet season, the correlation coefficients for all proportions except one and four were significant (proportion one, P = 0.058; proportion four, P = 0.14). In the dry season the correlation coefficients for the central positions (five, six and seven) were statistically significant, but those for proportions one, two-three, and four were not (P = 0.059, P = 0.077, and P = 0.071 respectively). However, on closer inspection of the individual proportions, I noticed that the lowest ranking female in group I was only ever in positions one and two, and was an obvious outlier in scatter plots of each proportion by dominance rank (Studentized deleted residual and Cooke's distance, Norusis 1993). I therefore reanalyzed the data after omitting this female and found all correlation coefficients to be significant (Table 2-1), except for proportion one in the wet

Figure 2-2: Regressions of edge ratio by rank. Edge ratio was calculated as the proportion of all spatial readings that an animal was on the edge of the group. (a) Wet season, log (edge ratio) was used to acheive normality (Shapiro-Wilks and K-S tests, $P < 0.05$, Norusis, 1993). Females: $Y = -0.456X - 0.169$, $r^2 = 0.523$, $P = 0.066$. Males: $Y = -0.426X + 0.103$, $r^2 = 0.811$, $P = 0.006$ (b) Dry season. Females: $Y = -0.612X + 0.802$, $r^2 = 0.611$, $P = 0.038$. Males: $Y = -0.655X + 1.165$, $r^2 = 0.630$, $P = 0.033$. The triangle represents a young male that was determined to be an outlier, and removed for this analysis (see text for explanation).


(a)
females
males
Log (Edge Ratio)
0.0
-0.1
-0.2
-0.3
-0.4
-0.5
-0.6
0.0
0.2
0.4
0.6
0.8
1.0
(b)
Edge Ratio
1.2
1.0
0.8
0.6
0.4
0.2
0.0
0.0
0.2
0.4
0.6
0.8
1.0
Dominance rank

season (P = 0.085). Thus, high ranking animals tend to be found in the three central positions, while subordinates tend to be found in the outer positions.

Since the area I defined as the front of the group is made up of one edge position (position 1) and one central position (position 5), this edge-versus-centre trend may mask any tendency for individuals to be in the front or back of the group. I therefore calculated the proportion of central readings (positions five, six and seven) that each animal was found in position five, and the proportion of edge readings (positions one, two-three and four) that each animal was found in position 1. These values were not correlated with dominance rank in either season (Pearson correlation coefficient. Position five: wet season = -0.28, one-tailed P = 0.66; dry season = 0.24, one-tailed P = 0.42; Position one: wet season = -0.16, one-tailed P = 0.57; dry season = -0.14, one-tailed P = 0.63). Thus, dominant animals are not more likely to be found in position five than positions six and seven, nor are they more likely to be found in position one than positions two-three and four.

Spatial Position and Vigilance

Animals were not more vigilant when on the edge of the group than when in the centre (wet season 1-tailed P = 0.93; dry season 1-tailed P = 0.49; Table 2-2). Similarly, animals were not more vigilant in the front positions than they were in the back positions (wet season 1-tailed P = 0.89; dry season 1-tailed P = 0.50). Since vigilance may have functions other than predator detection (see discussion), I examined the vigilance rates for individuals to see which group members were most vigilant. The most vigilant individuals

Table 2-1: Partial correlations (controlling for sex) of the spatial position proportions by rank. A positive value indicates the position is used to a greater extent by dominants, a negative value indicates the position is used to a greater extent by subordinates.

Season	Position 1	Position 2-3	Position 4	Position 5	Position 6	Position 7
Wet	-0.46	-0.73	-0.32	0.74	0.78	0.59
	p = 0.058	p = 0.002	p = 0.14	p = 0.002	p = 0.001	p = 0.017
Dry	-0.4543	-0.4198	-0.4303	0.8802	0.6403	0.8677
	p = 0.059	p = 0.077	p = 0.071	p = 0.000	p = 0.009	p = 0.000
Wet*	-0.42	-0.69	-0.70	0.76	0.76	0.58
	p = 0.085	p = 0.006	p = 0.006	p = 0.002	p = 0.002	p = 0.024
Dry*	-0.51	-0.68	-0.74	0.89	0.60	0.90
	p = 0.045	p = 0.007	p = 0.003	p = 0.000	p = 0.020	p = 0.000

Spatial proportions were calculated as the proportion of total readings that the animal was in that position. All p values are one-tailed.

* = analyses run with the lowest ranking female from group one removed (see text).

Table 2-2: Effects of spatial position on rates of vigilance (rates were calculated as time spent in vigilance behaviour divided by total time).

Season	Position	Mean ± SD	Z	No. Pairs	1-Tailed P
Wet	Edge	0.114 ± 0.050	-0.909	14	0.93
	Centre	0.120 ± 0.048			
Dry	Edge	0.058 ± 0.020	-0.454	14	0.49
	Centre	0.054 ± 0.029			
Wet	Front	0.122 ± 0.043	-1.818	15	0.89
	Back	0.115 ± 0.041			
Dry	Front	0.060 ± 0.031	-1.818	15	0.97
	Back	0.059 ± 0.019			

Pairs were compared using Wilcoxon matched-pairs tests.

were the two alpha males (0.17 and 0.20 versus a mean of 0.11), and this difference was significant for both alpha males during both seasons (one sample against the mean test, Sokal and Rohlf 1981, wet season: t = 4.47, P = 0.018; t = 7.73, P < 0.001; dry season: t = 4.33, P = 0.017; t = 2.66, P = 0.029).

Spatial Position and Density

The density of animals around an individual can affect the feeding competition it experiences, the benefit it receives from conspecific vigilance and dilution, and the size of its domain of danger. My measure of density was the number of animals within ten metres of the focal animal, which I predicted would be lower when an individual was on the edge than when it was in the centre. The density of animals was significantly lower on the edge in both seasons (Wilcoxon matched-pairs test: wet season, 1-tailed P = 0.005; dry season, 1-tailed P = 0.005; Table 2-3).

Spatial Position and Capture Success

Capture success was defined as the number of insects caught per time spent searching. If there is a depletion effect then an animal should have a higher capture success when foraging in the front positions of the group (positions one and five) than when foraging in the back of the group (positions two-three, four, six, and seven). The lowest ranking female in group I was excluded from this analysis because she was only observed in positions 1 and 2, and therefore I felt that she could not properly represent feeding in the back of the group. Animals experienced a higher capture success in the front than in the back during the dry season (1-tailed P = 0.015; Table 2-4), indicating that

Table 2-3: Spatial position and density (measured as the number of animals within ten metres of the focal animal; n = 14).

Season	Position	Mean + SD	Z	1-Tailed P
Wet	Centre	2.909 ± 0.77	-3.296	0.005
	Edge	1.834 ± 0.56		
Dry	Centre	2.522 ± 0.73	-3.296	0.005
	Edge	1.481 ± 0.48		

Pairs were compared using Wilcoxon matched-pairs tests.

Table 2-4: Spatial position and capture success, measured as the number of insects captured divided by the amount if time (in seconds) spent searching (n = 14).

Season	Position	Mean + SD	Z	P
Wet	Front	0.0127 ± 0.003	-0.596	1-tailed p = 0.28
	Back	0.0130 ± 0.003		
Dry	Front	0.0066 ± 0.002	-2.166	1-tailed p = 0.015
	Back	0.0050 ± 0.001		
Wet	1	0.0132 ± 0.004	-0.848	2-tailed p = 0.40
	5	0.0120 ± 0.005		
Dry	1	0.0063 ± 0.002	-0.160	2-tailed p = 0.88
	5	0.0065 ± 0.004		
Wet	Centre	0.0123 ± 0.003	-0.910	1-tailed p = 0.18
	Edge	0.0133 ± 0.003		
Dry	Centre	0.0053 ± 0.001	-0.220	1-tailed p = 0.41
	Edge	0.0054 ± 0.001		

Pairs were compared using Wilcoxon matched-pairs tests.

there was a significant depletion cost for animals foraging in the back of the group. The difference between the average values for animals in the front (0.0066) and back positions (0.0050) amounts to approximately 6 insects per hour. In contrast, there was no difference in capture success between the front and back positions during the wet season (Wilcoxon matched pairs, 1-tailed P = 0.276). Because I obtained different results for the wet and dry seasons, I tested for a seasonal effect on capture success and found that success was significantly lower in the dry season (mean = 0.0052, SD = 0.001) than in the wet season (mean = 0.0126, SD = 0.002; 2-tailed P < 0.001) The difference between the average values in the two seasons was 0.0074, which is equivalent to an additional 27 insects captured per hour of searching during the wet season.

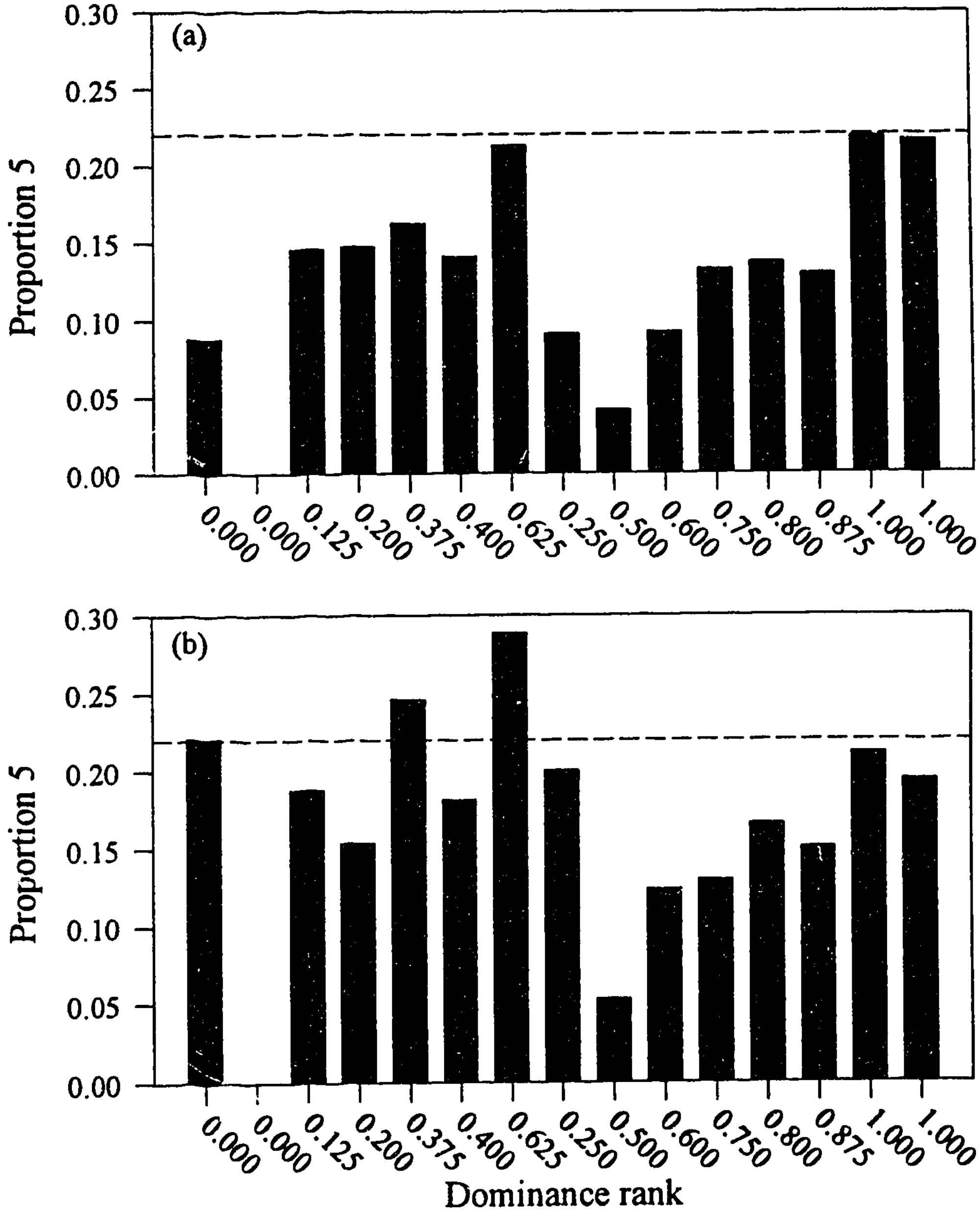
During the dry season dominance rank was positively correlated with proportion five, and negatively correlated with proportion one (Table 2-1), so dominant individuals tended to be in one of the front positions, but not the other. Therefore, I tested to see if animals experienced a different capture success in position one than in position five, and found no difference in either season (Wilcoxon matched pairs: 2-tailed P = 0.397 for the wet season and 2-tailed P = 0.875 for the dry season). Thus, the depletion cost experienced by animals is similar in both forward positions, and is significantly lower than in the back of the group only during the dry season.

Although both positions one and five represent a similar lack of depletion cost, position five (being a central position) should represent a higher benefit in terms of decreased predation risk. Therefore, dominant animals should be able to decrease their predation risk by being central, and still avoid depletion costs by being in position five.

However, as stated earlier, high ranking animals were not more likely to be in position five than in positions six and seven, and therefore were not showing any forward preferences within the centre of the group. Since the benefits I am proposing for position five involve foraging for insects, I performed the analysis again, using only those sessions where animals were foraging for insects. Using these samples, I again divided the number of readings that an animal was in position five, by the number of readings that it was in the centre of the group. This proportion was significantly correlated with dominance rank in the dry season (Pearson correlation coefficient = 0.4779, 1-tailed P = 0.042), but not during the wet season (Pearson correlation coefficient = -0.5273, 1-tailed P = 0.984).

In the dry season, three animals clearly spent the most time in position five (Fig. 2-3); these were the alpha males from each group (dominance rank = 1.000) and the alpha female from group two (dominance rank = 0.625). In the wet season there is no such pattern. Visual inspection of Fig. 2-3 (a) and (b) suggests that the two alpha males spent the same amount of time in position five in both seasons, but that most subordinates were in position five less during the dry season than they were in the wet season. A Wilcoxon matched-pairs test including all individuals except the alpha males, confirms that subordinate individuals were in position five less in the dry season than in the wet season (Z = -2.9810, 2-tailed P = 0.003). Thus, during the dry season, when there was a significant depletion cost in the back of the group, subordinate animals were less likely to be found in position 5 than they were during the wet season. However, the two most dominant individuals did not show a similar seasonal difference.

Figure 2-3: Proportion of time spent in position five by rank during the dry (a) and wet (b) seasons. Proportion five was calculated as the proportion of the group that is subordinate to the animal, and since there are two groups there are two ranks of zero (the lowest ranking animals) and two ranks of one (the highest ranking animals). The reference line represents proportion five for the alpha males during the dry season. The two alpha males have ranks of 1.000 and the alpha females from groups I and II have ranks of 0.400 and 0.625, respectively.


0.30
0.25
0.20
0.15
0.10
0.05
0.00
(a)
Proportion 5
0.000
0.000
0.125
0.200
0.375
0.400
0.625
0.250
0.500
0.600
0.750
0.800
0.875
1.000
1.000
(b)
Proportion 5
Dominance rank

I found that individuals had a higher density of neighbours when in the centre than when on the edge. Since a higher density of animals should increase depletion costs, I predicted that individuals should experience a lower capture success in the centre than on the edge. However, capture success was not significantly lower in the centre during either season (Table 2-4, Wilcoxon matched pairs: wet season, 1-tailed P = 0.181; dry season, 1-tailed P = 0.413).

Possible Mechanisms

As indicated in Fig. 2-2 (a) and (b), subordinate animals spent more time on the edge of the group than dominant animals. If dominant animals were actively excluding subordinates from the centre of the group, then individuals should have experienced higher rates of agonism when located in the centre of the group than on the edge. However, the rate of agonism (given and received) was not higher when animals were in the centre during either season (Wilcoxon pairs: wet season 1-tailed P = 0. 463; dry season 1-tailed P = 0.587; Table 2-5). Furthermore, although Fig. 2-3 shows that subordinates spent less time in position five during the dry season than during the wet season, the rate of agonism in position five was not higher in the dry season (mean = 0.0029, SD = 0.003) than in the wet season (mean = 0.0047, SD = 0.005; Wilcoxon matched pairs: Z = -1.5280, 1-tailed P = 0.938). Thus, although subordinates spent less time in position five during the dry season, they did not seem to be actively excluded from the position by dominant animals.

Capture success was lower in the dry season than in the wet season, suggesting that insects were less available in the dry season, and therefore that competition between

Table 2-5: Spatial effects on the rates of agonism and the proportion of proximity readings in which the animal had a dominant animal within 10 metres (referred to as Dom-prox).

Variable	Season	Position	Mean ± SD	Z	No. Pairs	1-Tailed P
Agonism	Wet	Centre	0.0059 ± 0.006	-0.094	14	0.46
		Edge	0.0050 ± 0.003			
Agonism	Dry	Centre	0.0026 ± 0.002	-0.220	14	0.59
		Edge	0.0031 ± 0.003			
Agonism	Wet	Total	0.0054 ± 0.004	-3.408	15	0.000
	Dry	Total	0.0028 ± 0.002			
Dom-prox	Wet	Centre	0.4825 ± 0.168	-2.845	14	0.002
		Edge	0.3492 ± 0.151			
Dom-prox	Dry	Centre	0.4308 ± 0.146	-2.934	14	0.002
		Edge	0.2808 ± 0.140			

Pairs were compared using Wilcoxon matched-pairs tests.

group members may have been higher. To see if foraging success for foods other than insects was lower in the dry season I used the amount of foraging time spent feeding, which is a rough estimate of return for unit effort. I have not used it to investigate the effects of spatial position on foraging success because, as argued by Janson (1990b), it is confounded by the movement of the group around the focal animal. If an animal stops to feed, the rest of the group may keep moving, and so the spatial position of the animal can change during the course of its feeding bout. Thus, the position in which an animal ingests an item is not necessarily the position it was in when it first found the food item. However, the ratio of foraging time spent feeding should represent an adequate measure of the general foraging success for individuals in each season. I calculated the ratio of time spent feeding to time spent foraging for each animal in each season, using only samples where individuals were not foraging for insects, and found that the feeding to foraging ratio was significantly lower in the dry season (mean = 0.37, SD = 0.076) than in the wet season (mean = 0.52, SD = 0.069; Wilcoxon matched pairs, 1-tailed $P < 0.001$).

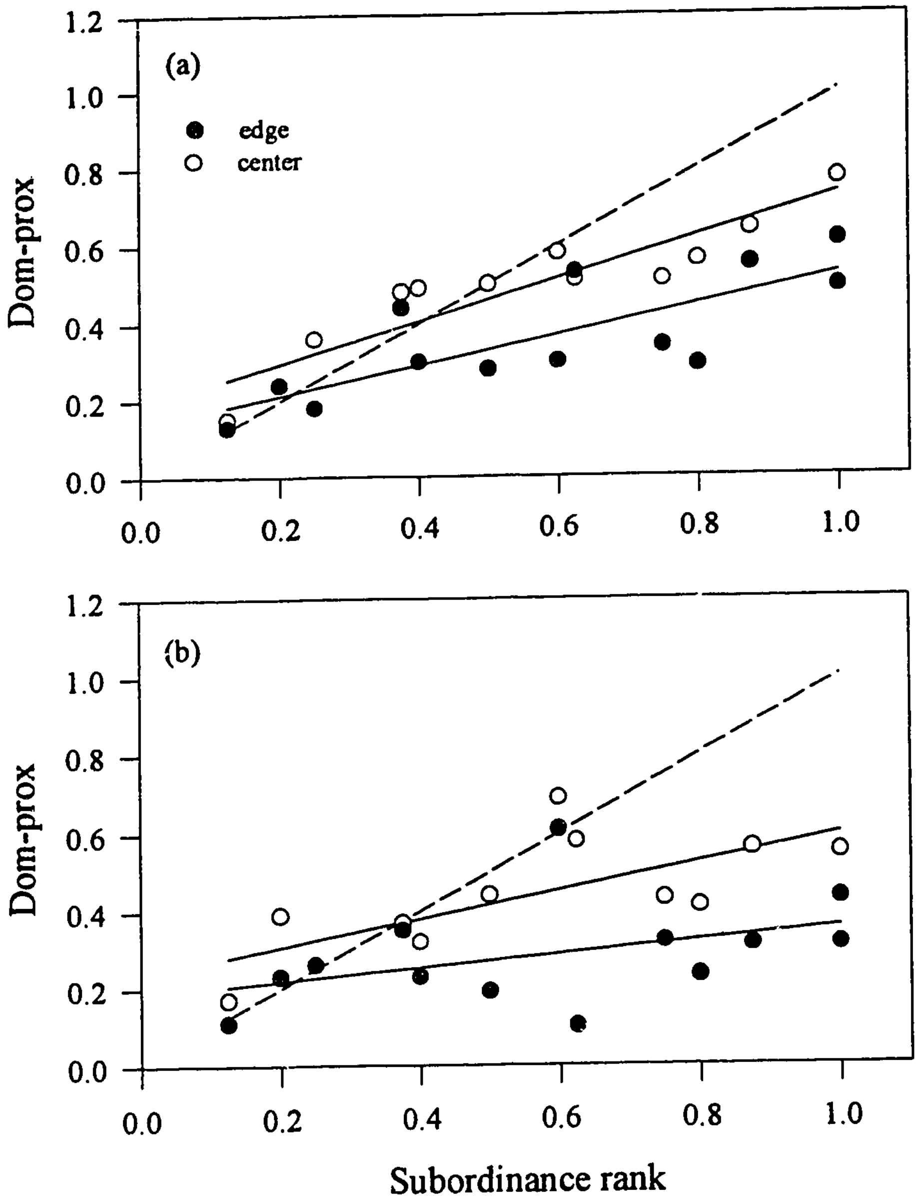
Since both capture success and the ratio of foraging time spent feeding were lower in the dry season than in the wet season, it is likely that animals experienced greater competition for food during the dry season. Therefore, if dominant animals were using aggression to exclude subordinates from preferred positions, the rate of aggression should have been higher in the dry season. An alternative explanation is that subordinates were avoiding central positions in order to avoid dominant animals, in which case the rate of agonism would not increase during the dry season. Animals did not experience higher rates of agonism in the dry season than during the wet season (Wilcoxon matched-pairs test, 1-tailed P = 0.9996; Table 2-5).

Janson (1990a) and Robinson (1981) both concluded that the amount of aggression received by an animal was more important than dominance rank in determining where individuals foraged. Specifically, those animals that received more aggression were more peripheral. However, in this study a partial correlation analysis (holding sex constant) showed that the edge ratio of an individual and the rate of aggression they received were not significantly correlated in either season (wet season: r = -0.19, P = 0.53; dry season: r = 0.27, P = 0.38). Thus, animals that received more aggression were not more likely to be on the edge of the group.

To investigate the possibility that subordinate animals were avoiding the centre of the group in order to avoid dominant animals, I tested whether an animal is less likely to have a dominant animal in proximity (defined as within ten metres), when on the edge. The variable used was the proportion of samples where the individual had a dominant animal in proximity (referred to as dom-prox in Table 2-5), the prediction being that this should be higher in the centre. The two dominant males were removed for this analysis, since it was not possible for them to have a dominant animal in proximity. There were highly significant differences in both seasons, with animals being more likely to have a dominant in proximity when in the centre than when on the edge (Wilcoxon matched-pairs tests: wet season, 1-tailed P = 0.002; dry season, 1-tailed P = 0.002). This result suggests that spending time on the edge would be a viable strategy for an individual to avoid having dominant animals in proximity. However, it does not show that subordinates are intentionally avoiding dominants; the same trend could occur if subordinates prefer the edge for some other reason.

In order to test whether subordinates were avoiding dominant animals, I calculated a "subordinance rank" for each animal, as the proportion of the group that ranks over that animal (similar to the dominance rank calculation described above, but replacing "s" with the number of animals in the hierarchy that are dominant to the animal). If animals are associating randomly, then the proportion of readings in which they have a dominant animal in proximity should be proportional to their subordinance rank. For example, an individual that has four animals ranking above it should be twice as likely to have a dominant animal in proximity as an animal that only has two animals that rank above it. Therefore, a regression of the variable dom-prox (from Table 2-5) by subordinance rank should have a slope of one. Figure 2-4 (a) and (b) shows this expected line with the origin through zero (i.e. $Y = X$), which would occur if animals always had other individuals in proximity to them. A change in slope can only occur if animals of different rank show differential association with dominant animals. If subordinates avoid dominants, and this tendency increases as subordinance rank increases (i.e. dominance rank decreases), then the slope should be less than 1. As shown in Fig. 2-4, subordinates were less likely to be in proximity to dominant animals than expected, both when in the centre and when on the edge. Furthermore, this trend was stronger on the edge than in the centre, and stronger in the dry season than in the wet season. In fact, the slope of the regression line for animals in edge positions during the dry season is not significantly different from zero, indicating that subordinate animals were no more likely than higher ranking animals to be in

Figure 2-4. Regressions of dom-prox (the proportion of all proximity readings during which an animal had a dominant animal within ten meters) by subordinance rank. The dashed line represents the expected line, if the origin went through zero ($Y = X$). All slopes were compared using analysis of covariance (Norusis, 1993), and then pairs of slopes were compared using the Tukey test (Zar, 1984). (a) Wet season: central readings, $Y = 0.547X + 0.186$, $r^2 = 0.84$, $P = 0.000$; edge readings, $Y = 0.390X + 0.135$, $r^2 = 0.60$, $P = 0.002$. The slopes of the regression lines for edge and center are both significantly different from the reference line ($P < 0.001$), and from each other ($P = 0.015$) (b) Dry season: center readings, $Y = 0.366X + 0.232$, $r^2 = 0.49$, $P = 0.011$; edge readings, $Y = 0.173X + 0.183$, $r^2 = 0.15$, $P = 0.20$. The slopes of the regression lines for edge and center are both significantly different from the reference line ($P < 0.001$), and from each other ($P = 0.023$). Additionally, the regression lines for center readings in the two seasons had significantly different slopes ($P = 0.012$), as did those for edge readings ($P = 0.009$).


(a)
● edge
○ center
Dom-prox
1.2
1.0
0.8
0.6
0.4
0.2
0.0
0.0
0.2
0.4
0.6
0.8
1.0
(b)
Dom-prox
1.2
1.0
0.8
0.6
0.4
0.2
0.0
0.0
0.2
0.4
0.6
0.8
1.0
Subordinance rank

proximity to a dominant. Thus, subordinates appeared to avoid dominants whether they were in the centre or on the edge, but they may have been able to do so more effectively on the edge. Seasonally, subordinates avoided dominants more during the dry season, when competition for food was highest, than during the wet season.

DISCUSSION

Spatial Position and Dominance rank

In my study groups, the tendency for an individual to be on the edge of the group was strongly affected by its dominance rank. Dominant animals were more likely to be in the centre than subordinate animals, and less likely to be on the edge. However, the spatial distribution of animals between the front and back of the group was not affected by dominance rank. I assume that dominant animals are able to distribute themselves according to their preferences for feeding positions, but that subordinates must also take into account factors such as the location of more dominant animals, and the degree of contest competition. My findings suggest that the centralness of a spatial position affects whether or not it is preferred by white-faced capuchins, but that the forwardness of a spatial position is only important when food items are low in abundance so that depletion by animals in the front of the group represents a significant cost to those in the back.

Spatial Position and Predation Risk

Hamilton (1971) introduced the concept of a "domain of danger", to describe the area in which an individual is vulnerable to attack from a hidden predator that strikes at the closest prey item. An individual's domain of danger is an area consisting of all points closer to the owner of the domain than to any other individual. Thus, animals at the periphery of a group have larger domains of danger than those in the centre of the group. This concept applies particularly well to boa predation on C. capucinus (Chapman 1986), as boas are ambush predators and so are expected to attack the first animal that comes within striking distance (Greene 1983). Vine (1971) furthered Hamilton's argument, dealing specifically with predation by a predator that approaches from outside the group, and concluded that there was a quantifiably higher risk for peripheral animals than for central animals. This scenario can be applied to predation by felids, coyotes, and tayras, which are also potential predators for capuchins in Santa Rosa (Freese 1983).

I found that spatial position had no effect on vigilance behaviour in my study groups. Although many studies have found that peripheral animals are more vigilant than central ones (see introduction), some have found that the spatial position of an animal does not affect its vigilance behaviour. For example, Underwood (1981) found that two out of five species of antelope did not exhibit differential amounts of vigilance across spatial positions within the group. Of particular interest to this study are the results from two studies on other species of capuchin monkeys. Janson (1990b) found that C. apella are more vigilant in the front of the group than at the back, but that adults do not prefer areas that are associated with low rates of vigilance (which Janson argues represent areas of lower predation risk). He did not examine the variation in vigilance rates between central and edge positions. Robinson (1981) found that correlations between vigilance and centralness in C. nigrivittatus do not show a consistent trend across age sex classes;

centralness correlates with a decrease in vigilance for females and juveniles, but not for adult and subadult males. Thus, studies of the vigilance across spatial positions within groups do not show consistent results; some animals adjust their rates of vigilance to their spatial position, while others do not.

Although the presence of a correlation between vigilance and peripheralness is often used to support the view that predation risk is higher on the edge, the absence of such a trend does not preclude the existence of a gradient in predation pressure. While increased vigilance is often correlated with higher predation pressure, the two are not always found together. Many other factors can affect an animal's vigilance behaviour, including social vigilance directed at other group members (Quenette 1990), and vigilance aimed at the detection of other groups (Fedigan and Rose 1994). These other forms of vigilance may mask vigilance intended for predator detection, and observers will likely be unable to discriminate between them. Additionally, not all behaviour relating to predator detection will be overt, and thus detectable to an observer. Animals may be more wary in certain spatial positions without demonstrating observable differences in vigilance behaviour. Thus, the lack of spatial effects on vigilance behaviour in this study does not imply that predation risk is equal between spatial positions. Furthermore, since I found that the alpha males were significantly more vigilant than other group members, my results lend support to the conclusion made by Fedigan and Rose (1994), that the vigilance behaviour of male C. capucinus in Santa Rosa National Park was directed primarily towards males in other groups, rather than towards potential predators.

The size of an individual's domain of danger is inversely related to its number of neighbours (Busse, 1984). Therefore, since capuchins had fewer neighbours when they foraged on the edge, they should have had larger domains of danger while on the edge than while in the centre. Additionally, they would have obtained lower benefits from conspecific vigilance and from the dilution effect. Thus, although animals foraging on the edge of the group probably had a lower predation risk than if they were solitary, the benefit gained was not as high as that gained when they foraged in more central positions.

Spatial Position and Feeding Competition

Robinson (1981) found that the tendency of an individual to be in the front of the group was correlated with greater success at capturing insects in C. nigrivittatus. In my study groups, capture success was higher when individuals foraged in the front positions than in the back positions, but only in the dry season. Since capture success was much lower in the dry season than in the wet season, it is likely that depletion was of little consequence in the wet season, but only influenced capture success when insects were relatively rare. Because dominance rank affects the distribution of animals between edge and centre, but not between front and back, the two positions that make up the front of the group (positions one and five) should contain animals of different rank. However, both positions represent similar capture success. Therefore, it seems that the tendency of high ranking animals to be in position five and not in position one was a strategy to reduce predation risk, rather than a strategy to increase foraging success. By foraging for insects in position five rather than in position one, dominant animals were able to take advantage of the increased capture success found in the front of the group, and the decrease in predation risk found in the centre of the group. The suggestion that position five was a preferred position is supported by rank-related seasonal differences in the amount of time individuals spent there. The tendency for subordinate animals to be in position five was lower in the dry season, while the two most dominant animals did not show a similar seasonal difference. Thus, during the dry season, an increase in scramble competition was associated with a change in the spatial behaviour of subordinate animals, but not dominant animals.

Contrary to my predictions, capture success was not lower in the centre of the group than on the edge, despite the higher density of animals in the centre. Since the edge of the group is made up of both the leading and trailing edges, any differences between edge and centre positions may be confounded by the depletion effect from front to back. Furthermore, it is likely that the depletion of insects is a very localized phenomenon. Thus, although foraging over areas that have already been searched by other animals may affect the capture success of an individual, having other animals foraging nearby may not. The effect of a given density will depend on the distance over which an animal can detect an insect, and therefore the radius around itself that it is able to search. As density increases, the degree to which an individual's search field overlaps with those of its neighbours will also increase. In order to minimize the effects of density, animals may space themselves so that their search fields will overlap as little as possible. Consequently, central animals will receive few depletion costs from their neighbours. However, at high densities, the borders of individual search fields should be very close together. Therefore, one row of animals will search an entire area, and individuals behind them will receive a depletion cost. Thus, animals may be able to space themselves so that they avoid depletion costs due to increased densities in the centre of the group, but they will still be subject to depletion costs from front to back.

Why Are Subordinates on the Edge?

Subordinates may be more peripheral because dominant individuals actively defend central positions, or because subordinate animals avoid central positions in order to avoid dominant animals. Since the rate of agonism experienced by animals was not higher in the centre of the group than on the edge, it does not appear that dominants were actively excluding subordinates from central positions. Furthermore, although my results show that subordinate animals were less likely to be in position five during the dry season than during the wet season, the rate of agonism in position five was not higher during the dry season, suggesting that active exclusion by dominant animals cannot explain the seasonal difference.

Alternatively, if contest competition is important for white-faced capuchins, subordinate animals may try to avoid foraging near dominant animals. During 500 hours of contact with the study groups in the 1995 dry season, I recorded 57 supplantations over food and 26 supplantations over water. This indicates that foraging capuchins are subject to contest competition , and that subordinates would therefore benefit from avoiding dominant individuals while foraging. My results suggest that subordinates do avoid dominant animals, and that they do so to a greater extent during the dry season. Since both capture success and foraging success were lower in the dry season, I argue that foraging competition was probably higher in the dry season. Thus, the fact that subordinates avoid dominant animals more in the dry season supports the hypothesis that subordinates avoid dominants as a strategy to deal with foraging competition. Since animals were less likely to have a dominant animal in proximity to them when they were on the edge than when they were in the centre, spending time on the edge would be an effective strategy for subordinates to avoid foraging in proximity to dominant animals.

Phillips (1995) has suggested that C. capucinus avoid contest competition by foraging in a dispersed group. My findings suggest that this may be a strategy used more by subordinate animals than by dominant animals. Since dominant animals will not receive as high a cost from contest competition, they are able to forage in central positions, where this form of competition is most likely. Subordinates, however, may disperse to the edge of the group in order to reduce the likelihood that they will be involved in contest competition.

Janson (1990a) found that aggression received, in particular aggression from the dominant male, affected the spatial preferences of subordinate C. apella. Robinson (1981) found a similar trend for C. nigrivittatus, except that aggression from the alpha female was the most important. The lack of correlation between aggression received and spatial preferences in my study, and the finding that aggression rates do not vary between spatial positions suggests that direct aggressive interaction is less important for spatial regulation in C. capucinus than in other Cebus species.

Spatial Benefits Afforded by High Rank

The animals in my study groups were faced with two cost-benefit gradients: predation risk increased from the centre of the group to the edge, while scramble competition for insects was greater in the back of the group than in the front (but only during the dry season). Dominant animals spent more time in the centre of the group, and thereby decreased their predation risk. In contrast, subordinates spent more time in the riskier edge positions, probably as a strategy to avoid contest competition from dominant animals. The interaction of the two gradients means that position five would have had the best cost/benefit ratio during the dry season. During the wet season, scramble competition was likely minimal, so all central positions should have been equally beneficial. As predicted, dominance rank was correlated with the preference of position five over positions six and seven while animals foraged for insects during the dry season but not during the wet season. Further support for this argument comes from the finding that, while dominant animals were able to maintained the proportion of time that they spent in position five during both seasons, subordinates decreased the time they spent there during the dry season, when competition for insects likely increased. Thus it appears that dominant animals are able to occupy the preferred positions within a group, while subordinates probably have to trade-off the benefits offered by preferred positions with the costs of being exposed to contest competition from dominant animals. In this study, it appears that the benefit of avoiding dominant animals outweighs any increased risk of predation on the edge of the group.

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Chapter Three. Dominance and diet: Patterns of aggression and avoidance

Increased competition for food is the primary cost incurred by living in a group (Alexander 1974; van Schaik 1983). This competition will occur in two forms: scramble (or indirect) competition, when some animals deplete a resource before others have a chance to feed, and contest (or direct) competition, when aggression or displacement between group members leads to a decreased intake for some group members (Janson and van Schaik 1988). In some species, contest competition may be more subtle, with subordinates actively avoiding dominants, but the consequences of this avoidance can lead to reduced access to preferred foods (van Schaik et al. 1983; Janson and van Schaik 1988). Presumably, animals should attempt to decrease either form of competition whenever possible. This study examines the effects of contest competition, mediated by dominance rank, in white-faced capuchins (Cebus capucinus).

Within groups organized by a social dominance hierarchy, the costs associated with competition for food may be skewed so that dominant animals receive a lower cost than subordinate animals. Contest competition will be more costly for subordinate animals than for dominant animals; animals of lower rank will have more animals above them in the dominance hierarchy, and so will have more animals that can exclude them from resources. Another foraging cost of group living that may be greater for subordinates than dominants is the cost imposed by scrounging. Scrounging occurs when an animal (the scrounger) uses the behavioural investment of another animal (the producer) to obtain a limited resource (Barnard and Sibly 1981). Food robbing (or kleptoparasitism) is a special case of scrounging that occurs when one animal takes a food item from the animal that found it (Brockman and Barnard 1979). Other forms of food-related scrounging include sharing patches found by a producer, and area copying, whereby animals search in the immediate area around an animal that has recently captured a prey item. Dominance rank will be an important component of food robbing, since a dominant animal is likely to take a food item from a subordinate without contest, while the reverse is probably unlikely (Ens et al. 1990). Dominance rank will also be important if scroungers supplant producers from patches of food, rather than sharing them (e.g. Rohwer and Ewald 1981; Czikeli, 1983; Gore 1993).

The distribution of food items will influence both the degree of contest competition over those items (and therefore the effect of dominance), and the likelihood of scrounging. When food items are small and cryptic, contest competition over clumped food items will be greater than over dispersed items, since clumps are defendable (Whitten 1983; Boccia et al. 1988; Caraco et al. 1989). Furthermore, since group members must feed in close proximity when exploiting clumped foods, animals will be more likely to be involved in aggressive encounters with other group members (Phillips 1995), and subordinates will be at a disadvantage, since they will be more likely to receive aggression. Scrounging will also be affected by the distribution of small food items, since the supplantation of subordinates from patches will be more likely if food is clumped (Giraldeau et al. 1990). This prediction is supported by the finding that dominant Harris' sparrows (Zonotrichia querula) used subordinates to find food only when the food was clumped (Rohwer and Ewald 1981).

The use of large food items, and food items with long handling times (either for the food item itself or the substrate in which it is found) may also be influenced by the dominance status of an individual. Since animals exploiting items with long handling times are stationary, other group members will be moving past them, and so they will be vulnerable to supplantation by more dominant animals (Janson 1990). Furthermore, food robbing is more likely to occur over larger, more conspicuous food items (Brockman and Barnard 1979), which frequently have a longer handling time. Ens et al. (1990) found that curlews (Neumenius arquata) attacked each other over large prey items, but never over small ones, and that handling time was significantly correlated with the rate of food robbing. Similarly, Thompson (1986) found that kleptoparasitic gulls (Larus ridibundus) stole only large worms from plovers (Vanellus vanellus and Pluvialis apricaria). If there is a cost associated with handling, then animals supplanted after they have handled an item but before they have ingested it will receive a cost, and no benefit but the supplanter will receive the benefit at a lower cost than if they had discovered the item themselves (a further benefit to kleptoparasitism). If the likelihood of having such an item taken away is high for subordinates, it may be advantageous for them to avoid these food items entirely.

Another factor that influences the likelihood of competition over a resource is the benefit gained from the resource (Popp and Devore 1979). Food resources of high value will include individual food items with a high nutritional value, and patches of food, which will be more valuable than single items of similar nutritional value (Rubenstein 1981). Since these items confer a large benefit on the animal that eats them, dominants will be more likely to initiate interactions over them. However, subordinates will also be more likely to escalate, rather than giving up the food item without contest, when the resource is of higher value (Rubenstein 1981).

Thus, the cost of obtaining a food item is influenced by both the dominance rank of the animal, and characteristics of the food item. Since optimal diet theory suggests that animals should include items in their diet based (in part) on the net energy gained from the item (energy contained in the food item minus the energy necessary to obtain it), an animal's dominance rank within a group may influence the foods it includes in its diet. The same prediction also arises from the model of Engen et al. (1988), who suggest that the inclusion of food items in the diet will be affected by the presence of competition, and therefore that the diet of subordinate animals should be influenced by the presence of dominants. Post et al. (1980) found that animals similar in rank have a greater dietary overlap than animals with a greater difference in rank, indicating that subordinates have different diets than dominant animals. Barnard and Brown (1981) found that shrews (*Sorex araneus* L.) decrease their selectivity for food items when a competitor is present. Pimm et al. (1985) showed that two subordinate species of hummingbirds (*Eugenes fulgens* and *Archilochus alexandri*) shifted first to a generalist strategy, and then to selecting the poorer patch, with increasing density of a dominant species (*Lampornis clemenciae*). Thus, I predict that subordinate *C. capucinus* will show a lower degree of dietary overlap with high ranking animals than with those of similar rank. Furthermore, if the presence of dominant animals causes subordinate animals to be less selective, then subordinate animals should have more diverse diets than dominant animals.

My aim in this study was twofold: first to investigate the effect of dominance rank on the diet of white-faced capuchins (C. capucinus), and second to determine the influence of the distribution and handling time of food items on rank-related dietary differences. Phillips (1995) concluded that contest competition is not important to C. capucinus, based on the low rate of aggression exhibited by this species. I argue that a more subtle form of contest competition, mediated by the avoidance of dominant animals by subordinates, is occurring, and attempt to support this with data on rank-related dietary differences. Specifically, I investigate the influence of rank on dietary diversity, dietary overlap between pairs of animals, and the relative use of clumped foods and foods with long handling times by animals of different rank.

METHODS

Study Site and Species

The study was conducted in the dry tropical forest of Santa Rosa National Park, Costa Rica. The climate is characterized by two distinct seasons; the dry season extends from mid-December to mid May, and the wet season runs from May through November (Chapman 1987).

The white-faced capuchin (C. capucinus) is a medium sized, arboreal monkey in which females weigh about 70% of the average male weight of three kilograms (Glander et al. 1991). White-faced capuchins live in multi-male, multi-female groups (Oppenheimer 1968; Buckley 1983; Mitchell 1989; Perry 1995), and in Santa Rosa the average group size is 14 individuals (Fedigan 1986; Fedigan et al. in press). Within these groups it is possible to determine a linear dominance ranking among adults, with adult males individually dominant over females, except for the alpha female who often ranks above some of the lower ranking males (Fedigan 1993). Cebus capucinus are omnivorous; the bulk of their diet is made up of fruit, and to a lesser extent insects (Chapman and Fedigan 1990; Freese and Oppenheimer 1981). In addition, they prey opportunistically on small vertebrates (Fedigan 1990; Perry and Rose 1994), and only rarely eat leaves and flowers (Oppenheimer 1968; Buckley 1983; Chapman and Fedigan 1990; Mitchell 1989). Capuchin monkeys exhibit a highly flexible diet, with differences between age-sex classes in diet and foraging strategies (Rose 1994; Fragaszy and Boinski In press).

Data Collection

Focal data were collected on the adult and subadult members of two groups. Group I consisted of three adult males, three adult females, five juveniles, and three infants. Group II consisted of three adult males, four adult females, two subadult males, ten juveniles, and four infants. Both groups were well habituated to observation, as they have been part of a long term study by Dr. L. M. Fedigan for the past 11 years.

Behaviour was sampled using the focal animal continuous sampling method (Altmann 1974), with a sample length of ten minutes. Sampling was performed daily, from dawn to dusk, throughout the periods of May 1994 to August 1994 (wet season), and January 1995 to March 1995 (dry season). Similar amounts of data were collected in each field season (169 hours in the wet season and 151 hours in the dry season), resulting in a total of 320 hours of data. An average of 11.32 hours of data were taken for each animal during the wet season (totals for individuals ranged from 10.79 to 11.88 hours), and an average of 10.09 hours of data was taken for each animal in the dry season (totals ranged from 9.93 to 10.34 hours). At the beginning and end of each focal session I recorded the identity of all animals within 10 metres of the focal animal.

In addition to focal sampling, all supplantations, threats, fear grimaces, and retreats (Appendix A) were recorded *ad libitum* (Altmann 1974) and used to construct a dominance hierarchy. Once dominance hierarchies had been established for each group, a dominance rank score was computed for each animal so that data from both groups could be pooled. The score represents the proportion of animals in the hierarchy over which that animal ranks, and is calculated as $s / N-1$, where s = the number of animals in the hierarchy that are subordinate to the animal, and N = the total number of animals in the hierarchy (Cheney & Seyfarth 1981). During the second (dry season) field season, the object over which the interaction occurred (if this was clear) was also recorded.

Dietary Comparisons

Dietary overlap between animals was measured using the simplified Morisita's index (Krebs 1989). The index was calculated as

$$C_H = \frac{2 \Sigma p_{ij} p_{ik}}{\Sigma p_{ij}^2 + p_{ik}^2}$$

where C_H = simplified Morisita index of overlap between individuals *j* and *k*, p_{ij} and p_{ik} = the proportion of time individuals *j* and *k* spent feeding on food type *i*. A mean dietary overlap was calculated for each rank difference (e.g. the overlap for the pair of animals ranking 0.2 and 1.0 was averaged with the overlap for the pair ranking 0 and 0.8, since the rank difference for both pairs was 0.8), yielding 13 mean overlap values (five for group I and 8 for group II). These values were then regressed against rank difference, to investigate whether overlap was greater for animals that were farther apart in the hierarchy.

Each food item was classified as dispersed (single food items spread out across the habitat), small clumps (multiple food items occurring together, but only one or two monkeys can feed in the clump at a time), or large clumps (more than two monkeys can feed in a clump at one time). There was only one food item (figs, Ficus sp.) for which some clumps were large enough that all of group I fed in a clump at the same time (group II was never seen to do this). With this exception large clumps held greater than two monkeys, but less than the whole group. Food items were also classified as having long or short handling times. Food items with long handling times either required some form of processing, or were large enough that they required more than one bite, and thus took more than a few seconds to consume. Appendix C contains a list of the foods eaten in the wet and dry seasons, and their classification by dispersion and handling time. To compare the use of different food items or food types (i.e. the three dispersions and two handling times) I used the proportion of feeding time spent feeding on that item or type. Proportions were arcsin transformed prior to applying statistical tests.

To investigate the effect of rank on the use of different food types I used a repeated measures ANOVA, with three within subjects factors (handling time, dispersion of the food source, and dominance rank class). Dominance rank class was divided into three classes: high (dominance rank of 0.67 to 1.00), medium (dominance rank of 0.34 to

0.66), and low (dominance rank of 0 to 0.33). Group was also included as a between subjects factor, to control for differences between groups. The terms of interest in the ANOVA were the second order interactions between rank class and dispersion, and between rank class and handling time.

To investigate whether supplantations and aggressive encounters occurred more frequently over certain food items, I examined the supplantations, threats, and chases observed *ad libitum* for which the item contested was easily discerned. I obtained the frequency of such acts per food item, and then divided these by the total amount of time the monkeys spent feeding on the item. This controlled for differences in the amount of time spent feeding on each item, and therefore the time available for aggression to occur over different food items. However, it is important to note that these numbers are not true rates of aggression, since the aggressive acts were recorded whenever they were seen, not only during focal samples, and therefore I will refer to the numbers obtained as aggression scores throughout this paper. These scores are presented in a bar graph in the results, but no statistical test was performed on them. Additionally, I tallied the number of foods over which aggression occurred, for each of the two handling time categories and in each of the three dispersion categories. I tested whether aggression was more likely to occur over certain food types, using a G-test on a three by two by two (dispersion by handling time by aggression or no aggression) contingency table.

Since scrounging involves the supplantation of an animal from a food item, the rate of supplantation received by an animal will be an indication of the cost it receives from scrounging. The rate of supplantation may be slightly higher than the rate of scrounging, because some supplantations occur that are not directly related to food. However, 85% of all supplantations observed were over food, so the rate of supplantation should be a close approximation for the rate of scrounging. The rate of supplantations received was calculated for each individual, in each field season, from the focal session data. These rates were then regressed against rank, to see if subordinate animals were supplanted at a higher rate than dominant animals.

To examine the effect of proximity to dominant animals on the proportion of time animals spent feeding on the different food types I used a repeated measures ANOVA. I included three within subjects factors (proximity, dispersion category of the food type, and handling time category) and one between subjects factor (group). There were two categories for proximity; the first occurred when the animal was in proximity (within ten metres) to at least one dominant animal, and the second occurred when the individual was in proximity to only subordinate animals, but no dominant animals. The relevant terms in the ANOVA were the terms for the interactions between dispersion and proximity, and between handling time and proximity. To determine whether subordinate animals monitor dominants, I tested whether subordinates were more vigilant when they had a dominant animal within ten metres, using a Wilcoxon matched pairs test, pairing the proportion of time an animal spent being vigilant when it had only subordinate animals within ten metres with the amount of time it spent being vigilant when it had at least one dominant animal within ten metres.

Dietary diversity was calculated using Levin's measure of niche breadth, which accounts for both the number of food types in the diet and the proportion in which they are eaten (Krebs 1989). Levin's measure is calculated as $B = 1 / \Sigma p_j^2$, where B = Levin's measure of niche breadth and p_j = the proportion of feeding time that the individual spent feeding on food item j ($\Sigma P_j = 1.0$). The measure was then standardized, to express it on a scale from 0 to 1.0, as $B_A = B-1 / n-1$, where B_A = Levin's standardized niche breadth, B = Levin's measure of niche breadth, n = the number of possible food items (Krebs 1989). This standardized measure was regressed against dominance rank to determine whether rank affected the diversity of an individual's diet.

RESULTS

Dietary Overlap

Mean dietary overlap decreased as the difference in rank between the animals being compared increased (Fig. 3-1). Thus, animals of similar rank had more similar diets than those further apart in the hierarchy. This trend was significant in both seasons (dry season $r^2 = 0.72$, $P = 0.0008$; wet season $r^2 = 0.65$, $P = 0.0002$), but the slope of the regression line was steeper in the dry season than in the wet season (T-test, Zar 1984, $P = 0.01$).

Since the two points with the lowest overlap differences were both the result of comparison's made in group II, the question of group differences for this trend is raised. I therefore recalculated the regression lines for both seasons, with the groups separate, and tested for a slope difference between the two groups. The slopes were not significantly different in either season (Tukey test, Zar 1984, dry season: $q = 1.04$, $P > 0.50$; wet season: $q = 1.26$, $P > 0.50$). In fact, all comparisons within group II are lower than those

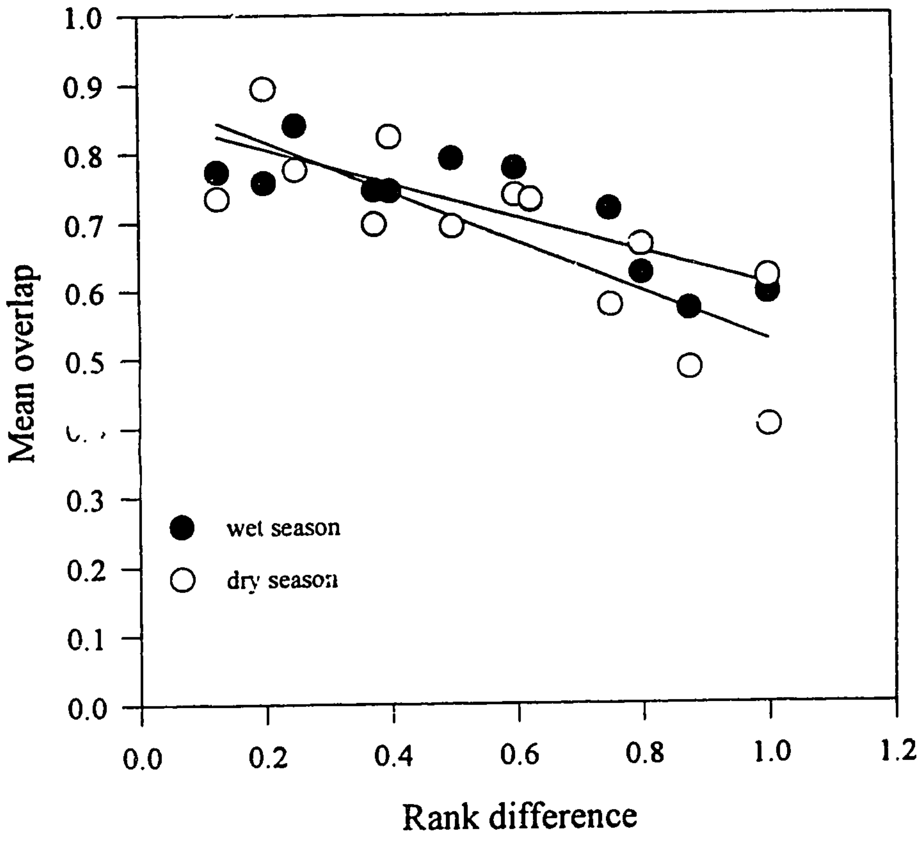

Figure 3-1: Mean dietary overlap between pairs of animals as a function of difference in rank ($Y = 0.86 - 0.25X$, $r^2 = 0.72$, $P = 0.0008$; wet season: $Y = 0.89 - 0.36X$, $r^2 = 0.65$, $P = 0.0002$). Overlap was calculated using the simplified Morisita's index (see text for details), and then means were obtained for each rank difference (5 values for group I and 8 for group II).

of group I during the dry season, but not during the wet season (the difference in the Y intercept between the two groups is 0.11 in the dry season and only 0.03 in the wet season), which is the reason that the two lowest points are from group II. The lower degree of overlap between animals in group II may be explained by the fact that group II was larger (22 individuals versus 15 in group I), and therefore individuals in group II may have experienced more competition. However, since the slopes of the regression lines for each group do not differ, rank has a similar effect on dietary overlap in both groups.

Dominance Rank and the Use of Different Food Types

Dominance rank affected the use of dispersion types, but not handling time types. The interaction between rank class and dispersion was significant in the dry season (P = 0.002), but not in the wet season (P = 0.45). As indicated in Fig. 3-2, during the dry season high ranking animals spent a greater proportion of their time feeding on food items in large clumps than moderate or low ranking animals. The reverse trend is shown for food items that occur in small clumps, and very little trend is shown for dispersed food items. The interaction term for rank class by handling time was not significant in either season (P = 0.34 in the dry season and P = 0.57 in the wet season). In case the absence of a trend for dispersion types during the wet season was due to the inclusion of figs (the one food source where all group members of group I could feed in the clump at the same time), the wet season data was reanalyzed with the time spent feeding on figs excluded. Dispersion class still did not significantly influence feeding time by rank.

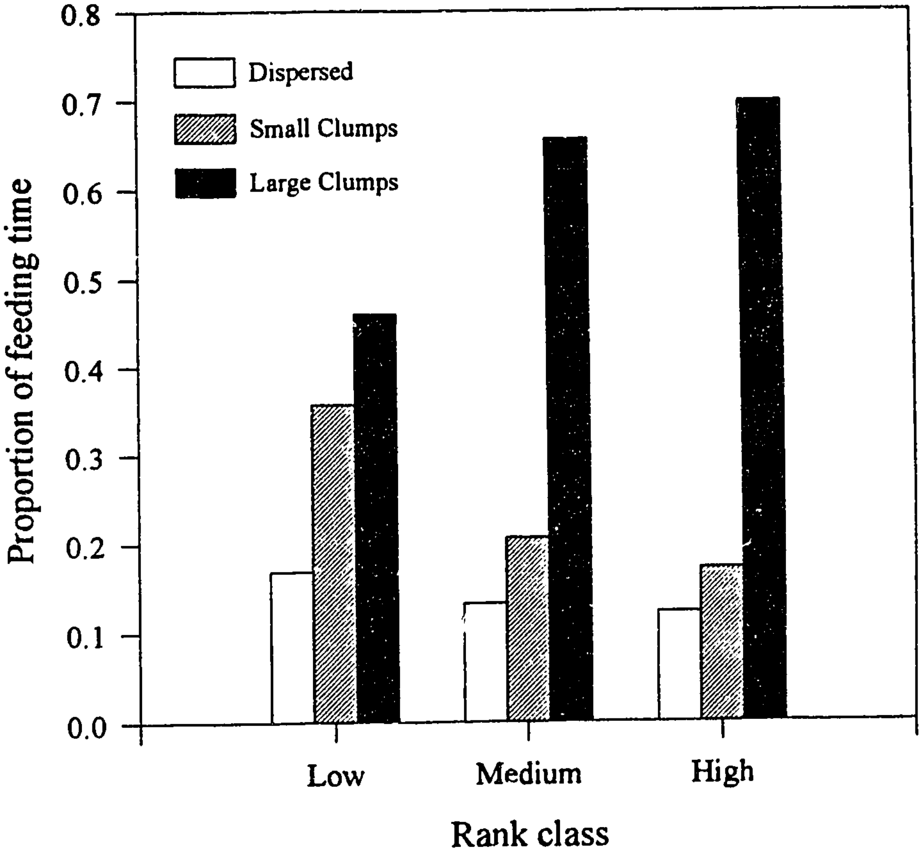

Figure 3-2: The use of food items in the dry season that were dispersed, or occurred in small or large patches by animals of low, medium, and high rank (see text for definition). Values are expressed as the proportion of total feeding time that animals spent feeding on foods of each type.

Supplantations Over Food Items

Aggressive acts occurred over 13 of the 41 food items that the monkeys were observed to eat during the dry season. Aggression scores were especially high for bee hives and squirrels, which are large, conspicuous items with very long handling times (Fig. 3-3). The likelihood of supplantation or aggression did not differ between the dispersion types (G = 1.202, D. F. = 2, P = 0.56; Table 3-1), but did differ between the handling time types (G = 6.280, D. F. = 1, P = 0.013; Table 3-1). Thus, animals were not more likely to be supplanted or receive aggression over clumped food items (regardless of the size of the clump), but were more likely to receive aggression or be supplanted over food items with long handling times. Low ranking animals received a higher rate of supplantation than higher ranking animals (linear regression, wet season: $r^2 = 0.43$, P = 0.008; dry season: $r^2 = 0.29$, P = 0.04).

Proximity To Dominant Animals

Proximity to dominant animals did not affect the use of the different food types. The use of foods that were dispersed, or occurred in small or large clumps, was not influenced by proximity to dominant animals (wet season, P = 0.35; dry season, P = 0.34). Similarly, the interaction between handling time and proximity was not significant (wet season, P = 0.12; dry season P = 0.92). During the dry season, subordinates were more vigilant when they had a dominant animal within ten metres than when only lower ranking animals were within ten metres (Z = -2.69, P = 0.007). However, this trend was not shown in the wet season (Z = -0.245, P = 0.81).

Figure 3-3: Aggression scores for the 14 foods over which aggressive acts occurred during the dry season. Aggression scores were calculated as the number of aggressive acts recorded for each food item (these data were recorded *ad libitum*), divided by the amount of time the monkeys fed on the food item during focal samples (see text for further explanation). The dashed reference lines divide the food items into foods that are dispersed, or occur in small or large clumps. Hatched bars represent food items with long handling times, and white bars represent those with short handling times. The labels 'Large e. in' and 'Small e. in.' represent large and small embedded insects.

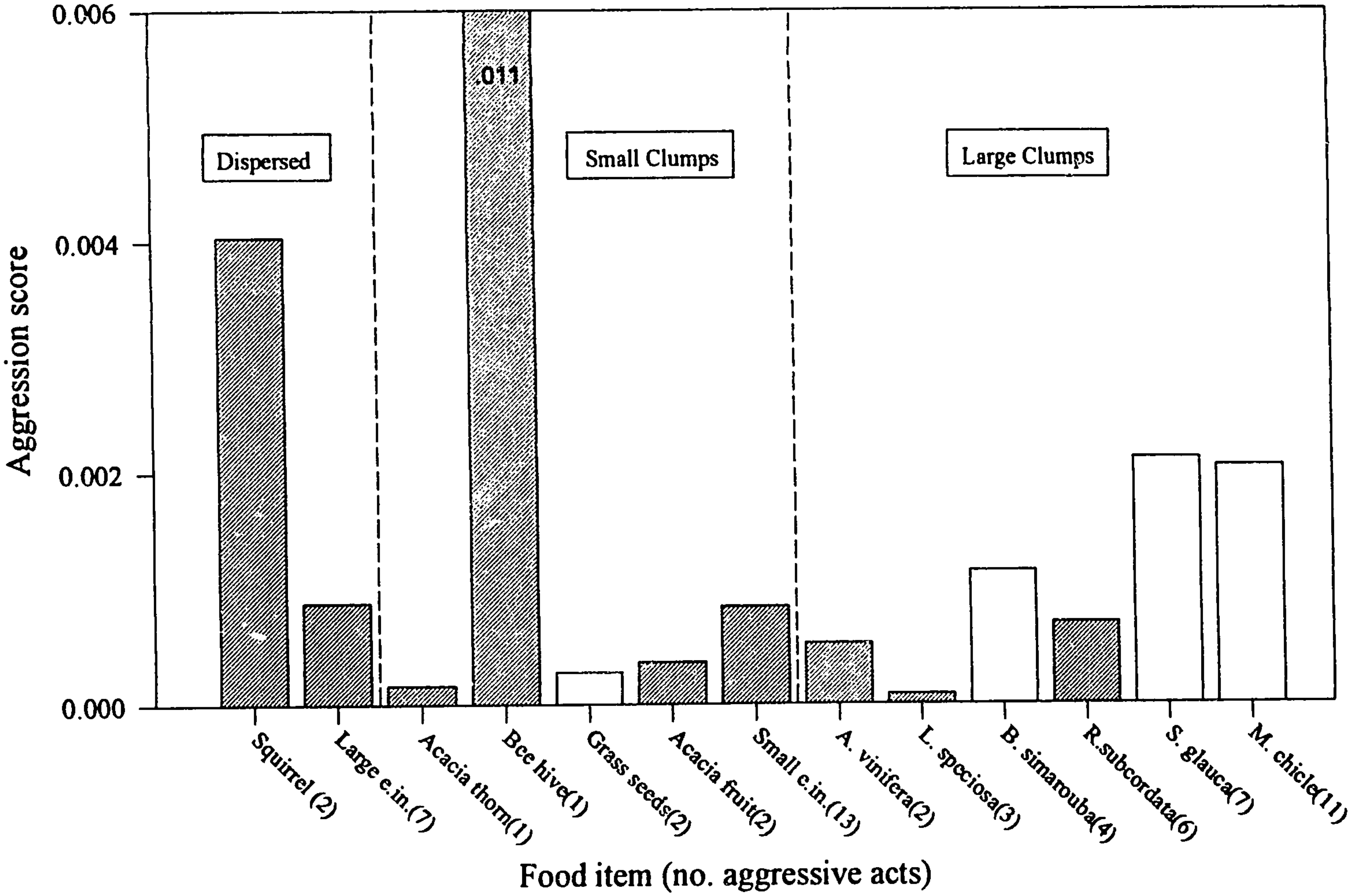
0.006
0.004
0.002
0.000
Aggression score
Dispersed
Small Clumps
Large Clumps
.011
Squirrel (2)
Large e.in.(7)
Acacia thorn(1)
Bee hive(1)
Grass seeds(2)
Acacia fruit(2)
Small e.in.(13)
A. vinifera(2)
L. speciosa(3)
B. simarouba(4)
R.subcordata(6)
S. glauca(7)
M. chicle(11)
Food item (no. aggressive acts)

Table 3-1: Frequencies of aggressive acts over different food types.

	Dispersion			
	Dispersed	**Small Clumps**	**Large Clumps**	**Total**
Aggression	2	5	6	13
No Aggression	6	14	8	28
Total	8	19	14	41

	Handling Time		
	Long	**Short**	**Total**
Aggression	9	4	13
No Aggression	9	19	28
Total	18	23	41

Dietary Diversity

Levin's standardized measure of niche breadth was significantly affected by dominance rank in the dry season (linear regression; $r^2 = 0.344$, $P = 0.022$), but not in the wet season ($r^2 = 0.028$, $P = 0.583$). During the dry season, low rank was associated with greater dietary diversity, and high rank with low dietary diversity (Fig. 3-4). However, this relationship was not reflected in the number of foods used by individuals, since a regression of this variable by dominance rank was not significant ($r^2 = 0.007$, $P = 0.773$). Thus, the trend must have been due to a difference in the way that animals distributed their time across the food items in their diet. I calculated dietary evenness for each individual during the dry season as $E = B / B_{MAX}$, where B = Levin's measure of niche breadth and B_{MAX} = the maximum value possible for B, which is equal to the number of food items (Krebs 1989). As expected, evenness decreased with increasing rank (linear regression, $r^2 = 0.468$, $P = 0.005$), suggesting that the trend found for dietary diversity was the result of a tendency for high ranking animals to specialize on a few food items.

In white faced capuchins, dominance rank is highly correlated with sex, and the majority of males within a group are dominant over females. Hence, distinguishing between sex differences and differences based on dominance rank is difficult. In an attempt to separate these factors, I performed the regression of Levin's standardized measure of niche breadth again, separately for each sex. These results should be interpreted with caution, however, since sample sizes are small (seven females and eight males). There was no significant trend within either sex (dry season: males, $r^2 = 0.016$ $P = 0.77$; females, $r^2 = 0.000$, $P = 0.99$; wet season: males, $r^2 = 0.40$, $P = 0.095$, females,

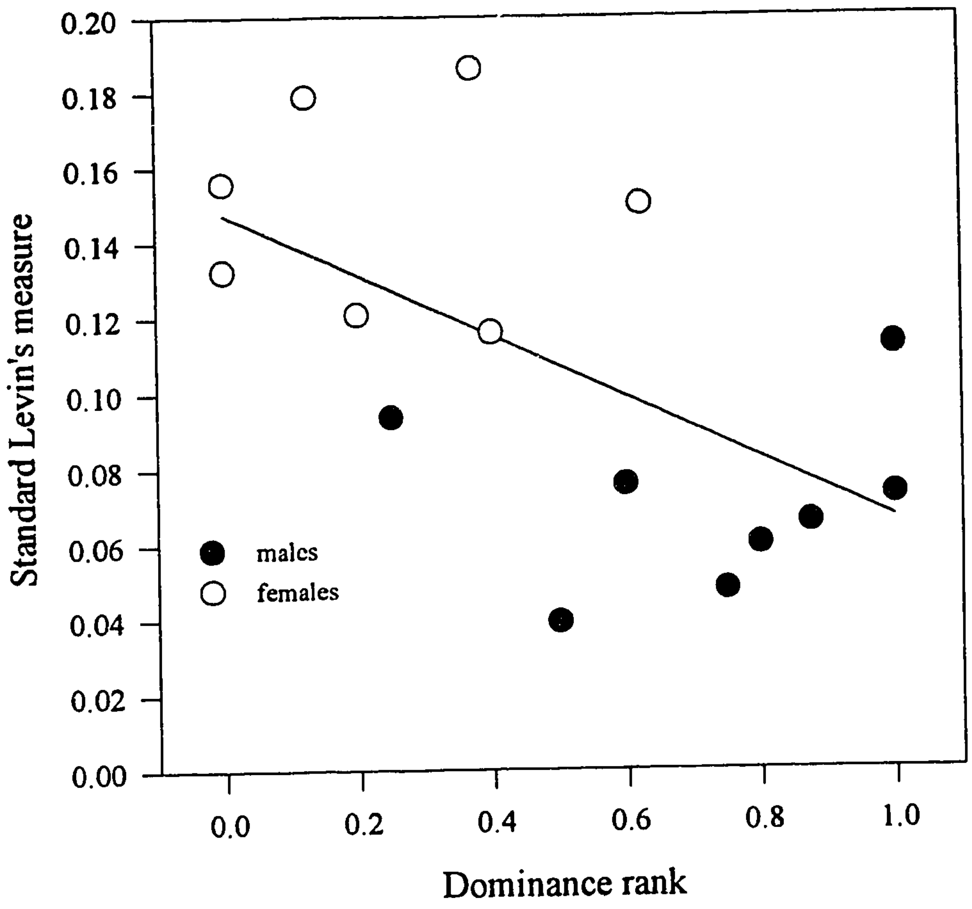

Figure 3-4: Dietary diversity as a function of dominance rank during the dry season ($Y = -0.081 + 0.14X$, $r^2 = 0.34$, $P = 0.022$). Dietary diversity was measured using the standardized Levin's measure (see text for further explanation).

$r^2 = 0.000$, $P = 0.99$). Furthermore, high ranking females and low ranking males have similar ranks (ranging from 0.25 to 0.62) but high ranking females exhibited a higher dietary diversity than low ranking males (Fig. 3-4). Thus, it appears that sex influenced dietary diversity more than dominance rank.

By far, the food item used most by the monkeys during the dry season was the seeds of Luehea speciosa (Appendix C). I therefore looked at the proportion of time animals spent feeding on this food to see if the trend in diversity may have been related to their use of this food. The proportion of time that animals spent feeding on this fruit was strongly related to dominance rank; dominant animals spent a much higher proportion of their time feeding on it than did subordinates (linear regression, $r^2 = 0.44$, $P = 0.007$; Fig. 3-5). As indicated in Fig. 3-5, the two most dominant animals spent 34 and 42 percent of their feeding time feeding on L. speciosa, while the two most subordinate animals spent only one and 13 percent. Again, this relationship depends more on sex than dominance *per se*, as the trend is not significant within either sex (males: $r^2 = 0.020$, $P = 0.74$; females $r^2 = 0.28$, $P = 0.22$), and low ranking males spent a greater proportion of their time feeding on L. speciosa than females of similar rank (Fig. 3-5). The proportion of feeding time an animal spent feeding on L. speciosa was significantly correlated with its standard Levin's measure for the dry season (Spearman Correlation, $r = -0.95$, $P = 0.000$). Animals that used L. speciosa more showed a consistent trend to use certain other food items less (Table 3-2). In group I, animals that used L. speciosa less, spent more time foraging on the fruit of Acacia sp. trees, and also the larvae of the ants which live in the thorns of this tree, while individuals in group II spent more time feeding on the fruit from Randia

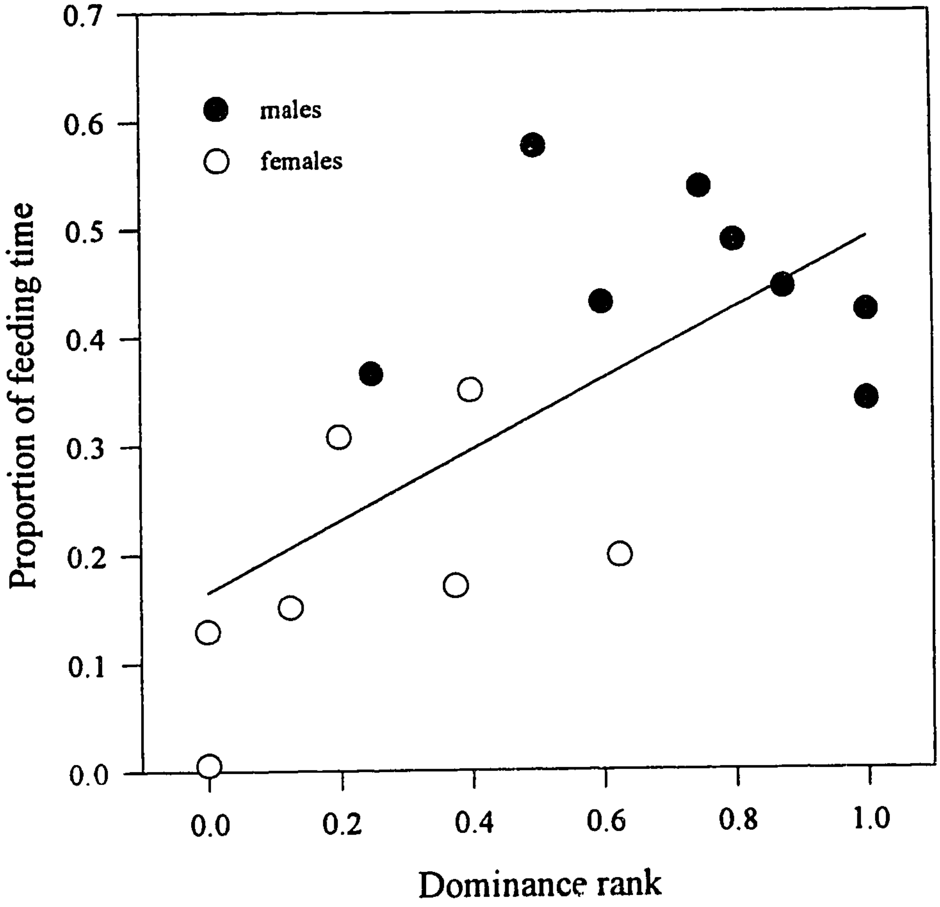

Figure 3-5: Proportion of feeding time spent feeding on Luehea speciosa during the dry season, as a function of dominance rank ($Y = 0.17 + 0.34X$, $r^2 = 0.44$, $P = 0.007$).

Table 3-2: Correlations between time spent feeding on *L. speciosa* and other food items, for animals in groups I and II.

	Group I		**Group II**	
Food Item	**Correlation Coefficient**	**P**	**Correlation Coefficient**	**P**
Small imbedded insects	-0.943	0.005	-0.883	0.002
Acacia sp. fruit	-0.829	0.042	-0.365	0.334
Acacia sp. ant larvae	-0.829	0.042	-0.383	0.308
R. subcordata fruit	0.6571	0.156	-0.900	0.001

Correlation coefficients are Spearman correlation coefficients (Norusis, 1993), and all P-values are 2-tailed. N = 6 for group I and N = 9 for group II.

subcordata. In both groups, animals substituted small imbedded insects and larvae, which they found in dead branches. Thus, males appeared to specialize on L. speciosa, while females maintained a more diverse diet, replacing L. speciosa with an increase in the use of a variety of foods.

DISCUSSION

The composition of an individual's diet was significantly affected by its dominance rank. Animals of similar rank had similar diets, while those further apart in the hierarchy had diets that overlapped less. Furthermore, the influence of dominance rank on diet was stronger in the dry season than in the wet season. Foraging success was lower in the dry season than in the wet (Chapter Two), and subordinate animals avoided dominants more during the dry season than during the wet season (Chapter Two). These findings indicate that competition was stronger during the dry season than during the wet season. Thus, the finding that rank-based dietary differences are stronger in the dry season than in the wet season can be interpreted as a response to increased competition in the dry season.

During the dry season, dominant animals spent more time feeding on foods that occurred in large clumps, while subordinates spent more time feeding on foods that occurred in small clumps. One factor influencing the trend for dominant animals tospend more time feeding on foods that occurred in large clumps may have been that large clumps represent an abundance of food in a localized area, so that they could obtain a large amount of food before having to search for a new clump. The tendency for low ranking animals to spend less time feeding on foods that occur in large clumps may have been due to the avoidance of aggression, either through the avoidance of large clumps of food, where direct competition was more likely, or through the avoidance of dominant animals. Large clumps usually contained more than one monkey, and therefore the potential for direct competition within these clumps was probably high. Thus, subordinate animals may have avoided large clumps of food, and instead fed in small clumps of food, where they were less likely to be subject to competition. Furthermore, if dominant animals specialized on foods that occurred in large clumps, then one consequence of avoiding dominants may have been reduced access to food that occurred in large clumps. This interpretation is supported by the fact that rank-related differences in the use of clumped foods were present in the dry season but not in the wet season, and subordinates avoided dominant animals more during the dry season than during the wet season (Chapter Two).

An alternative explanation is that subordinate animals were actively excluded from large clumps of food by dominant animals. However, examination of aggression over the different food types during the dry season suggests that this is not the case, since aggression scores did not differ between the three dispersion types. This is in accord with the findings of Whitten (1983) who concluded that there was no clear relationship between the frequency of supplantation and the influence of rank on the inclusion of foods in the diets of female vervet monkeys (Cercopithecus aethiops).

A number of other studies have stressed the importance of avoiding higher ranking animals during foraging. Using a cost-benefit analysis, Popp and Devore (1979) predicted that subordinates, who are unlikely to win aggressive encounters with dominant individuals, should avoid both dominant animals and situations that have a potential for conflict. Caraco et al. (1989) found that subordinate juncos (Junco hyemalis) avoid dominants while foraging, even if doing so involves choosing a lower feeding rate. Ens and Goss-Custard (1984) suggested that subordinate oystercatchers (Haematopus ostralegus) face a trade-off between searching for mussels in high quality areas and having them stolen, and avoiding dominant birds by foraging in lower quality areas. Thouless (1990) also argued that the avoidance of dominant animals decreased the foraging efficiency of grazing red deer hinds (Cervus elaphus) Thus, avoidance may be an important factor mediating contest competition within groups where dominance relationships exist.

In contrast to the results found for dispersion of the food item, the use of food items with long or short handling times was not influenced by dominance rank. However, aggression occurred over foods with long handling times significantly more than it did over foods with short handling times. This may be related to the value of the food item, since items with long handling times tend to be larger, and therefore may be of more value. Certainly, the two food items that had the largest aggression scores (bee hives and squirrels) were two of the largest food items obtained by capuchins, and were also rarely obtained. Consequently, the benefit obtained from food items with long handling times may be worth risking the cost of aggression from dominant animals. This is supported by anecdotal evidence, in that supplantations over large food items frequently involved attempts by the subordinate animal to retain the item. For instance, supplants over large food items were often preceded by chases, unlike the more common form of supplantation, where the subordinate quickly gave up the food item and vacated the area.

Thus, the results of dominance mediated contest competition for food appear to represent an interaction between the value of the food item, the dispersion and size of the food item, and the dominance rank of the animal. When food items are of high nutritional value, and are either clumped or large and conspicuous, animals exhibit the highest rates of aggression, but not dietary differences. When items are of lower nutritional value, but still clumped, animals exhibit rank-related dietary differences. Finally, when food items are dispersed (and probably also when they are of low food value), animals do not exhibit either high rates of aggression or rank-related dietary differences.

Although subordinates spent less time feeding on food items that occurred in large clumps during the dry season, and although they were supplanted from items with long handling times significantly more than from items with short handling times, they did not change their likelihood of feeding on different food types when dominants were in close proximity (less than ten metres). Thus it seems that dietary adjustments occurred over the long term, rather than over the short term. However, during the dry season subordinates were more vigilant when dominant animals were nearby, suggesting that they were monitoring dominants, and therefore that having a dominant animal in proximity is a cost, both because time spent being vigilant cannot be spent foraging and because of the risk of supplantation.

Are Subordinates Less Selective?

Dietary diversity appears to have been influenced by rank, sex, or a combination of both during the dry season, but not during the wet season. Furthermore, this trend appears to be due, at least in part, to the tendency of dominant animals to specialize on L. speciosa during the dry season, whereas subordinate animals maintained a more diverse diet. Examination of Figs. 3-4 and 3-5 shows that this trend may be the result of a sex difference in dietary diversity. In fact, the lack of a significant trend within the sexes suggests that the trend may be due more to sex than to dominance. However, since the majority of adult males are dominant to adult females in white-faced capuchins, it is difficult to discern which factor is the source of the trend. Possibly, both factors are operating, since a sex difference that caused males to specialize more heavily on L. speciosa may have been reinforced by the tendency of females (as subordinate animals) to avoid L. speciosa trees.

The factors behind the differential tendencies of the sexes to eat L. speciosa are not easily discerned. Luehea speciosa, being a seed, may be a good source of protein (Richards 1985). It is therefore interesting that two of the foods substituted by individuals who eat less L. speciosa are insects (small imbedded insects and ant larvae in Acacia sp. thorns), which will also be good sources of protein. Furthermore, when monkeys eat the fruit of R. subcordata, they seem to concentrate mainly on the black, soft substance in the centre of the fruit, which appears to consist mainly of seeds, and therefore may also be high in protein. Thus, the reason for the sex difference is not obvious, since there are no overt characteristics of the food items involved that suggest differences in nutritional content.

Interestingly, the differences in dietary diversity did not result from rank-related differences in the number of foods included in the diet as was predicted by the model of

Engen et al. (1988). Instead, it resulted from differences in the time spent feeding on different items. Thus, it appears to have been mediated by the tendency of females to avoid L. speciosa clumps, and instead forage on alternative food items. Consequently, the results from this study do not support the model of Engen et al. (1988).

Do Dominant White-faced Capuchins Scrounge?

It can be argued from the presence of supplantations, and other aggressive acts over food items, that dominant animals were scrounging in my study groups. Moreover, subordinates received more supplantations than dominants, and therefore should have received a greater cost from scrounging, as predicted by Vickery et al. (1991). However, the overall rates of supplantation and aggression were low; supplantations occurred at a rate of about 0.144 per hour in the wet season and 0.072 per hour in the dry season, and aggressive acts in general (including chases, threats, contact aggression, and supplantations) occurred at a rate of about 1.78 per hour in the wet season and 1.69 per hour in the dry season. Therefore, it is unlikely that dominant individuals specialized in scrounging, as described by Barnard and Sibly (1981). Presumably, dominants behaved like the opportunist strategy in the model of Vickery et al. (1991), searching for their own food, but taking advantage of any scrounging opportunity that arose.

Dominance Rank and Intragroup Competition for Food

Subordinate white-faced capuchins faced scrounging from dominant animals over items with long handling times, and likely also face an increase in the likelihood of interference when feeding in large clumps of food. Additionally, subordinates avoided dominant animals (Chapter Two), and therefore may have faced a trade-off between feeding on foods that occurred in large patches, and avoiding dominant animals in order to avoid interference from them. During the dry season, subordinates spent less time feeding on foods that occurred in large patches, and specialized instead on small patches of food. However, they did not spend less time than dominant animals feeding on food items with long handling times, nor did they decrease their use of these items when dominant animals were nearby. Similar trends were not apparent in the wet season, when competition for food was likely lower (Chapter Two). I argue that diet choices made by subordinates must take into account, not only the benefit gained from the food item and the abundance of foods included in the diet, as predicted by foraging theory, but also the likelihood of receiving aggression from dominant animals when feeding on that item. Thus, rank-related differences in diet will reflect the trade-offs between the likelihood of receiving aggression, and the benefit received from the food source.

In this study, the presence of rank-related differences in diet suggests that dominance plays a role in the diet of dominant white-faced capuchins. However, those food types that show dietary differences do not show high rates of aggression, and those that show high rates of aggression do not show rank-related dietary differences. The lack of correlation between rank-related dietary differences and the occurrence of aggressive acts suggests that researchers must be careful when assuming that a lack of aggression is evidence that dominance is not important within a system, When dominance hierarchies exist, subordinates may be better off to avoid interactions with dominant animals over food, since they are unlikely to win the contest (Popp and Devore 1979). Thus, in some systems dominance may be important, even though there is very little overt aggression, since subordinates will benefit by avoiding aggressive competition with dominant animals.

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Chapter Four. General discussion and conclusions

In this thesis I have examined the interaction between the social system and foraging behaviour of the white-faced capuchin monkey (Cebus capucinus). Living in a group affords protection from predators, but also imposes increased competition for food between group members. Therefore, when groups are organized by a social hierarchy, dominant animals should use their rank to maximize the benefit they obtain, while minimizing the cost. In Chapter Two I examined rank-related differences in the use of spatial positions within the physical boundaries of the group, and in Chapter Three I discussed rank-related dietary differences. In both, I argued that the avoidance of dominant animals by subordinate animals, rather than the aggressive exclusion of subordinates from preferred spatial positions and feeding areas, was the mediating factor.

Popp and Devore (1979) used cost-benefit analysis to model the decisions made by individuals faced with the possibility of aggressive competition for a resource. They argue that there are four variables of primary significance to an animal contemplating an aggressive encounter: (1) the probabilities of access to the disputed resource through aggression or through alternative strategies, (2) the benefit of access to the object of competition, (3) the effects of the competition on relatives of the actor, and (4) the intrinsic competitive abilities of the actor and his competitor. If the net benefit competing aggressively (i.e. the benefit obtained from the resource minus the involved in aggressive competition) is not greater than the benefit obtained by not competing aggressively, taking into account the probabilities of obtaining the resource each way, an animal should avoid the interaction.

When there is an established dominance relationship between the two competitors the subordinate animal knows from past experience that it is unlikely to win (and hence that the benefit it can expect is zero), and thus it should avoid an aggressive encounter entirely. Therefore, within groups where dominance relationships exist, subordinates will benefit by avoiding dominant animals. This avoidance can occur on a small scale, with subordinates reacting to the proximity of a higher ranking animal, or on a large scale, with subordinates avoiding areas of the habitat where dominants are present in high densities.

Thouless (1990) concluded that the efficiency of grazing red deer hinds was decreased by the presence of more dominant animals, because they were more likely to move away, and to stop feeding while doing so, if a neighbouring individual was socially dominant. Similarly, as overall bird densities increase on mussel beds, subordinate oystercatchers (Haematopus ostralegus) must spend more time avoiding dominant animals, and therefore experience a decreased intake rate (Ens and Goss-Custard 1984). Subordinate juncos (Junco hyemalis) avoid dominant animals, even if doing so involves moving to an area that provided a lower feeding rate (Caraco et al. 1989). Such avoidance can impose costs on subordinate animals by decreasing the efficiency with which they forage. By taking evasive actions, subordinate animals may lose search time, or may be distracted from searching by the need to monitor dominant animals, and hence be less effective foragers (Ens and Goss-Custard 1984).

When food is patchily distributed, the avoidance of dominant animals may influence the behaviour of subordinates on a larger scale. For instance, subordinate oystercatchers refrain from landing on mussel beds when bird densities on the beds are high, and instead feed in less preferred areas (Ens and Goss-Custard 1984). Female vervet monkeys (Cercopithecus aethiops) of similar rank feed and range together, and low-ranking females rarely enter a clump of food in which dominant females are feeding. Instead, low ranking females feed on a separate food source while they wait for the higher ranking females to finish feeding in the clump, at which time most of the food in the clump is gone (Whitten 1983). When preferred foods are clumped, or patches occur where food densities are greater, this large scale avoidance of dominant animals will result in a lower intake of preferred resources by subordinate animals.

White-faced capuchins showed both small scale and large scale avoidance. Small scale avoidance was observed in the form of "retreat" behaviour, whereby a subordinate animal saw a dominant animal approaching, and avoided it by leaving the area. During these interactions the dominant animal did not exhibit any aggression, or acknowledge the subordinate in any way. However, by leaving the area, the subordinate often had to stop feeding, and then search for a new patch of food, and so was presumably incurring a cost. Subordinates also avoided dominant animals on a larger scale, by spending time on the edge of the group, and avoiding large patches of food. This form of avoidance presumably imposed both a greater predation risk on subordinate animals, and a decreased access to foods that occurred in large clumps.

When the benefit gained from a resource is very high, it may outweigh the cost imposed by the risk of aggression from higher ranking animals. In other words, when the contested item is of high value, the social system may break down, and scramble competition may prevail. Animals are therefore unlikely to exhibit dietary differences for resources of high value. Furthermore, if the animal that finds a very valuable item is approached by a higher ranking individual, it may not surrender the item without contest. However, the contest need not be in the form of a direct aggressive encounter. For example, if the item is portable, the individual may run away, taking the item with it. Thus, animals will show rank-related differences in the use of items which are not valuable enough to outweigh the costs of aggression from high-ranking animals, but not show differences in the use of items that are highly valuable.

The environment of a subordinate animal can therefore be envisioned as a matrix of resources and higher ranking animals. When making decisions about where to forage, subordinates must take into account the location of the various resources, the benefits offered by different resources, and the probability of receiving aggression from a dominant animal while exploiting different resources. Thus, while dominant animals may be able to select resources (whether they be spatial positions, food items, or otherwise) based on their characteristics, subordinates must also take into account the differential probability of aggressive interactions with dominant animals over the various resources. In this study, the avoidance of dominant animals and situations where conflict was more likely appeared to be an important factor mediating the access of subordinate white-faced capuchins to central spatial positions and highly clumped foods.

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Appendix A: Description of behaviours used to construct dominance hierarchies.

Retreat
An animal moves away from an approaching animal, accompanied by submissive body postures and head-checking behaviour. Different from a supplant in that the animal moves away before the approaching animal arrives at it's location, and the approaching animal is not threatening or staring while it approaches.

Fear Grimace
An animal has its mouth slightly open and lips stretched back, head and/or eyes lowered. Often accompanied by vocalization and lowered body posture.

Supplantation
An animal approaches another animal in a very deliberate fashion (usually accompanied by a direct stare or threat face), the other animal leaves (usually accompanied by head-checking behaviour), and the first animal occupies the spot or obtains the resource previously being used by the second animal.

Threat
An animal makes a threat face toward another individual with the canines fully exposed. Usually accompanied by a stiff-legged, tense quadrupedal posture and slight piloerection.

Appendix B: Supplantations and aggressive acts per hour of focal data in the wet and dry seasons. Agonism includes supplantations, threats, and chases.

Season	Behaviour	Mean	S.D.	Range
Wet	Supplantation	0.34	0.17	0 - 0 64
Dry	Supplantation	0.47	0.21	0.10 - 0.88
Wet	Agonism	0.78	0.35	0.27 - 1.42
Dry	Agonism	0.75	0.23	0.30 - 1.07

Appendix C: List of foods eaten in the wet and dry seasons. Dispersion classes are: Dispersed = single food items are spread out over the habitat, Small clumps = multiple food items occur together, but only one or two monkeys can feed in the patch at one time, Large clumps = multiple food items occur together and more than two monkeys, but not the whole group, can feed in the clumps at one time (*Ficus sp.* is the one exception because all of group I was occasionally seen feeding in one *Ficus sp.* tree, but group II was never seen doing this). Handling time classes are: Long = some form of processing was required before the item was eaten, or the item was large enough to require multiple bites, and so was held in the animal's hands for more than a few seconds, Short = no processing was required and the item was small enough to go directly into the mouth. Mean P = the mean proportion of time animals spent feeding on each food item.

Food Item	**Dispersion**	**Handling Time**	**Mean P:**		
			Total	**Group I**	**Group II**
WET SEASON					
Fruit:					
Bromelia pinquin	Small clumps	Long	<0.01	<0.01	<0.01
Byrsonima crassifolia	Large clumps	Short	0.03	0.04	0.03
Cecropia peltata	Large clumps	Short	<0.01	<0.01	<0.01
Chlorophora tinctoria	Large clumps	Short	0.04	<0.01	0.03
Cetrum ferruginia	Large clumps	Short	0.01	<0.01	<0.01
Cordia panamensis	Small clumps	Short	<0.01	<0.01	<0.01
Curatella americana	Large clumps	Short	<0.01	<0.01	<0.01
Erythroxylon havanense	Large clumps	Short	0.15	0.10	0.18
Ficus sp.	Large clumps	Short	0.15	0.22	0.10
Guettarda macrosperma	Large clumps	Short	0.08	0.05	0.11
Krugiodendron sp.	Small clumps	Short	0.01	0.02	<0.01
Lasiasas sorghoides	Large clumps	Short	<0.01	<0.01	<0.01
Miconia argentea	Small clumps	Short	<0.01	<0.01	<0.01
Muntingia calabura	Large clumps	Short	<0.01	<0.01	<0.01
Ocotea veraguensis	Small clumps	Short	<0.01	<0.01	<0.01
Passiflora platylōba	Small clumps	Long	0.01	<0.01	<0.01
Paullinia cururu	Small clumps	Short	0.01	<0.01	<0.01
Rourea glubra	Small clumps	Short	<0.01	<0.01	<0.01
Sciadodendron excelsum	Large clumps	Short	0.03	0.02	0.04
Sidium guayaba	Large clumps	Short	0.04	0.10	<0.01
Solanum hazenii	Large clumps	Short	0.01	<0.01	0.02
Spondias mombin	Large clumps	Short	<0.01	<0.01	0.01
Stemmadenia obovata	Small clumps	Long	0.05	0.01	0.08
Trichilia sp.	Small clumps	Short	<0.01	<0.01	<0.01
Xilosma flexuosum	Large clumps	Short	<0.01	<0.01	<0.01
Zeulania guidonia	Large clumps	Long	0.01	<0.01	0.02
Seeds:					
Apeiba tibourbou	Small clumps	Long	<0.01	0.01	<0.01
Luehea candida	Large clumps	Long	0.01	<0.01	<0.01
Luehea speciosa	Large clumps	Long	<0.01	<0.01	<0.01
Quercus oleoides	Large clumps	Short	<0.01	<0.01	<0.01

Food Item	Dispersion	Handling Time	Mean P: Total	Group I	Group II
Plant Shoots:					
Bromelia pinquin	Small clumps	Long	<0.01	<0.01	<0.01
Vertebrate Prey:					
Bird eggs	Small clumps	Short	<0.01	<0.01	<0.01
Invertebrate Prey:					
Insects	Dispersed	Short	0.20	0.17	0.22
Insect eggs	Large clumps	Short	<0.01	<0.01	<0.01
Large imbedded insects	Dispersed	Long	<0.01	<0.01	<0.01
Small imbedded insects	Small clumps	Long	0.03	0.05	0.02
Ant larvae in *Acacia sp.* thorns. *Pseudomyrmex sp.*	Small clumps	Long	0.04	0.09	0.01
Bee hive	Small clumps	Long	0.02	0.01	0.02
Larvae in *Sebastiana confusa* seeds	Large clumps	Short	0.02	0.05	0.01
DRY SEASON:					
Fruit:					
Acacia sp.	Small clumps	Long	0.04	0.10	<0.01
Acrocomia vinifera	Large clumps	Long	0.04	<0.01	0.07
Annona purpurea	Disperses	Long	<0.01	<0.01	<0.01
Bursera simaruba	Large clumps	Short	0.03	0.04	0.02
Byrsonima crassifolia	Large clumps	Short	<0.01	<0.01	<0.01
Diospyros nicaraguensis	Large clumps	Short	<0.01	<0.01	<0.01
Guettarda macrosperma	Large clumps	Short	<0.01	0.01	<0.01
Lasiasas sorghoides	Large clumps	Short	<0.01	<0.01	<0.01
Manilkara zapota	Large clumps	Short	0.06	0.03	0.08
Muntingia calabura	Large clumps	Long	<0.01	<0.01	<0.01
Randia subcordata	Large clumps	Long	0.09	0.06	0.11
Simarouba glauca	Large clumps	Short	0.03	0.04	0.02
Spondias mombin	Large clumps	Short	<0.01	<0.01	<0.01
Stemmadenia obovata	Small clumps	Long	0.01	<0.01	0.01
Seeds:					
Luehea candida	Large clumps	Long	<0.01	<0.01	<0.01
Luehea speciosa	Large clumps	Long	0.33	0.35	0.31
Sloanea terniflora	Large clumps	Long	0.02	<0.01	0.03
Quercus oleoides	Large clumps	Short	<0.01	<0.01	<0.01
Graminea - black seeds	Small clumps	Short	0.06	0.08	0.04
grass with long seeds	Small clumps	Short	<0.01	<0.01	0.01
Leaves:					
Bromelia pinquin	Small clumps	Long	0.01	0.02	<0.01
Guaria Morada	Small clumps	Long	<0.01	<0.01	<0.01

Food Item	**Dispersion**	**Handling Time**	**Mean P:**		
			Total	**Group I**	**Group II**
Flowers:					
Bauninia ungulata	Large clumps	Short	0.01	<0.01	<0.01
Vertebrate Prey:					
Sciurus variegatoides	Dispersed	Long	0.01	<0.01	0.01
Unknown mammal young	Dispersed	Long	<0.01	<0.01	<0.01
Invertebrate Prey:					
Insects	Dispersed	Short	0.09	0.06	0.11
Large imbedded insects	Dispersed	Long	0.03	0.03	<0.01
Small imbedded insects	Small clumps	Long	0.06	0.06	0.07
Ant larvae in *Acacia sp.* thorns. *Pseudomyrmex sp.*	Small clumps	Long	0.05	0.10	0.02
Bee hive	Small clumps	Long	<0.01	<0.01	<0.01
Small insects in *Combretum farinosum.* flowers	Small	Short	<0.01	0.01	<0.01