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SEX DIFFERENCES IN FORAGING BEHAVIOUR AND BENEFITS AND COSTS OF RESIDENT MALES IN WHITE-FACED CAPUCHINS

By

LISA M ROSE ©

A THESIS

SUBMITTED TO THE FACULTY OF GRADUATE STUDIES AND RESEARCH

IN PARTIAL FULFILMENT OF THE REQUIREMENT FOR THE DEGREE

OF MASTER OF ARTS

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Lisa M. Rose
#203-250 East 2nd Street
North Vancouver, B.C. V7L 1C5

Date [illegible]

UNIVERSITY OF ALBERTA

FACULTY OF GRADUATE STUDIES AND RESEARCH

The undersigned certify that they have read, and recommend to the Faculty of Graduate Studies and Research for acceptance, a thesis entitled SEX DIFFERENCES IN FORAGING BEHAVIOUR AND BENEFITS AND COSTS OF RESIDENT MALES IN WHITE-FACED CAPUCHINS submitted by LISA M ROSE in partial fulfillment of the requirements for the degree of MASTER OF ARTS.

L. M. Fedigan

Dr. L.M. Fedigan

Jan O. Murie

Dr. J.O. Murie

Dr. N. Lovell

Date: 4 August 1992

ABSTRACT

Sex differences in diet and foraging behaviour are examined in white-faced capuchin monkeys (*Cebus capucinus*) in a tropical dry forest at Santa Rosa National Park, Costa Rica. Three hypotheses to explain sex differences in diet and foraging behaviour are tested: 1) sexual dimorphism; 2) the demands of pregnancy and lactation; and 3) competition avoidance. Three hypotheses regarding the benefits and costs of males to females are also tested: 1) males afford greater benefits to females than do other females; 2) males impose greater costs on females than do other females; 3) the benefits and/or costs associated with resident males are unequally distributed among females. I collected 380 hours of focal data on 15 adults (8 females and 7 males) in two study groups over a five month period.

Sexual dimorphism offered the best explanation of sex differences in *C. capucinus* diet and foraging behaviour, accurately predicting that males do more strenuous foraging activity, make less use of small foraging supports, spend more time on or near the ground, and eat more animal protein. Females eat more embedded invertebrates, while males eat more large invertebrates and take more vertebrate prey. Pregnant and lactating females spent more time resting and less time foraging than other females, increasing their foraging return by focusing on foods requiring little handling time. There was little evidence of competition avoidance between the sexes.

For females, males provide greater benefits than other females, but they also impose higher costs. The main benefit afforded by males is their vigilance against potential predators or extra-group males. Females may benefit from male protection of infants, but the risk of infanticide may be a concomitant cost, as demonstrated by the killing of an infant by one male after a change in male dominance ranks. Males impose costs on females through increased feeding competition and related agonism. Females may be unable to effectively exclude males from groups, and their best alternative may be to form individual alliances with males. High-ranking females benefit most from the presence of males by forming alliances with the alpha male.

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CHAPTER 1: INTRODUCTION

In this study I examine foraging and social behaviour in a neotropical primate, *Cebus capucinus*. First, I consider the foraging behaviour of males and females in the light of evolutionary hypotheses of sex differences in primate foraging. Second, I consider the relative benefits and costs of male group members to females, with an emphasis on foraging considerations. In this first chapter I discuss the theoretical background to the questions posed, review relevant primate field studies, and introduce the study species.

THEORETICAL BACKGROUND

The primary strategies through which individuals attempt to maximise inclusive fitness differ between the sexes (Trivers 1972). In non-human primates, female reproductive success is not generally constrained by mate availability. Hence the primary strategy of females is food acquisition, while that of males is mate acquisition (Wrangham 1980, 1983; Janson 1984; O'Brien 1991). Sex differences in primate foraging and social behaviour can be predicted on the basis of differing primary strategies. Females are expected to be 'energy maximisers' (*sensu* Schoener 1971), while males minimise foraging time in favour of other fitness-increasing activities such as sexual behaviour or predator vigilance (Iwamoto 1987; Boinski 1988a).

Female strategies are widely considered to be the predominant factor shaping primate social systems, as male strategies depend largely on the distribution and behaviour of females (Emlen and Oring 1977; van Schaik 1989; Mitchell *et al.* 1991). However, social organisation represents the interaction of both female and male strategies (Wrangham 1980), and social groups are a compromise between conflict and co-operation among group members (Crook 1970; Walters and Seyfarth 1986; Dunbar 1989). For females, the presence of resident males will have both benefits and costs. If females tolerate males within a social group, the benefits that these males provide would be expected to equal or exceed the costs that they impose. However, if females are unable to effectively exclude males from a group, then males may impose a net cost on females, who would then be predicted to follow behavioural strategies which minimise these costs.

SEX DIFFERENCES IN FORAGING BEHAVIOUR

Three explanations of sex differences in primate foraging behaviour are widely proposed (Clutton-Brock 1977a):

a) Sexual selection has led to sexual dimorphism in body size, which may produce coincidental variations in foraging behaviour.

b) The costs of pregnancy and lactation have led to selection for sex differences in diet and foraging behaviour.

c) Selection may favour individuals who avoid competing for limiting resources with their mates or offspring.

The three proposed explanations are not mutually exclusive. In species where males are 25-50% heavier than females, the opposing effects on energy needs of sexual dimorphism and pregnancy and lactation would tend to cancel each other out. Bioenergetic considerations (especially female reproductive effort) and the exploitation of different niches by males and females have been proposed as underlying causes of sexual dimorphism (see Fedigan 1982 for a detailed discussion). Various proximate factors contribute to sex differences in foraging behaviour, including social constraints on food access (Janson 1984, 1985), spatial position (Robinson 1981a; Janson 1990a, 1990b), food preferences (Hladik 1981; Hobi and Glaser 1983), foraging competence (Boesch and Boesch 1984; Fragaszy 1986), and response to perceived predation risk (Fragaszy 1990). However, discussion at this point will be limited to the three ultimate factors described above.

Sexual Dimorphism

Many primate species exhibit sexual dimorphism in body weight; in most cases, males are heavier than females. Body weight directly affects the amount of food an animal requires. For mammals, basal metabolic rate (the minimum energy expenditure required to support life while an animal is at rest) can be roughly calculated as a function of body weight raised to the exponent 0.75 (Kleiber 1961). Thus, large animals have higher overall energy needs than small ones, but use less energy per unit body weight. For example, using Kleiber's formula (BMR = 70 $W^{0.75}$, where W = body weight in kg), predicted BMR for a 10 kg male would be 394 kcal, while that of a 7 kg female would be 310 kcals. Coehlo (1974) confirmed that Kleiber's formula closely predicted measured metabolic rates in several primate species under laboratory conditions. An individual's energy requirements vary according to its level of activity; actual energy intake may be three times predicted BMR (Richards 1985). Smaller animals not only metabolise energy faster than large ones; they have less food storage and digestive capacity, and thus need to eat more frequently and/or rely on more nutritious and easily digested foods (Temeren *et al.* 1984).

Body weight can also influence diet and foraging behaviour by limiting the substrates on which an animal can feed. In arboreal species, lighter individuals can move along slender supports and forage on terminal branches that would not support heavier conspecifics (Kummer 1971; Mendel 1976; Fleagle and Mittermeier 1980; Robinson 1981a; Cant 1987; Boinski 1989). Larger individuals may also be less vulnerable to predators, and tend to forage in more exposed locations. Increased body strength and large, stout canines may promote strenuous foraging activies such as branch breaking and bark stripping (Waser 1977), and allow more efficient exploitation of 'hard-to-open' foods such as large nuts or tightly packed fruits (Rodman 1977; Janson 1985, 1986a).

Female Reproductive Factors

Reproduction is energetically costly for a female primate. Pregnancy and lactation increase her metabolic rate by up to 25% and 50% respectively (Portman 1970; Coehlo 1974). Lactation is the greater burden because throughout this period, as a mother requires sufficient energy to maintain her own weight and to support her infant's activity and growth, using a system which is less efficient than placental nourishment (Altmann 1980; Jolly 1985; Dunbar and Dunbar 1988). She will have increased protein and mineral needs (Sadleir 1969; Harrison 1983; Demment 1983), and the costs of foraging for high quality food will frequently be inflated by the cost of carrying her dependent infant (Altmann 1980; Lee 1989). As Fedigan (1992) remarks, a female non-human primate spends most of her adult life either pregnant or lactating, and thus her nutritional needs will usually exceed those of conspecific males, except in cases of extreme sexual dimorphism.

A female primate might increase her nutritional intake in two primary ways. First, she can increase her overall food intake, by either spending more time feeding, or by eating faster. Second, she can change the composition of her diet, expanding it to include a wider variety of items, or narrowing it by selecting high quality (low fibre, high protein) foods. Young leaves or shoots and arthropod or small vertebrate prey are two major protein sources: fruits are rich in carbohydrates but contain little protein - usually about 5% of dry weight (Hladik 1981). A female might also conserve energy by reducing her activity level, if her foraging needs still can be met by doing so (Kemnitz *et al.* 1986).

Avoiding Competition

Increased competition for food is an obvious consequence of group living, and can be correlated with clear fitness effects on individuals, including increased mortality and lowered female reproductive rates (Janson and van Schaik 1988). Because of their higher nutritional requirements, pregnant and lactating females are more likely to be adversely affected by feeding competition than males. A female's nutritional condition influences the rate at which she produces offspring, and affects her infant's health and survival as well as her own (Richard 1985; Robinson 1988; van Schaik 1989). As male and female reproductive success are linked by a common stake in offspring survival, behaviours which reduce competition between males and females, especially lactating females, would be adaptive for both sexes.

Selander (1972) first suggested that selection favours individuals who avoid competing for limiting resources with their mates or offspring. Niche separation or resource partitioning are common outcomes of competition among different species or groups (Begon *et al*). Feeding competition within groups may be similarly reduced if age and sex classes have slightly different diets (Chalmers 1979; Clark 1980), or spatially segregate during foraging. Clutton-Brock (1977a) suggested that competition avoidance would be most advantageous when i) animals are territorial and feed outward from a fixed base; ii) feeding rate is limited by search time rather than handling time; and iii) the adult sex ratio is close to parity. Clutton-Brock largely dismissed competition avoidance as an explanation of sex differences in primate foraging. However, as Lovejoy (1981) and Fedigan (1982) pointed out, he himself described what appears to be niche separation between the sexes in several primate species.

BENEFITS AND COSTS OF MALES TO FEMALES

Much attention has been paid to the benefits and costs of primate sociality (e.g. van Schaik 1983, 1989; Terborgh and Janson 1986; Robinson 1988, Dunbar 1989), but these factors have seldom been considered from the perspective of a female non-human primate. How does the presence of males within a social group affect females? Do males represent a greater benefit or a lesser cost to females than do other females within the same group? Four ways in which resident males may directly or indirectly affect female fitness are:

1. Group defence activities: intergroup competition and predator protection.
2. Mating stability and contribution to infant care.
3. Interference with female food acquisition through contest competition.
4. Aggression directed toward females or their offspring in non-feeding contexts.

Some males may offer greater benefits and impose fewer costs than others, and females may structure their patterns of association accordingly (O'Brien 1991). Females may also attempt to influence male behaviour in order to increase their own success in contest competition, enhance their social status, or gain priority of access to reproductive partners. The benefits and costs associated with resident males may not be shared equally amongst females within a group: high-ranking females may receive a disproportionate share of the benefits, while others bear most of the costs (O'Brien 1991).

Benefits of Males to Females

1. Group Defence

Competition for access to high-quality food patches and increased protection from predators are the two most widely cited explanations of primate sociality (Wrangham 1980, 1983; Alexander 1974; van Schaik 1983, 1989; Terborgh and Janson 1986; Mitchell *et al.* 1991; Sherman 1991). Males play an important role in both resource and predator protection. As their primary reproductive strategy is mate acquisition, males would be expected to protect their access to females by defending their social group. Females, with their greater commitment to feeding, may have less time available for group defence. Females may also be less likely than males to engage in high-risk confrontations with outside groups or potential predators.

Wrangham (1980, 1983) suggests that females attract males to groups in order to increase their success in intergroup dominance. The number of resident adult and subadult males in a group may determine its success in intergroup competition, and its subsequent access to resources (Robinson 1988). Male participation in group defence thus contributes indirectly to female fitness by increasing the group's overall access to feeding sites (O'Brien 1991). Males also play an important role in group defence against predators. Active confrontation of predators provides direct protection to group members, and can act as an effective predator deterrent (Cheney and Wrangham 1987). Male vigilance may be also be advantageous in many species. Vigilance improves the chance of detecting a potential predator and alerting others to its presence and identity (van Schaik and van Noordwijk 1989). The presence of vigilant males may also allow a female to spend more time foraging, and relieve her need to accompany and closely monitor vulnerable infants.

2. Mating Stability and Infant Care

The availability of a known and accepted reproductive partner is a benefit difficult to assess. Robinson (1988) suggests that resident males may reduce immigration and breeding takeover by outgroup males, contributing to social stability and contributing to female reproductive success. Infanticide by incoming males may be an extreme response to intense competition for females under conditions of limited male breeding tenure (Hrdy 1974, 1977), suggesting that long-term residence by breeding males may be of considerable benefit to females.

Male care of infants ranges from simple tolerance to intensive caretaking, and varies considerably both within and between species (Whitten 1987). Some males assist females in caring for their offspring by carrying, grooming, or 'babysitting' infants (Izawa 1980). Strong affiliative bonds with individual males may provide important benefits for infants, including protection from conspecifics and improved access to food resources (Altmann 1980; Whitten 1987). Other effects of males on infants may be subtle and difficult to measure; for example, adult males may provide role models for male infants.

Costs of Males to Females

3. Interference with female food acquisition

Within-group competition can take two forms: scramble or contest (Janson and van Schaik 1988; van Schaik 1989). Scramble competition occurs when all group members exploit the same food supply and none are able to obtain more than others through overt behaviour. The intensity of scramble competition is primarily determined by group size, and the sex of individual competitors is not a significant factor. In contest competition, one competitor actively prevents another's access to resources through aggression or displacement, allowing some individuals to obtain a greater share of resources than others. The outcome of contest competition is affected by social factors, especially dominance. Feeding success is often greater for dominant individuals, who gain priority of access to many foods, feed longer, and/or experience fewer interruptions than subordinants (Post *et al*. 1980; Robinson 1981b; Whitten 1983; Janson 1985). Dominants can exclude subordinants from rich feeding patches, and restrict them to areas of poor foraging yield and/or high predation risk (Janson 1985, 1990b). Males are the dominant sex in many primate species, so contest competition may be a means by which males can secure food resources at the expense of females.

4. Harassment of Females and Infants

In addition to interfering with female food acquisition, males may harass females or their offspring in non-feeding contexts. Agonistic exchanges with males could reduce the time available to females for rest, infant care, or other social activities. Females may spend time grooming males as a form of appeasement, promoting male tolerance of themselves and their offspring (Janson 1985; O'Brien 1991). Male hostility toward infants, of which infanticide is an extreme case, is an additional way in which males can reduce female reproductive success.

FINDINGS FROM PRIMATE FIELD STUDIES

Sex Differences in Foraging Behaviour

Sex differences in foraging behaviour have been reported in many primate species. Females often spend more time foraging or feeding than conspecific males, as in red colobus (Clutton-Brock 1974; Marsh 1981), mangabeys (Waser 1977), baboons (Dunbar 1977; Post 1981; Demment 1983), rhesus monkeys (Lindburg 1977; Seth and Seth 1986), howlers (Smith 1977), capuchins (Fragaszy 1986, 1990; van Schaik and van Noordwijk 1989), Japanese macaques (Iwamoto 1987), and squirrel monkeys (Boinksi 1988a, 1989). Female titi monkeys simply eat faster than males (Kinzey 1977). Female indris, gibbons, and siamangs eat both faster and for longer (Pollock 1977; Raemakers 1980; Chivers and Raemaekers 1986) However, the reverse is true in several species: female gorillas (Fossey and Harcourt 1977), orangutans (Rodman 1977; Rodman and Mitani 1987), chimpanzees (Ghiglieri 1984, 1988), and green monkeys (Harrison 1983) spend less time foraging than males. Strier (1991) found that the only sex difference in woolly spider monkey diets was the greater proportion of feeding time females devoted to flowers.

The apparent trend of prolonged female feeding, even in species where males are larger than females, suggests that the total energy needs of a large male body are outweighed by other factors which increase the energy requirements of female conspecifics. Alternatively, males may feed more efficiently than females, or feed on items that require less handling time. The most obvious factor increasing female energy needs is pregnancy and lactation, and this is frequently suggested in explanation of increased female foraging (e.g Pollock 1977; Waser 1977; Lindburg 1977; Demment 1983, Chivers and Raemaekers 1986; Fragaszy 1986). In addition, male wedge-capped capuchins may be more efficient foragers than females, obtaining a higher foraging yield per unit time (Fragaszy 1986). Clutton-Brock (1977a) suggested that in gorillas and orangutans, differences in body weight are so pronounced that the male feeds for longer periods than the female despite her energetic committment to pregnancy and lactation. Male chimpanzees make long 'border patrols' and spend more time travelling than females, and may increase their feeding time to support this additional energy expenditure (Chiglieri 1984, 1988). Harrison (1983) found that sex differences in the amount of time green monkeys spent foraging disappeared once he corrected for differences in male and female body weights; on a per-unit-body-weight basis, females actually spent slightly more time foraging than males. Strier (1991) suggested that the absence of sex differences in feeding time for woolly spider monkeys (a monomorphic species) may have been due to the lack of food stress in her study group, or the fact that only one female was lactating during the study.

Researchers comparing females of different reproductive status report mixed findings. Smith (1977) found that female howlers with infants fed for longer than those without. Female baboons spent more time feeding as their unweaned infants grew (Altmann 1980), but Post *et al* (1980) found that lactating females spent less time feeding than pregnant females. Boinski (1988a) found few differences among pregnant, lactating, and non-reproducing female squirrel monkeys. Harrison (1983) found that green monkey mothers actually spent less time feeding than other females. Harrison suggested that green monkeys have an overall 'low cost/high yield' strategy, and that females respond to the additional energy demands of lactation by increasing rest rather than increasing foraging time.

It is difficult to translate foraging times into nutritional values under field conditions, especially if feeding rates differ among food types, and/or some foods are difficult to identify (Clutton-Brock 1977b; Galdikas and Teleki 1981; Richards 1985; Barton 1992). However, many females are reported to eat more protein-rich foods than conspecific males. Some females eat more arthropods, as in guenons (Gautier-Hion 1980), capuchins (Robinson 1981a; Fragaszy 1986), siamangs (Chivers and Raemaekers 1986), and rhesus monkeys (Seth and Seth 1986). Female indris and guenons eat more young leaves, and many female baboons eat less fibre than conspecific males (Iwamoto 1979; Dunbar 1977; Demment 1983). There is an opposite trend in species which prey on relatively large vertebrates; female chimpanzees, baboons, and capuchins typically eat less meat than males (Teleki 1973, 1981; Goodall 1986; Boesch and Boesch 1984; Harding 1973; Strum 1975, 1981; Fedigan 1990).

Sexual dimorphism may account for differential substrate use and exploitation of tough foods, while pregnancy and lactation costs account for the greater exploitation of protein-rich foods by females. Gautier-Hion (1980) suggested that sex differences in the diets of guenons may reduce competition between males and pregnant or lactating females. Rodman (1977) also proposed competition avoidance as an explanation of the orangutan foraging pattern, in which males and females tend to segregate and use different feeding sites. Galdikas and Teleki (1981) referred to the foraging pattern of both orangutans and chimpanzees as 'ecological separation between the sexes', and suggested that this pattern represents an 'incipient division of labour'. However, Sugardijito and van Hooff (1986) attributed sex differences in orangutan foraging behaviour primarily to sexual dimorphism. Dimorphism may also influence sex differences in predation on relatively large vertebrates. Males, by virtue of their larger size and larger, stouter canines, may be more effective predators and less vulnerable to prey defences than conspecific females. Fedigan (1990) suggested that females may be unwilling to incur the high energy cost, physical danger, and uncertain returns of vertebrate predation, and may opt instead for the more reliable and less costly alternative of invertebrate predation, especially when pregnant or carrying an infant.

Benefits and Costs of Males to Females

Males are often the most frequent and aggressive participants in intergroup encounters, as has been reported for capuchins (Oppenheimer 1968, 1982; Defler 1979, 1982; de Ruiter 1986; Janson 1986a, 1986b; Robinson 1988; Fedigan in press), barbary macaques (Deag 1973), howler monkeys (Klein 1974; Klein and Klein 1975), rhesus monkeys (Lindburg 1977), baboons (Cheney and Seyfarth 1977), black and white colobus (Oates 1977), red colobus (Struhsaker 1980), langurs (Struhsaker and Leland 1987), gorillas (Stewart and Harcourt 1987), and chimpanzees (Ghiglieri 1984,1988; Goodall 1986). However, females often participate actively in group defence

(Fedigan 1982), and female titi monkeys (Robinson 1981b), tamarins (Terborgh 1983) and vervets (Cheney 1981) can be more active than males in intergroup encounters. The extent of female participation in many species varies among groups and according to circumstances; females usually defend territory or resources against outgroup females, while males defend their access to females and typically direct most of their aggression toward other males (Wrangham 1980; Cheney 1987). Females may be less likely to participate in intergroup encounters where males are considerably larger than themselves (Cheney 1987).

Males in many species devote more time to vigilance behaviour ('scanning') than conspecific females, as reported for black and white colobus (Oates 1977), guenons (Gautier-Hion 1980), vervets (Cheney and Seyfarth 1981; Baldellou and Henzi 1992), capuchins (de Ruiter 1986; van Schaik and van Noordwijk 1989; Fragaszy 1990; Fedigan in press), and squirrel monkeys (Boinski 1988a). Male capuchins are more active than females in confronting predators (Defler 1979; Janson 1986a, 1986b; Chapman 1986; Boinski 1988b; Escobar-Paramo 1989). However, female langurs are the main participants in snake-mobbings (Srivastava 1991). In field experiments, capuchin males detected model predators faster and more frequently than females, and were more likely to approach and mob both real and model predators (van Schaik and van Noordwijk 1989). Van Schaik and van Noordwijk suggested that for females, the benefits of male 'anti-predator services' may outweigh the costs of increased feeding competition.

The effects on females of feeding competition from resident males has yet to be directly investigated in the field. However, some findings suggest that females may adjust their foraging patterns in response to aggression from dominant males. Capuchin females may avoid interference while foraging by occupying positions close to the edge of their group rather than the more advantageous forward-central positions (Robinson 1981a; Janson 1990a).

Males are responsible for almost all reported cases of infanticide in non-human primates. Infanticide has been observed in a number of colobine species (reviewed in Struhsaker and Leland 1987), redtail monkeys (Struhsaker 1977), blue monkeys (Butynski 1982), baboons (Collins *et al.* 1984), howler monkeys (Crocket and Sekulic 1984; Clarke 1983), capuchins (Valerrama *et al.* 1990; pers.obs.), lemurs (Pereira and Weiss 1991), gorillas (Fossey 1984; Watts 1989), and chimpanzees (Goodall 1977; Takahata 1985; Spijkerman *et al.* 1990). Most infant killings were committed by an immigrant male who had not previously copulated with the infant's mother, usually soon after group takeover or rise in rank. Sugiyama (1967) noted that in langurs, the loss of an infant had the effect of advancing female estrus, an observation subsequently refined by Hrdy (1974, 1977) into the sexual selection 'advanced estrus' hypothesis, which considers infanticide as a male reproductive strategy. However, some cases have been observed in which no male reproductive advantage could be inferred (e.g. Goodall 1977; Takahata 1985; Spijkerman *et al.* 1990; Valerrama *et al.* 1990). Sugiyama (1987) emphasised that proximate factors arising from environmental and social conditions must also be considered in explaining infanticide. Unfortunately, the prevailing focus on the potential reproductive benefits of infanticide to males neglects the huge concomitant cost to females. The potential for male harm to infants may have been a potent selective force operating on female behaviour even in species where infanticide has not been observed in the wild (Smuts 1987).

In groups of both wedge-capped and brown capuchins, females preferentially associate with the alpha male (O'Brien 1991; Janson 1984). O'Brien suggested that this represents a female breeding strategy; mating exclusively with the dominant male reduces the chance that he will kill or injure subsequent infants, and may ensure that they are tolerated at feeding sites. In brown capuchins, the alpha male's ability to control access to fruit trees may allow him to provide a feeding benefit to females and their offspring (Janson 1984). By monopolising access to the dominant male, high-ranking females may receive a disproportion of the benefits of having males within the group (O'Brien 1991).

THE STUDY SPECIES

The white-faced capuchin, *Cebus capucinus*, is a New World (platyrrhine) primate, its geographical range extending from Belize to northern Colombia (Freese and Oppenheimer 1981). The genus includes three other species: the white-fronted capuchin *C. albifrons*, the wedge-capped capuchin *C. olivaceus* (formerly *C. nigrivittatus*), and the brown capuchin *C. apella*. All capuchins are diurnal, medium-sized quadruped climbers, and although all four species spend at least some time on the ground, they are primarily arboreal (Freese and Oppenheimer 1981). All have prehensile tails, opposable thumbs, and great manual dexterity (Robinson and Janson 1987; Fragaszy *et al.* 1990). *Cebus capucinus* is a moderately dimorphic species: body weights range from 0.9 kg to 2.6 kg for females, and from 1.2 kg to 3.3 kg for males (Buckley 1983). Mean body weights for three males and three females captured at Santa Rosa National Park, Costa Rica, were 3.3 kg and 2.3 kg respectively (Glander *et al.* 1991). Males are 25-35% larger than females, with larger shoulders, heavier jaw development, and longer canines (Oppenheimer 1968; Fedigan 1990). Females have an elongated clitoris that superficially resembles the male penis. Males reach full adult size and are considered mature at about eight years of age; females are mature at about four years (Oppenheimer 1968). Females can produce a new infant each year, but tend to give birth every second year (Robinson and Janson 1987). The gestation period is approximately five months (average 153 days in captive brown capuchins [Wright and Bush 1977]). It is not known how long capuchins live in the wild, but ages of at least 40 years have been attained in captivity (Fragsazy *et al*. 1990).

Capuchins are omnivores, renowned for their dietary plasticity and ability to exploit a broad spectrum of plant and animal foods (Izawa 1979; Freese and Oppenheimer 1981; Buckley 1983; Moscow and Vaughan 1987; Brown and Zunino 1990; Fragaszy *et al*. 1990). Populations living in different habitats can have widely differing diets, and considerable variability has been found among white-faced capuchin groups even within the same area (Chapman and Fedigan 1990). Animal foods, mostly insects, comprise up to 20% of total food intake (Oppenheimer 1982; Buckley 1983; Chapman 1988). A relatively short colon (among the shortest in primates) is consistent with a reliance on easily digested, energy-rich foods (Fragaszy *et al*. 1990), and animal foods are probably an essential dietary component. White-faced capuchins have been seen to eat such diverse foods as wasp nests, oysters and crabs, bird eggs, and small vertebrates such as lizards, squirrels, birds, and nestling coatis (Oppenheimer 1968; Buckley 1983; Newcomer and de Farcy 1985; Fedigan 1990; pers.obs.). Capuchins reqire drinking water, which they obtain from streams, waterholes, and tree holes or other natural basins where rainwater has collected (Oppenheimer 1968; Freese 1978).

Capuchins are extremely manipulative and opportunistic feeders, searching through and unrolling leaves, reaching into holes and crevices, stripping bark, and breaking twigs and branches (Oppenheimer 1968; Freese and Oppenheimer 1981; Buckley 1983; Fragaszy 1986, 1990; Moscow and Vaughan 1987). As successful generalists, capuchins occupy a New World niche analogous to that of chimpanzees in the Old World. The manipulative and cognitive abilities which capuchins demonstrate in captivity are often compared with those of the great apes, and may be intimately associated with their foraging strategy (Parker and Gibson 1977; Jolly 1985; Gibson 1986; Visalberghi 1988).

White-faced capuchins live in multi-male, multi-female groups of 6 to 30 or more individuals, with an average group numbering about 15 (Oppenheimer 1968; Buckley 1983; Fedigan *et al.* 1985; Massey 1987). Most groups have well-defined home ranges, and while overlaps do occur, at least some boundaries are defended (Oppenheimer 1968, 1982; Buckley 1983). Sub-adult males generally migrate from their natal groups, while females are philopatric. However, females occasionally transfer as well, and an all-female group can maintain and defend a home range, at least temporarily (Oppenheimer 1968; pers.obs.). Most groups have an unambiguous alpha male (cf Buckley 1983), and males are usually dominant over females. The alpha female ranks close to or immediately below the alpha male in some groups (Fedigan in press). Some researchers report a lack of rigid linear dominance hierarchies (Freese 1978; Buckley 1983), but although not readily apparent, linear rankings are found some *C. capucinus* groups (Fedigan, in press).

PURPOSE AND RELEVANCE OF THE PRESENT STUDY

In the present study, I follow the theoretical framework that male and female capuchins differ in their primary reproductive strategies; male behaviour is primarily directed toward gaining access to mates, while female behaviour is directed toward gaining access to food resources. I examine sex differences in foraging behaviour, and attempt to relate these differences to various evolutionary explanations. Can sex differences in the foraging behaviour of white-faced capuchins best be explained by sexual dimorphism, the costs of pregnancy and lactation, or competition avoidance? Within the context of differing male and female strategies, I also examine the benefits and costs of resident males to females. These benefits and costs are not directly comparable, making difficult to determine whether benefits exceed costs. I address the question in the form 'for females, how do the benefits and costs of males compare with those of females within the same social group?' Are the benefits and costs of males shared equally among females? Do females attempt to alter the balance of benefits and costs through male-directed behaviours?

White-faced capuchins are highly suitable subjects for this study. Their dietary flexibility and ability to exploit a wide range of resources promotes the development of intra- and inter- group differences in foraging behaviour. Their multi-male, multi-female social organisation is appropriate for comparing foraging and social behaviour between the sexes. Behavioural flexibility and the opportunities for learning provided by a long lifespan favour the development of complex social interactions. The study builds upon previous work on sex differences in foraging (Fragaszy 1986, 1990) and female-male association patterns (O'Brien 1991) in wedge-capped capuchins, and feeding competition in brown capuchins (Janson 1985, 1988, 1990a, 1990b). The work is part of a long-term study of population dynamics and individual life histories of three primate species at Santa Rosa National Park, Costa Rica, under the supervision of Dr. Linda M. Fedigan.

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CHAPTER 2

SEX DIFFERENCES IN THE DIET AND FORAGING BEHAVIOUR OF WHITE-FACED CAPUCHINS (*CEBUS CAPUCINUS*) AT SANTA ROSA NATIONAL PARK, COSTA RICA.

INTRODUCTION

The primary reproductive strategies through which individuals attempt to maximise inclusive fitness differ between the sexes: the primary strategy of females is food acquisition, while that of males is mate acquisition (Trivers 1972; Wrangham 1980, 1983; O'Brien 1991). Thus females are expected to maximise foraging time, while males minimise foraging time in favour of other fitness-increasing activities such as sexual behaviour and predator or competitor vigilance (Schoener 1971; Iwamoto 1987; Boinski 1988). Sex differences in activity patterns and diet have been reported in free-ranging groups of many non-human primate species (Gautier-Hion 1980; Robinson 1981; Galdikas and Teleki 1981; Marsh 1981; Demment 1983; Harrison 1983; Ghiglieri 1984, 1988; Chivers and Raemaekers 1986; Fragaszy 1986, 1990; Seth and Seth 1986; Iwamoto 1979, 1987; Rodman and Mitani 1987; Boinski 1988; and see Clutton-Brock 1977 for an earlier review). In most cases, females spent more time foraging than conspecific males, and/or ate more protein-rich foods.

Three evolutionary explanations of sex differences in diet and foraging behaviour are generally proposed: sexual dimorphism, the costs of pregnancy and lactation for females, and competition avoidance (Clutton-Brock 1977). Differences in body size affect the amount of food an individual requires, the types of food it can efficiently exploit, the substrates where it can feed, and its vulnerability to predators (Coehlo 1974; Robinson 1981; Janson 1985; Richard 1985; de Ruiter 1986; Cant 1987; Boinski 1989). Pregnancy and lactation increase a female's energy cost by up to 25% and 50% respectively, and also increase her protein and mineral requirements (Portman 1970; Coehlo 1974; Altmann 1980; Demment 1983; Dunbar and Dunbar 1988; Lee 1989). Differences in diet, or spatial separation, both of which reduce competition between the sexes, could be adaptive for males as well as females (Selander 1972; Chalmers 1979).

In this study I examine sex differences in foraging behaviour and diet in the white-faced capuchin, *Cebus capucinus*. These neotropical primates are moderately dimorphic; males are 25-35% larger than females, with larger shoulders, heavier jaws, and longer canines (Oppenheimer 1968; Fedigan 1990). Mean body weights for three males and three females captured at the study site were 3.3 kg and 2.3 kg respectively (Glander *et al*. 1991). White-faced capuchins live in multi-male, multi-female groups of 6 to 30 individuals, with an average group size of about 15 (Oppenheimer 1968; Buckley 1983; Fedigan *et al*. 1985; Massey 1987). Males are typically dominant over females, but in at least some groups the alpha female ranks immediately below the alpha male and above other males (Fedigan in press).

White-faced monkeys are omnivorous, and animal foods comprise up to 20% of their diet (Oppenheimer 1982; Buckley 1983; Chapman 1988; Moscow and Vaughan 1987). Their relatively short colon is consistent with a reliance on easily-digested, energy-rich foods (Fragaszy *et al.* 1990), and animal foods may be an essential dietary component. These monkeys eat a wide variety of invertebrates, and small vertebrates such as lizards, squirrels, birds, and nestling coatis (Oppenheimer 1968; Buckley 1983; Newcomer and de Farcy 1985; Fedigan 1990). They are highly opportunistic foragers, and their manual dexterity allows them to manipulate a wide range of materials and substrates in search of food. Capuchins are noted for their dietary plasticity, adaptability, and behavioural variability (Izawa 1979; Brown and Zunino 1990; Chapman and Fedigan 1990; Fragaszy *et al.* 1990).

To date, the wedge-capped capuchin (*Cebus olivaceus*) is the only capuchin species on which a field study emphasising sex differences in foraging behaviour has been done. Fragaszy (1986) found that *C. olivaceus* males spent proportionally less time foraging and more time resting than females; they devoted more time to vigilance behaviour, and spent more time on the ground. Robinson (1981) and de Ruiter (1986) have made similar observations on this species. Fragaszy suggested that *C. olivaceus* females may be less efficient foragers than males, obtaining a lower yield per unit foraging time. In a recent study of *C. capucinus*, Fedigan (in press) found that males and females spent similar amounts of time foraging, but that males were more vigilant and spent more time on the ground than females.

Hypotheses and Predictions

The objective of my study is to determine whether there are sex differences in foraging behaviour and/or diet in *Cebus capucinus*, and if so, to relate these differences to the three evolutionary explanations which have been proposed: sexual dimorphism, the costs of pregnancy and lactation, and competition avoidance. Each explanation is presented as a separate hypothesis, and associated sex differences in diet and foraging behaviour are predicted.

Hypothesis I:

Sexual dimorphism is the primary cause of sex differences in the diet and foraging behaviour of white-faced capuchins.

Predictions:

In order to meet the increased energy requirements associated with their larger body weight:

1. males spend more time foraging or feeding than females.
2. Males eat more protein-rich animal foods than females

As a result of their greater strength and larger canines:

3. males spend more time in physically strenuous foraging such as bark-stripping and branch-breaking than females.

As a result of their greater size and weight:

4. males use fewer small foraging supports than females.
5. males make greater use of lower substrates (including the ground) than females.

Hypothesis II:

The energy costs of pregnancy and lactation for females are the primary cause of sex differences in the diet and foraging behaviour of white-faced capuchins.

Predictions:

As a result of the increased energy requirements associated with pregnancy and lactation:

1. Females spend more time foraging and/or feeding than males.
2. Females eat more animal foods than males.
3. Pregnant or lactating females spend more time foraging and/or feeding than other adult females.
4. Pregnant or lactating females eat more animal foods than other adult females.

Hypothesis III:

Avoidance of competition between males and females is the primary cause of sex differences in the diet and foraging behaviour of white-faced capuchins.

Predictions:

1. Males and females have differences in diet not readily explained by sexual dimorphism.
2. If individuals who are close together tend to eat similar foods, then males and females are found in proximity less often than individuals of the same sex.
3. If males and females have successfully diverged in foraging such that competition between sexes is less intense than competition within sexes, there will be less foraging-related agonism between males and females than between females or between males.

The competition avoidance hypothesis does not readily lend itself to unambiguous predictions, and the rigor of testing this hypothesis is lower than that of the other two. The three hypotheses are not mutually exclusive, and it may not be possible to choose one and discard the remainder. However, one hypothesis may more accurately predict sex differences in foraging behaviour and diet than the others.

METHODS

Study Site and Groups

Santa Rosa National Park is situated near the Pacific coast of Costa Rica, adjacent to the Pan American Highway and about 35 km northwest of Liberia, Guanacaste. Established in 1970, Santa Rosa is a 10 800 ha mosaic of dry tropical forest, semi-evergreen forest, and reclaimed pasture in varying stages of secondary succession. The area experiences a distinct wet and dry season: almost all of Santa Rosa's 900-2400 mm of annual rainfall occurs between mid-May and mid-December (Glander *et al.* 1991). The park is home to a great diversity of wildlife: 115 species of mammals, 253 of birds, 100 of amphibians and reptiles, and over 10,000 insect species (Boza 1988). Three non-human primate species are present at Santa Rosa: the mantled howler monkey (*Aloutta palliata*), the red spider monkey (*Ateles geoffroyi*), and the white-faced capuchin (*Cebus capucinus*). A total of 28 capuchin groups were censused in 1983-1984, with an average group size of 15 individuals (Fedigan *et al.* 1985). Potential predators on white-faced monkeys are constricting snakes, felids, and raptors (Freese 1983; Chapman 1986).

The two main study groups were the Los Valles (LV) group and the Cerco de Piedra (CP) group (Appendix A). The LV group contained between 14 and 19 individuals (4-5 adult females, 2 adult males, 2 subadult males, 2-4 juveniles, and 4-6 infants). The CP group contained 12 to 14 individuals (4 adult females, 1-2 adult males, 0-1 subadult male, 4 juveniles, and 3-4 infants). Individuals could be recognised by facial characteristics and, for most adult males, scars. During the study period, three females gave birth, two CP group males left their group (one returned after a two-month absence), and one LV group male transferred to a neighbouring group.

The LV and CP group ranges covered approximately 100 ha and 45 ha respectively (Appendix B). The LV range was considerably richer in food resources than the CP range, with a higher proportion of forest over 100 years old, many productive fruit trees, and a permanent natural waterhole. The CP range included an artificial waterhole provided after clearing of ranchlands north of the park desiccated the previously existing natural waterhole (L.M. Fedigan, pers.comm.). The CP group has been the subject of previous studies at Santa Rosa (Fedigan 1990; Chapman and Fedigan 1990; Fedigan in press), and both groups were habituated to human observers. Visibility varied throughout the two ranges but was excellent in many areas, especially during the dry season. Observation distances of five to ten metres were common.

Data Collection

Preliminary observations for this study were made in May-July 1990 and January 1991. Extensive behavioural sampling of adults was conducted between 1 February and 30 June 1991. I collected 380 hours of focal data in the form of ten-minute continuous-time sessions (Altmann 1974), and additional *ad lib.* data on comparatively rare events such as vertebrate predation. I sampled from dawn until dusk across all group activities. The mid-day period (1130 h to 1330 h) was under-represented throughout the dry season, as monkeys and observer generally rested during this, the hottest part of the day.

Data were collected in alternating ten-day blocks for each group. I obtained 1063 focal sessions on LV group adults (4 females and 4 males) and 1210 on CP group adults (4 females and 3 males). Given the dispersed nature of the groups and the difficulty in locating particular individuals, it was not practical to follow a rigid sampling regimen. However, I attempted to sample each focal subject within a group before beginning a new round of observations, and in the LV group, to alternate males and females as focal subjects. I kept a continuous record of the number of samples obtained for each individual to ensure that sampling was evenly distributed. If a focal subject disappeared from view for more than 90 seconds, the session was abandoned and the data discarded.

I recorded the location and general activity of the group prior to each focal session, and the closest three neighbours within ten metres of the focal animal immediately before and after each session. All foraging behaviour was recorded according to type and target (Table 1); a complete ethogram of behaviours recorded is supplied in Appendix C. Most plant foods were identified to the species level (Appendix D); I collected samples of unknown food items wherever possible for later identification. Support height and size were recorded for all foraging behaviours. Branches or other supports classed as LARGE were those on which the individual could easily walk quadrupedally (diameter c.>10 cm). MEDIUM supports (diameter 1-10 cm) required some grasping with feet

Table 2.1: Foraging categories and food types used in analyses.

Foraging Behaviour

FEEDING

- CATCH AND EAT exposed or mobile prey.
- eat EMBEDDED INVERTEBRATES
- PICK AND EAT fruit, seeds, flowers, buds, leaves, emergent aggregate caterpillars.
- PICK AND PROCESS (e.g. rub and remove spines; bang, bite or peel open) fruit, seeds, snails.

MANUAL FORAGE

- break open and investigate stems, vines, surface bark.
- manipulate and search through live or dead vegetation.
- explore tree holes and crevices.
- grab at but fail to catch mobile prey.
- sample fruit by holding, biting, sniffing and/or poking.

- HEAVY FORAGE: break branches, strip bark

VISUAL FORAGE
- visually inspect vegetation

OTHER FORAGE
- includes drink, lick leaves, chase prey, nest raid.

Food Types

ANIMAL FOODS:

- VERTEBRATES: e.g. squirrels, nestling coatis,birds, eggs.
- EMBEDDED INVERTEBRATES: small invertebrates or larvae embedded in plant material.
- CATERPILLARS
- OTHER INVERTEBRATES: non-embedded invertebrates (excluding caterpillars). Primarily arthropods, but includes some gastropods (snails).

FRUIT: fruit, nuts or seeds

OTHER PLANT MATERIAL flowers, buds, shoots, stems, leaves.

or hands. SMALL supports were terminal twigs or thin vines (<1 cm diameter) which were grasped, usually using the tail as additional or sole support. 'OTHER' supports were adjacent to, above, or below the tree in which feeding occurred. Foraging height was classed as HIGH (> 15m), MEDIUM (5-15m), LOW (< 5m) or GROUND. Use of GROUND was noted across all activities.

Data Analysis

Data were coded and entered onto the computer using PRIMA 1.1 (PRimatologist Information Management and Analysis), a programme specifically designed for this project by Frameworks Management Corp, Victoria, British Columbia. PRIMA generates frequencies and durations of specified behaviours in a wide variety of combinations for each or all focal subjects.

Statistical analyses were carried out using the SPSS and SPSS-PC computer packages. For analysis of time budgets, the time an individual devoted to each behaviour was expressed as a percentage of the total time that animal was observed. Foraging behaviours and use of each substrate height and support size class during foraging were expressed as percentages of an individual's foraging time. The data were tested for sex and group differences using a two way analysis of variance at the $p < 0.05$ level. Group differences were non-significant unless otherwise indicated (detailed sex and group comparisons are supplied in Appendix E). To investigate patterns of proximity, I calculated the distribution of proximity scores within and between the sexes from the results of the proximity scans before and after each focal session. I compared this with a random distribution of proximity scores based on the number of males and females available. As some males were not present for the entire study period, the 'number of available males' reflected the percentage of samples for which each male was present in the group. Similarly, I compared the observed distribution of agonism between and within sex classes with a random distribution based on the availability of potential partners for each sex.

RESULTS

Summarised activity budgets for adult males and females are provided in Figure 2.1. Males scored higher than females for SCAN (F=41.32, $p<0.001$) and REST (F=6.55, p=0.027); females scored higher than males for FORAGE (F=4.97, p=0.046) and SOCIAL behaviour (F=23.28, $p<0.001$). The only significant difference between the two groups was the greater proportion of time devoted to SOCIAL behaviour by the LV group (F=17.12, p=0.002).

Time spent foraging and feeding:

Females devoted approximately 5% more of their time to foraging than males (Figure 2.1). Females did not differ significantly from males in the distribution of their time across major foraging categories (Figure 2.2), including the

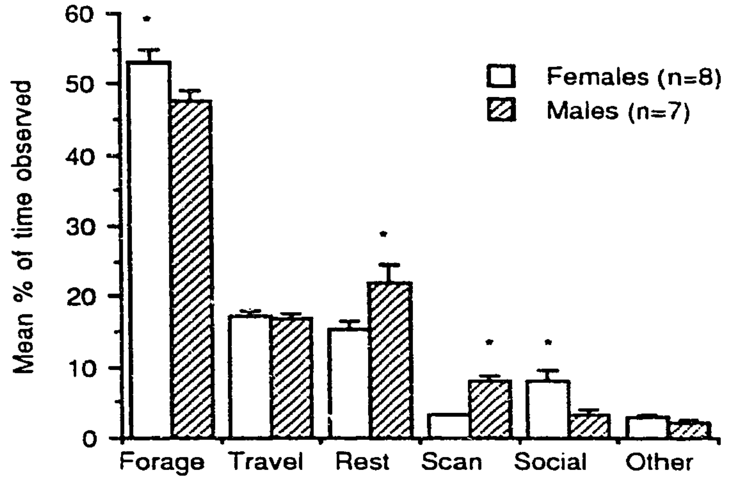

Figure 2.1: Mean percent (and SE) of time devoted to particular activities by males and females. An asterisk above a comparison indicates a level of significance in an ANOVA test of $p < 0.05$.

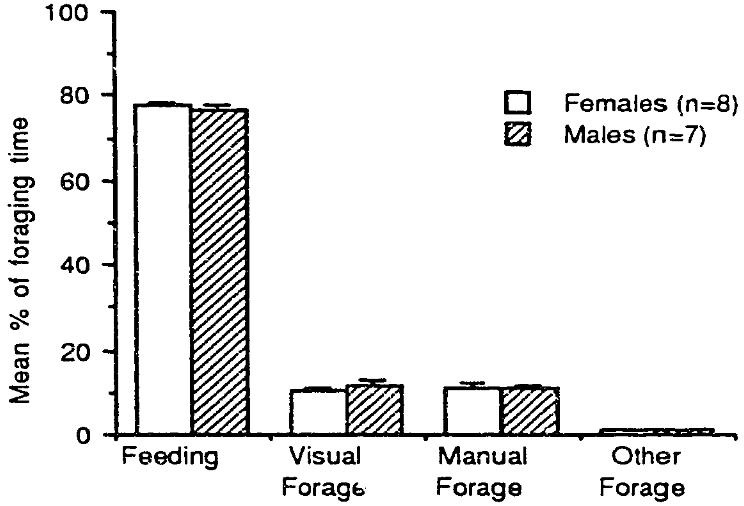

Figure 2.2: Mean percent (and SE) of foraging time devoted to particular types of foraging activities by males and females.

proportion of time they spent FEEDING (F=1.65, p=0.225). As handling time can affect the amount of food actually consumed, I examined the proportion of foraging time that males and females devoted to foods requiring manual processing prior to eating (PICK AND PROCESS). There was no consistent difference between the sexes (F=1.81, p=0.205). Males scored higher than females in the LV group; females scored higher than males in the CP group.

Diet and animal foods:

Males and females had broadly similar diets, with no significant difference in the proportion of ANIMAL FOOD eaten (F=0.39, p=0.546) (Figure 2.3). There was an intergroup difference in consumption of OTHER PLANT MATERIAL (F=6.42, p=0.028), primarily due to feeding on *Enterolobium cyclocarpum* leaf buds by the LV group. Within the class ANIMAL FOOD, females ate more EMBEDDED INVERTEBRATES than males (F=15.02, p=0.003) (Figure 2.4). Males spent more time eating VERTEBRATES (F=8.30, p=0.018), and caught more vertebrate prey per capita (Table 2.2). The CP group spent more time than the LV group exploiting EMBEDDED INVERTEBRATES; the LV group ate more CATERPILLARS (F=10.63, p=0.008; F=548.17, p<0.001).

The category OTHER INVERTEBRATES was mainly composed of motile arthropods, recorded under foraging category CATCH AND EAT. I examined foraging success within this category (excluding vertebrate prey), distinguishing between small prey

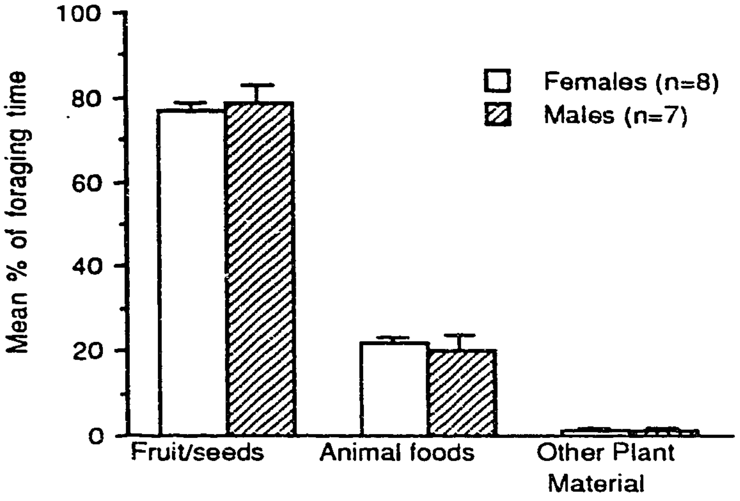

Figure 2.3: Mean percent (and SE) of foraging time spent exploiting particular food types by males and females.

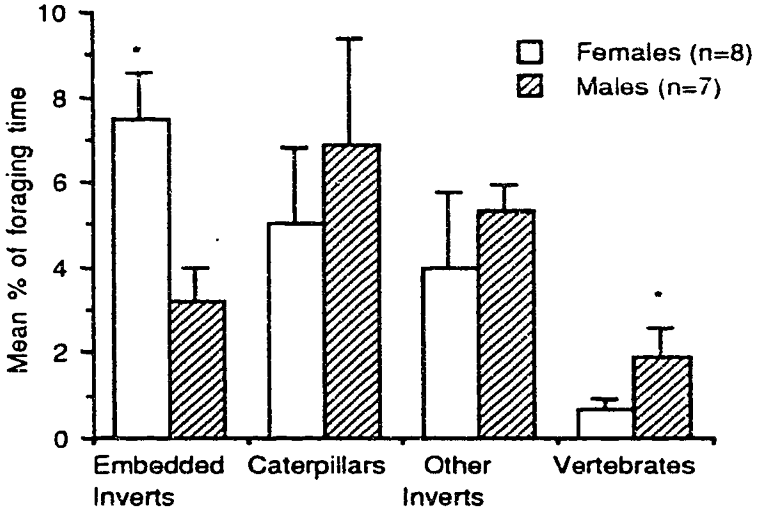

Figure 2.4: Mean percent (and SE) of foraging time spent exploiting particular types of animal food by males and females. An asterisk above a comparison indicates a level of significance in an ANOVA test of $p < 0.05$.

Table 2.2. Vertebrate predation by LV and CP groups: number and types of prey taken by males and females. Data taken from focal and *ad lib.* observations.

	Lizard	bird/egg nestling	Squirrel	coati	TOTAL	per[1] capita
LV males n=4	2	6	1	3	12	3.4
LV females n=4	1	6	0	2	9	2.3
CP males n=3	4	3	2	5	14	7.8
CP females n=4	0	1	0	6	7	1.8
TOTAL	7	16	3	16	42	3.2
MALES n=7	6	9	3	8	26	5.0
FEMALES n=8	1	7	0	8	16	2.0
LV group n=8	3	12	1	5	21	2.8
CP group n=7	4	4	2	11	21	3.6

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[1] Adjusted rate per capita, reflects number of individuals and proportion of time each was present in the group.

items (less than one monkey mouthful) and large prey items (more than a mouthful). Male and female capture rates were similar, but males caught more large invertebrates while females caught more small invertebrates (F=5.25, p=0.043; F=5.06, p=0.046) (Figure 2.5). Almost 65% of the 398 large invertebrate captures recorded occurred within 5 m of the ground. Males caught 31% of their large invertebrates on the ground, and 45% at heights of less than 5 m. Male success in catching large invertebrates increased with time spent ON THE GROUND (Figure 2.6).

Branch Breaking and Bark Stripping

On average, males spent 3.7% of their foraging time in HEAVY FORAGING, significantly more than the 0.5% spent by females (F=11.99, p=0.005).

Size of Foraging Supports:

Males spent less time than females on SMALL foraging supports, and more time on LARGE supports (F=156.59, p<0.001; F=45.57, p<0.001) (Figure 2.7). The only significant intergroup difference was the greater time spent on OTHER supports by the CP group (F=23.66, p=0.001).

Substrate Height

Males made more use than females of LOW supports and GROUND (F=33.20, p<0.001; F=30.19, p<=0.001) (Figure 2.8).

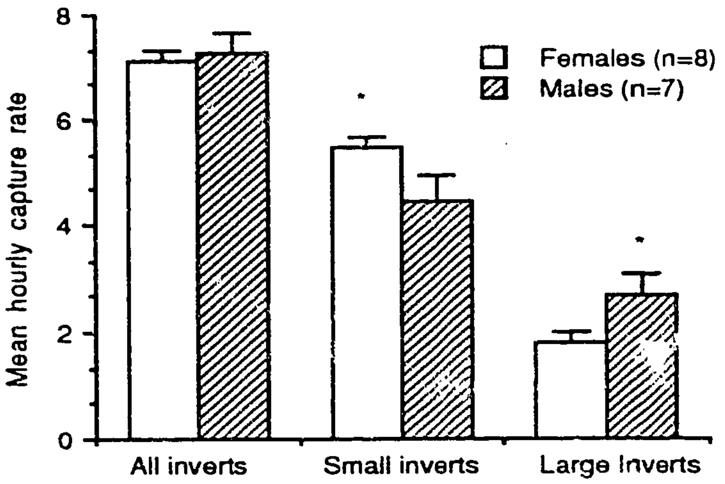

Figure 2.5: Mean capture rate (and SE) of large and small invertebrates by males and females per hour of foraging. n = 398 recorded captures. An asterisk above a comparison indicates a level of significance in an ANOVA test of $p < 0.05$.

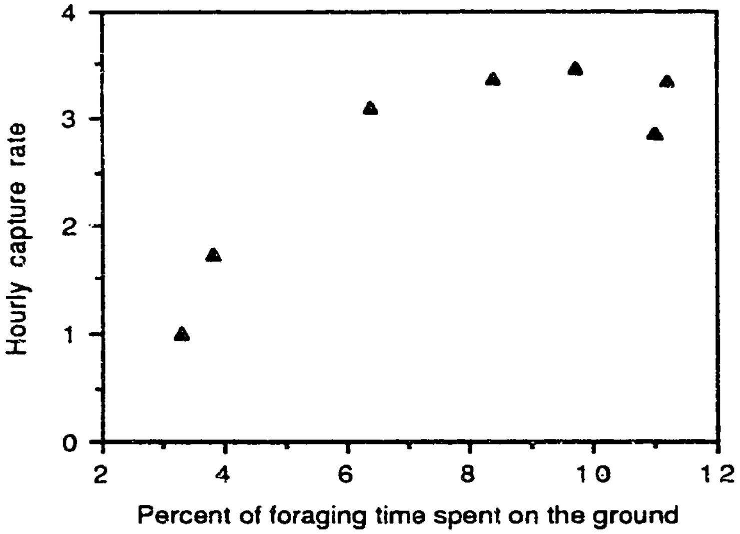

Figure 2.6: Percent of foraging time spent on the ground and hourly rate of large invertebrate capture for males.

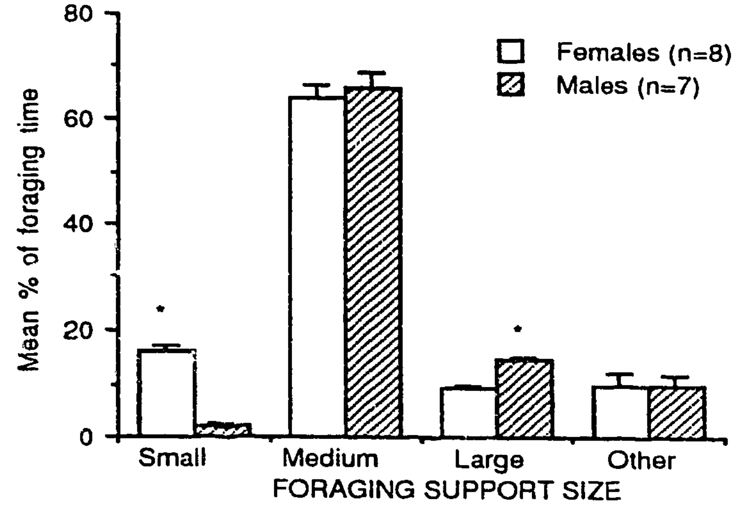

Figure 2.7: Mean percent (and SE) of foraging time spent on diffferent sized foraging supports by males and females. An asterisk above a comparison indicates a level of significance in an ANOVA test of $p < 0.05$.

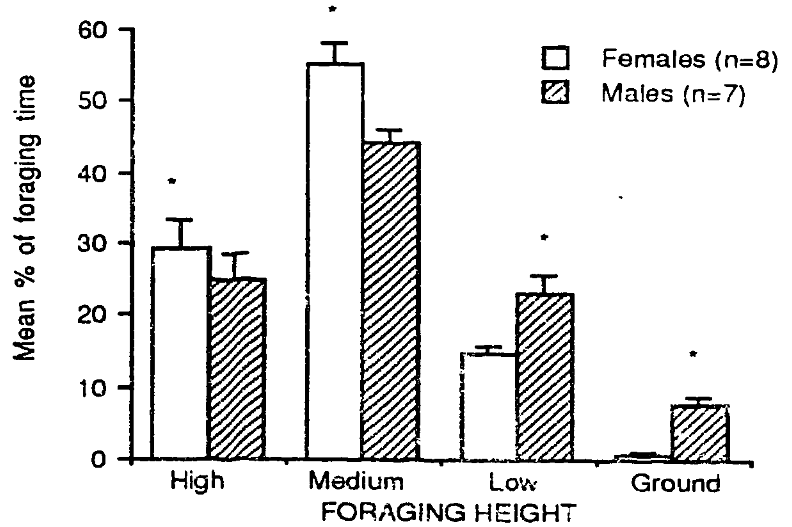

Figure 2.8: Mean percent (and SE) of foraging time spent at different foraging heights by males and females. An asterisk above a comparison indicates a level of significance in an ANOVA test of $p < 0.05$.

Females used more HIGH and MEDIUM supports ($F=7.86$, $p<=0.001$; $F=44.45$, $p<0.001$). The two groups differed in the greater use of HIGH supports by the LV group ($F=80.82$, $p<0.001$), and the greater use of MEDIUM and LOW supports by the CP group ($F=32.73$, $p<0.001$; $F=28.51$, $p<0.001$). In both groups, males spent more time ON THE GROUND during all activities ($F=23.82$, $p<0.001$).

Reproductive condition and time spent foraging:

Two LV group females gave birth in late April and late May respectively. One CP group female gave birth on April 15; her infant was killed on April 17 by a male who had recently risen from beta to alpha position. The three "birth females" spent less time foraging and more time resting than other females. The greatest differences were in the months that they produced and began nursing their infants (Figure 2.9). The LV group females foraged least in the month that their infants were born and in the month following birth. The CP female foraged least in the month that she gave birth. All three females rested more than others in the month that they gave birth and in the following month (Figure 2.10).

Reproductive condition and diet

There were considerable intergroup and seasonal differences in the time that females spent exploiting animal foods, but no consistent differences between birth females and

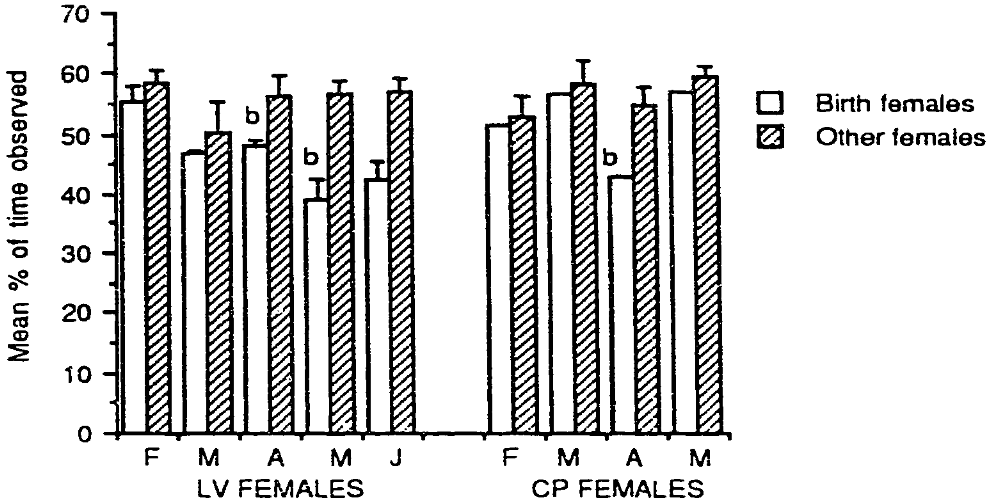

Figure 2.9: Mean percent and (SE) of time spent foraging each month by birth females (LV n=2, CP n=1) and other females (LV n=2, CP n=3). June data incomplete and thus omitted for CP group. "b" indicates months in which a birth occurred.

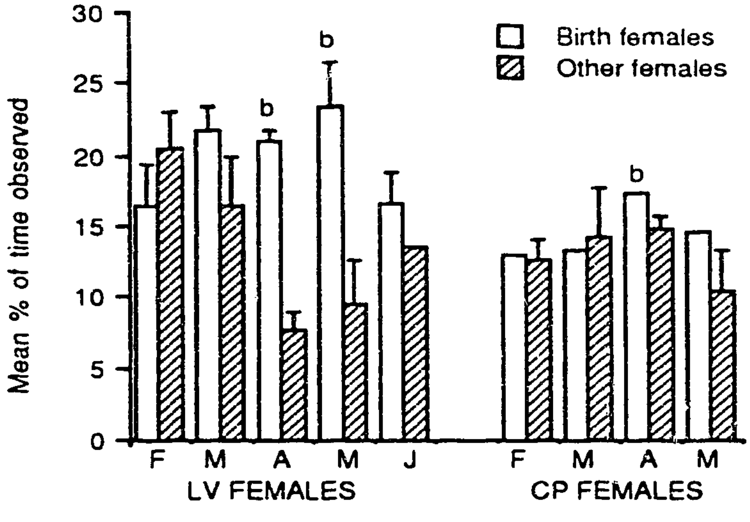

Figure 2.10: Mean percent and (SE) of time spent resting each month by birth females (LV n=2, CP n=1)and other females (LV n=2, CP n=3). "b" indicates birth months.

other females (Figure 2.11). However, birth females invested less time than others in the feeding categories EMBEDDED INVERTEBRATES and PICK AND PROCESS (Figure 2.12). In April and May, the two LV birth females caught more large invertebrates per foraging hour than other females (mean hourly rate for birth females: April 3.24, May 1.68; other females: April 1.68, May 1.09). In June, when most caterpillar feeding occurred, LV birth females spent 55% of their foraging time eating caterpillars, compared with 43% for other females.

Proximity of males and females.

The observed occurrence of proximity between males and females was similar to that predicted by a random distribution (Figure 2.13). Females were found in proximity to each other slightly more often than predicted, while males were found in proximity to each other less often than predicted ($X^2 = 8.69$, df=2, $p < 0.05$).

Agonism during foraging

The proportion of foraging-related agonism occurring between males and females was considerably higher than predicted by a random distribution, while the proportions occurring within each sex class were lower than predicted (X^2 =12.94, df=2, $p < 01$; Figure 2.14). The frequency of foraging-related agonism was higher in the CP group than in the LV group (F=9.44, p=0.011).

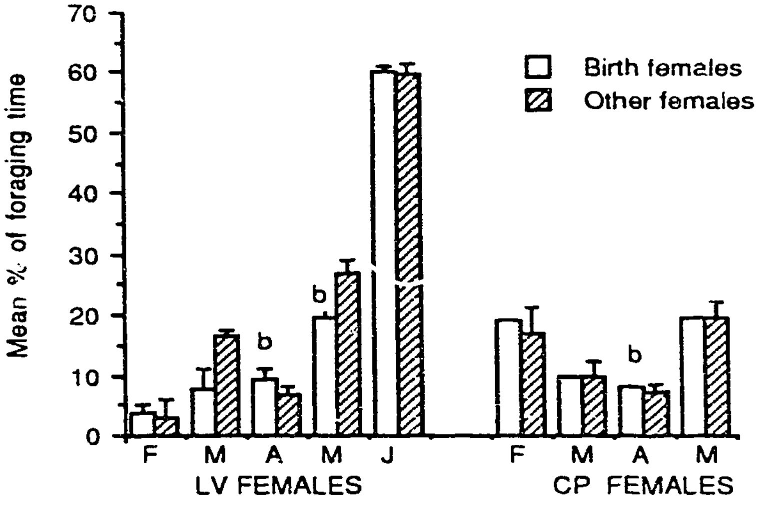

Figure 2.11: Mean percent (and SE) of foraging time spent exploiting animal foods each month by birth females (LV n=2, CP n=1) and other females (LV n=2, CP n=3). "b" indicates months in which births occurred.

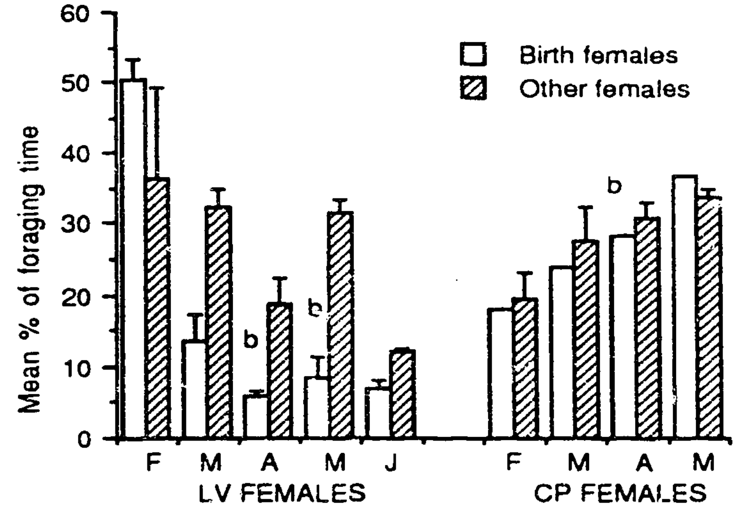

Figure 2.12. Mean percent and (SE) of foraging time exploiting foods requiring processing and embedded invertebrates each month by birth females (LV n=2; CP n=1) and other females (LV n=2; CP n=3). "b" indicates birth months.

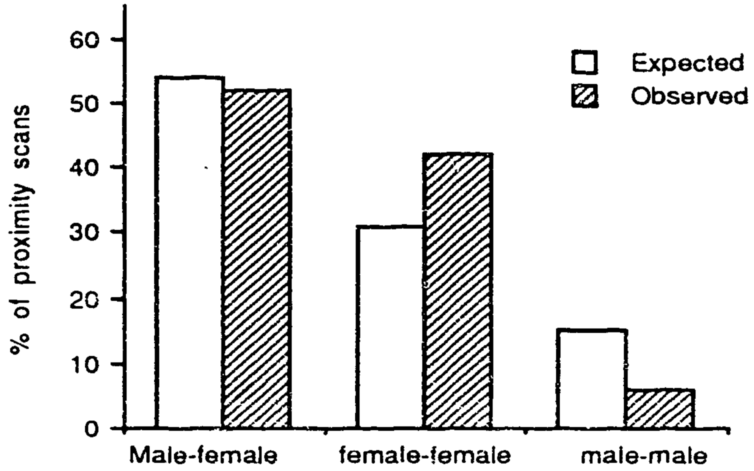

Figure 2.13: Expected and observed distribution of proximity within and between sexes. Expected distribution based on number of male-female, male-male and female-female dyads. n=15 (8 females, 7 males)

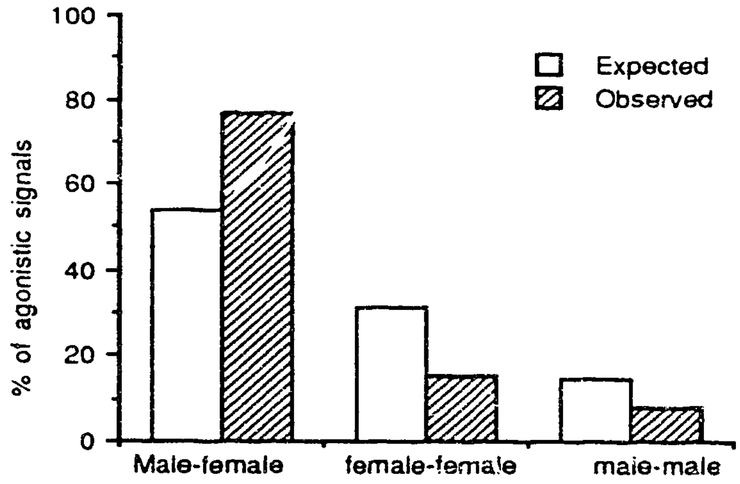

Figure 2.14: Expected and observed distribution of foraging-related agonism within and between sexes. Expected distribution based on number of male-female, male-male, and female-female dyads. n= 15 (8 females, 7 males).

DISCUSSION

Hypothesis I: Sexual Dimorphism

The sexual dimorphism hypothesis is strongly supported by the findings that males made less use than females of small foraging supports, spent more time on or near the ground, and devoted more time to strenuous foraging activities.

The larger size and weight of males apparently restricted their use of slender supports and terminal branches, as has been reported for other sexually dimorphic species (Mendel 1976; Fleagle and Mittermeir 1980; Robinson 1981; Cant 1987; Boinski 1989). The finding that males spent more time than females on or near the ground is consistent with previous reports for this and other capuchin species (Robinson 1981; Fragaszy 1986; de Ruiter 1986; Fedigan in press). Fragaszy (1990) attributed this sex difference in *Cebus olivaceus* to intrinsic psychological factors affecting response to perceived predation risk, rather than differences in foraging return or body size *per se*. Because males are larger, they may be less vulnerable to predators than females, and thus less constrained to avoid areas of high predation risk (Boinski 1989). At Santa Rosa, positions on or near the ground are likely to be those incurring the highest risk of predation. The danger from predators on the ground is attested by Chapman's (1986) account of a boa constrictor preying on a juvenile capuchin. Five felid species are also present in the park, but their impact on the monkeys is unknown. Santa Rosa has three aerial predators conceivably capable of taking small monkeys: the collared forest falcon (*Micrastur semitorquatus*), crested caracara (*Caracara plancus*), and great black hawk (*Buteogallus urubitinga*) (T.Langden, pers. comm.). Raptors may be a threat to monkeys on the ground as well as in higher strata. I twice observed a collared forest falcon on a low branch apparently watching capuchins that were foraging on the ground nearby. Several monkeys gave repeated alarm calls, after which the bird flew away.

The presence of an observer may have initially inhibited some females from foraging on the ground. It is unlikely that this significantly biased the results of the study, as all subjects were fully habituated by the end of the first month's data collection. However, the obvious wariness that several females initially showed in coming down to the ground with an observer present lends support to Fragaszy's conclusion that females perceived the ground as a 'high risk' area.

Physically strenuous foraging behaviours typically occurred when the capuchins attempted to extract prey items lodged beneath bark or in tree crevices. Woody material was usually loosened by repeated biting and pulling before it was torn away and the prey exposed. Leverage was often increased by placing the feet below the target area and using both hands to pull bark from above. The greater body weight and strength of males, in conjunction with robust canines and jaws, clearly increased their efficiency in performing such behaviours.

Contrary to what was predicted under the sexual dimorphism hypothesis, males did not spend more time foraging than females. As in Fragaszy's (1986, 1990) study of *Cebus olivaceus*, males spent less time foraging and more time resting. However, I considered the possibility that the increased energy demands associated with a larger body could be met in some way other than through increased foraging time. For example, males could spend more of their foraging time feeding, they could eat faster, or they could select more high-energy, protein-rich foods.

The males in this study did not spend more of their foraging time feeding than females. I did not obtain sufficient data on the rates at which males and females ate comparable foods for detailed analysis, but observations of feeding bouts on fruits large enough to be individually counted (e.g. *Luehea candida*, *Zuelania guidonia*, *Spondias* and *Anona* sp.) suggested that there were no marked or consistent sex difference in rates of fruit consumption. Males in the CP group devoted less of their foraging time to fruits requiring processing prior to eating (mainly *Slonea terniflora* and *Luehea candida*), and may thus have received a slightly higher foraging return on fruit than females. However, as this was not the case in the LV group, it is unlikely to represent a consistent difference between the sexes.

Several findings indicate that males obtained more animal protein than females. The first is their greater consumption of vertebrate prey, which represent large, concentrated packages of high-quality protein (Fedigan 1990). This is consistent with previous reports for this and other species in which vertebrate predation has been observed (e.g. Fedigan 1990; Harding 1973; Strum 1981; Teleki 1981; Goodall 1986). Second, males obtained more large invertebrates than females. Many of these were orthopterans, cockroaches or cicadas up to eight cm in length, also a rich protein source. For example, the protein content of orthopterans typically ranges between 50% and 75% (Myers 1982). Third, consistent with Fedigan's (1990) findings and those of Fragaszy (1986, 1990) for wedge-capped capuchins, males invested less time than females in exploiting embedded invertebrates. Many of these were small larvae encased in woody material, offering a comparatively low return for foraging time and effort expended.

Caterpillars were a particularly abundant and readily obtainable source of protein in the early wet season; in June, the LV group spent almost half of its recorded foraging time feeding on them. The small amount of caterpillar feeding recorded for the CP group partially reflects a sampling bias, as caterpillars emerged *en masse* during an LV sampling period. However, caterpillars were far more abundant in the LV range, which included at least 10 large *Enterolobium cyclocarpum* trees covered by tiny emergent caterpillars of the family Geometridae, and many of the small *Randia* trees favoured by caterpillars of the family Sphingidae (E.Olson, pers. comm.).

As noted by Fragaszy (1986, 1990) and Fedigan (1990), males tended to exploit more large or exposed prey, while females preferred smaller or embedded items. This may indicate that males are more efficient foragers, as Fragaszy (1986) has suggested for wedge-capped capuchins. An alternate view, suggested by Fedigan (1990), is that females follow the foraging strategy that gives the most reliable return, while males are more opportunistic. This does not imply that females 'work' at foraging and males do not. For example, during the study I frequently saw males expend considerable time and physical effort extracting large arthropods from crevices, or patiently wait to capture prey flushed by army ant raiding parties. However, males may tend to take the foods most readily available in the areas where they forage, while females select the 'safest' foraging targets. Embedded larvae may provide a relatively small protein return for foraging effort expended, but once located, the prey are unlikely to escape. By contrast, large invertebrates and small vertebrates are typically mobile, and may elude capture. The vertebrate prey most commonly obtained by females were bird eggs or nestlings with limited motility.

As Fedigan (1990) has observed, dominance and body size may contribute to sex differences in vertebrate predation. Males are larger than females, and individually dominant over them. Thus, if a female captures a large prey item within sight or hearing of a male, she may risk losing it to him. For example, I saw a CP group male take a lizard from one female, and watched two LV group males chase a young female for almost five minutes before she finally eluded them and was able to eat two nestling birds that she had caught. The greater success of males in capturing larger prey may reflect both their larger size and the greater proportion of time that they spend on or near the ground. Vertebrate prey such as squirrels and lizards tended to be caught on or near the ground. In addition, 65% of all large invertebrates captures were recorded within 5 m of the ground. I was not able to compare the abundance of large invertebrates at different foraging heights in order to determine whether this reflected greater prey availability or enhanced capture success. In either case, to the extent that sex differences in animal foods exploited reflect differences in substrate use, they may be coincidental effects of sexual dimorphism.

Hypothesis II: Pregnancy and Lactation

As predicted under this hypothesis, females spent more of their time foraging than males. The difference was smaller than that reported by Fragaszy (1986) for *Cebus olivaceus*. Fragaszy found that adult females foraged on 70% of scan samples and males on only 44%, compared with mean foraging budgets of 53.1% and 47.5% respectively in this study. The higher proportion of foraging recorded for the *C. olivaceus* females may reflect different sampling regimes, a phylogenetic difference, or dissimilar habitats. The small sex difference in *C. capucinus* foraging time seems insufficient to account for the 25-50% increase in energy demands associated with pregnancy and lactation. It could be argued that the increased metabolic requirements associated with greater male body weight should be taken into account (e.g. see Harrison 1983). Based on mean body weights of 3.3 kg for males and 2.3 kg for females (Glander *et al.* 1991), and Kleiber's (1961) model in which basal metabolic rate varies with the 0.75 power of body weight, females would have approximately 76% the caloric needs of males. Thus the finding that females spent more time foraging than males may be more significant than the small percentage difference suggests.

Contrary to what was predicted under this hypothesis, females did not eat more animal foods than males. As discussed above, females may have obtained less animal protein than males, and gained a lower protein return for foraging time expended. Increased female foraging time can be at least partially explained by their heavier reliance on small, embedded animal protein sources.

The behaviour of the three birth females suggests that increased female foraging was not a response to the increased energy demands of pregnancy and lactation. During pregnancy, a female's energy requirements increase with the growth of the infant she carries. Lactation imposes a heavier energy burden because a mother must feed a larger, growing infant using a system which is less efficient than placental nourishment, and usually carry it as well (Altmann 1980, Jolly 1985; Dunbar and Dunbar 1988). Females would thus be predicted to increase their foraging time with advancing pregnancy and especially during lactation. Yet the females who gave birth during the study did quite the opposite; they spent less time foraging than other females in their groups. The most striking reduction in foraging times occurred during the time of heaviest energy requirements - late pregnancy and subsequent lactation. The association between reduced foraging time and reproductive state is supported by the data for the female PA, whose infant lived only a few days. During April, the month in which she gave birth, PA spent 10% less time foraging than in any other month, and 12% less than the average for other CP group females. In May, when she was no longer pregnant or lactating, PA's foraging returned to its previous level, close to the female average.

It appears that rather than meeting increased energy demands through additional foraging, the pregnant and lactating females in this study opted to conserve energy by increasing the time they spent resting. A similar strategy has been reported for the green monkey, *Cercopithecus sabaeus* (Harrison 1983). Following the birth of their infants, the two LV females received almost constant grooming during group rest periods, and frequently rested or groomed together even when others were foraging. The favouring of social activity over foraging and the general healthy appearance of these females suggested that they were not experiencing severe nutritional stress, implying that they were meeting their nutritional needs despite their reduced foraging time.

The prediction that pregnant and lactating females eat more animal foods is based on the increased protein requirements associated with infant growth (Sadleir 1969; Altmann 1980). Focusing on protein-rich animal foods might also allow energy requirements to be met more quickly. Yet, contrary to this prediction, females who gave birth did not spend more time eating animal foods than other females. There was no observable increase in their exploitation of animal foods in the months approaching and following birth; in May, the two LV birth females actually spent less time exploiting animal foods than other females in the group. However, their greater consumption of large invertebrates and emergent caterpillars may have increased their protein yield per unit foraging time.

In both groups, birth females devoted less time to foods which required extensive handling time. Examples include *Luehea candida* seeds, which the monkeys removed from their woody cases by repeated banging against hard surfaces, large snails, which were banged in a similar manner, and larvae embedded in woody stems, thorns, or seedcases. The difference was small in the CP group, but striking in the LV group, especially in the months surrounding births. This may reflect greater availability of alternative foods in the LV range. Caution is obviously needed in extrapolating from such a small sample of females. However, it seems likely that in this study, pregnant and lactating females saved foraging time and effort by focusing on foods that required little handling time. This 'low effort' strategy, in conjunction with a high protein return from large invertebrates, may have enabled them to meet their nutritional requirements more rapidly, allowing time for increased rest and social activity.

In Harrison's (1983) study of green monkeys, births occurred during the early dry season. Harrison suggested that pregnant and lactating females who minimised foraging during this period (perhaps using fat reserves) were able to compensate by increasing feeding time with the onset of rain, when high-protein foods became abundant. This 'low-cost, low-yield' foraging option was consistent with the overall strategy of his study population, in which time spent feeding increased with increased food availability, and vice versa. White-faced capuchins at Santa Rosa do not exhibit marked birth seasonality, although there is a tendency for births to peak in the early dry season (L.M. Fedigan, pers.comm.). In the year of this study, animal protein - especially in the form of emergent caterpillars - became abundant within a month of the births within the study groups. Seasonality in the availability of easily-obtained animal protein may be an important factor shaping the foraging strategies of reproducing females. Unfortunately, I lacked the necessary data on seasonal food availability and foraging responses to explore this possibility further.

Hypothesis III: Competition avoidance

My study provided little support for this hypothesis. The diets of males and females were similar, and I saw no foods eaten by males that were not also eaten by females. The one sex difference in diet that could be interpreted as a form of competition avoidance was the tendency of females to eat small or embedded invertebrates while males eat larger, mobile animal prey. Females may have responded to males' superior competitive ability in capturing and keeping large prey by specialising in smaller, less 'desirable' animal foods. However, the distribution of most animal foods appeared to be random rather than clumped, and spatial separation between males and females would seem a more predictable outcome of competition for this resource. As discussed earlier, sex differences in the exploitation of animal foods may more readily be explained by the tendency of females to focus on more reliable protein sources, and the greater proportion of time males spent on or near the ground.

There was some indication of niche separation through vertical stratification, with males tending to forage in the lower strata and females tending to forage in the higher strata. O'Brien (1991) noted that similar partitioning of vertical foraging space may have reduced feeding competition between the sexes in *C. olivaceus.* However, sex differences in *C. capucinus* foraging height may have been a consequence of sex differences in body weight and response to predation risk. The proximity data did not suggest a pattern of sexual segregation during foraging. Even when most group members were eating the same foods - a fairly common situation due to the prominence of seasonal fruits in the capuchin diet - most females did not appear to avoid being in proximity to males, or vice versa.

The finding that more foraging-related agonism occurred between sexes than within sexes suggests that males and females have not successfully diverged in their diet or foraging behaviour. Almost 80% of the agonism between males and females occurred in a foraging context, suggesting that there was considerable feeding competition between the sexes (see Chapter Three). The higher frequency of foraging-related agonism in the CP group was consistent with increased competition in response to reduced food abundance. The lesser food abundance in the CP range was reflected in the monkeys' physical condition: individuals were thinner than those in the LV group (based on less rounded stomachs and more prominent bony angles), with thinner, duller coats. The CP group spent slightly more time travelling and foraging than the LV group, and significantly less time engaged in social behaviour, suggesting a greater preoccupation with obtaining food.

Conclusion

Of the three hypotheses considered, sexual dimorphism proved to be the best predictor of sex differences in foraging behaviour. This hypothesis accurately predicted that males made less use of small foraging supports, spent more time foraging on or near the ground, did more strenuous foraging, and obtained more animal protein. Increased time spent on or near the ground may reflect sex differences in vulnerability to predation as well as in body weight *per se*. Differential substrate use may in turn promote sex differences in foraging yields for animal protein.

Males and females differed in the types of animal protein they exploited; males ate more large or mobile prey, and females exploited more small or embedded invertebrates. This finding may reflect both differential substrate use and a sex difference in foraging strategy: females opt for the most reliable return and males are more opportunistic. Males may obtain a higher protein yield per unit foraging time, meeting their energy requirements more quickly than females and allowing them more time for rest and vigilance behaviours.

Based on the small sample of females available, the energy costs of pregnancy and lactation do affect female foraging behaviour. However, the pregnant and lactating females in this study did not respond to increasing energy demands by increasing their foraging time; they conserved energy by resting and increased their foraging return by focusing on larger protein packages and foods requiring little handling time. Rather than promoting sex differences in foraging, pregnancy and lactation seemed to result in females following a 'low effort' strategy similar to that of males. As in *Cercopithecus sabaeus*, the foraging strategies of *Cebus capucinus* females may be shaped by the seasonal availability of easily obtained animal protein. This suggestion might be tested using a larger sample of females in different reproductive states over several seasons.

The competition avoidance hypothesis showed little predictive power in this study. Competition between the sexes was evident in both study groups. Niche separation through vertical stratification may serve to reduce competition, but also can be explained by sexual dimorphism in body size. Sex differences in diet may reflect different strategies for obtaining animal protein, greater male foraging efficiency, and differential substrate use due to sexual dimorphism.

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CHAPTER 3

BENEFITS AND COSTS OF RESIDENT MALES TO FEMALES IN WHITE-FACED CAPUCHINS (*CEBUS CAPUCINUS*) AT SANTA ROSA NATIONAL PARK, COSTA RICA.

INTRODUCTION

Males and females attempt to maximise their inclusive fitness through different primary reproductive strategies. Females maximise food acquisition, while males maximise mate acquisition (Trivers 1972; Wrangham 1980, 1983; O'Brien 1991). Female strategies are considered to be the predominant factor shaping primate social systems, as male strategies depend largely on the distribution and behaviour of females (Emlen and Oring 1977; van Schaik 1989; Mitchell *et al.* 1991). However, social organisations result from the interaction of male and female strategies (Wrangham 1980). For females, the presence of males within a social group will have both benefits and costs. Benefits that males might afford females include group defence, infant care, and reproductive stability; costs include interference with food acquisition and aggression directed toward females or their offspring.

Male participation in group defence against predators decreases the probability of mortality for females and infants. Excluding non-group conspecifics also contributes indirectly to female reproductive success by maintaining or increasing the group's access to resources (Wrangham 1980; van Schaik 1983; 1989; Robinson 1988; O'Brien 1991). Male vigilance may provide protection for females and their infants, allowing them more time for foraging activity. Males may contribute to infant care by carrying, grooming, or 'babysitting' infants, or providing protection from conspecifics (Izawa 1980; Altmann 1980). Resident males may reduce immigration and breeding takeover by unfamiliar males, contributing to social stability and reducing the likelihood of infanticide (Robinson 1988).

The addition of males to a group imposes a cost on females by increasing feeding competition. Individual success in contest competition is strongly influenced by social factors, especially dominance rank and aggressive behaviour (Janson 1985; van Schaik 1989). In many primate species, males are dominant over females, and may obtain a disproportionate share of food resources through their greater success in contest competition. Male harassment may reduce the time available to females for rest, infant care, or social activity. Infanticide, which has been suggested to be a male 'reproductive str[illegible] (Hrdy 1977), can drastically reduce a female's reproductive success.

The benefits and costs associated with resident males may not be shared equally among females; some females may monopolise the benefits, while others bear most of the costs (O'Brien 1991). Females may attempt to alter the balance of benefits and costs or to increase their success in female-female competition through male-directed behaviours.

If females could exclude males, but tolerate them within a social group, then the benefits that these males provide would be expected to equal or exceed the costs that they impose. However, if females are unable to effectively exclude males, then males may impose a net cost on females, and females would be predicted to follow behavioural strategies which minimise these costs (O'Brien 1991).

In this study I examine the benefits and costs of resident males to females in the white-faced capuchin (*Cebus capucinus*); an arboreal, neotropical primate. White-faced capuchins live in multi-male, multi-female groups of 6 to about 30 individuals, with an average group size of 15 (Oppenheimer 1968; Buckley 1983; Fedigan *et al.* 1985; Massey 1987). Most groups have well-defined home ranges, and while overlaps do occur, at least some boundaries are defended (Oppenheimer 1968; Buckley 1983). Females generally remain and breed in their natal groups, whereas most males migrate to other groups prior to maturity (Robinson and Janson 1987). Males are 25-35% larger than females, and are typically dominant over them (Oppenheimer 1968; Buckley 1983; Fedigan 1990). Most researchers identified an unambiguous alpha male (cf. Buckley 1983) but could not readily distinguish linear dominance hierarchies (e.g. Freese 1978). However, both male and female dominance hierarchies have been determined in several groups, with the alpha female ranking immediately below the alpha male (Fedigan in press).

Previous studies found that males of all four capuchin species spent more time than females in vigilance behaviours, were more frequently involved and more aggressive in intergroup encounters, and were more active in detecting and confronting predators (Oppenheimer 1968, 1982; Defler 1979, 1982; de Ruiter 1986; Fragaszy 1986; 1990; Janson 1986a, 1986b; Robinson 1988; Escobar-Paramo 1989; van Schaik and van Noordwijk 1989). Little information is available regarding male care of infants in capuchins, but Escobar-Paramo (1989) emphasised the affiliative relationship between infants and the alpha male in *Cebus apella*, and Izawa (1980) reported that the *C. apella* alpha male groomed, carried, and 'babysat' infants. Several cases of infanticide by wedge-capped capuchin males have been reported (Valderrama *et al.* 1990), and one case was observed in this study. Male interference with female food acquisition has yet to be directly addressed through field study. However, an individual's position within the group has been shown to affect foraging success (Robinson 1981; Janson 1990a). Robinson found that in *C. olivaceus,* the dominant male and female occupied the most advantageous foraging position at the centre of the group. Janson suggested that *C. apella* females avoid the centre of the group to reduce interference from males while forgaging for insects.

Hypotheses and Predictions

Because the benefits and costs of males to females are not directly comparable, making it difficult to determine whether benefits exceed costs, I have devised several hypotheses of the form "how do the benefits/costs of males to females compare with those of other females within the same social group?". Predictions are made on the basis of each hypothesis.

Hypothesis I:

The benefits that resident males provide for females exceed the benefits provided by other females.

Predictions:

1. males exhibit more vigilance behaviour than females.
2. males are more active than females in detecting and confronting actual or potential predators.
3. males are more active and aggressive than females in intergroup encounters.

Hypothesis II:

The costs that resident males impose on females exceed the costs imposed by other females:

Predictions:

1. More agonism occurs between males and females than among females, especially in a foraging context.
2. Males tend to direct aggression toward females, while females direct submissive signals toward males.
3. Female foraging is more often interrupted by males than by females.
4. Female foraging success decreases with increased time

spent in proximity to males.

5. Female foraging success decreases with increased agonism involving males.

Hypothesis III:

Some females receive greater benefits and/or bear fewer costs from male presence than others:

<u>Predictions</u>:

1. Some females show strong patterns of association with males, while others do not.
2. Females with strong male associations solicit male support in agonistic encounters with other females, or engage in other male-directed behaviours which may increase their success in female-female competition.
3. Females with strong patterns of male association and support have greater foraging success than other females.
4. Male aggression is unevenly distributed among females.

The three hypotheses are not mutually exclusive, and may be independently accepted or rejected. Hypotheses I and II generate four possible outcomes: i) males provide greater benefits and impose lower costs than females, ii) males provide greater benefits but impose higher costs, iii) males provide lower benefits but impose lower costs, or iv) males provide lower benefits and impose higher costs.

METHODS

Study Site and Groups

Santa Rosa National Park is situated near the Pacific coast of Costa Rica, adjacent to the Pan American Highway and about 35 km northwest of Liberia, Guanacaste. Santa Rosa covers approximately 10 800 ha of dry tropical forest, semi-evergreen forest, and reclaimed pasture in varying stages of secondary succession. The park is home to three non-human primate species: the mantled howler monkey (*Aloutta palliata*), the red spider monkey (*Ateles geoffroyi*), and the white-faced capuchin (*Cebus capucinus*). Capuchin home ranges often overlap with those of spider and howler monkeys. Potential predators on capuchins at Santa Rosa include large snakes, felids, and probably large raptors (Freese 1983, Chapman 1986). The harpy eagle (*Harpia harpyja*), a major predator on small monkeys in other areas, is not present. Tayras (*Eira barbara*) may pose a minor threat to young capuchins (Defler 1980; de Ruiter 1986).

The two study groups were the Los Valles (LV) group and the Cerco de Piedra (CP) group (Appendix A). The LV group consisted of 14-19 individuals (4-5 adult females, 2 adult males, 2 subadult males, 2-4 juveniles, and 4-6 infants); the CP group consisted of 12-14 individuals (4 adult females, 1-2 adult males, 0-1 subadult male, 4 juveniles, and 3-4 infants). Individuals could be recognised by facial characteristics and, for most adult males, scars. Dominance hierarchies were constructed for both sexes from the direction of aggressive and submissive signals. A change in the CP male hierarchy occurred after a fight (inferred from wounds to both males) between the alpha and beta male. During the study period, two CP group males left their group (one, the displaced alpha male, returned within two months), an LV male transferred to a neighbouring group, and three females gave birth. The CP group has been the subject of previous studies (Fedigan 1990; Chapman and Fedigan 1990; Fedigan in press), and both groups were habituated to human observers. Visibility varied throughout the two ranges but was excellent in many areas. Observation distances of five to ten metres were common, especially in the late dry season.

Data Collection

Preliminary observations for this study were made in May-July 1990 and January 1991. Extensive behavioural sampling of adults was conducted between 1 February and 20 June 1991. I collected 380 hours of focal data in the form of ten-minute continuous-time sessions (Altmann 1974), and additional *ad lib* data on comparatively rare events such as predator mobbing and intergroup encounters. Data were collected in alternating ten-day blocks for each group. I obtained 1063 focal sessions for LV group adults (4 females and 4 males) and 1210 for CP adults (4 females, 3 males). Given the dispersed nature of the groups and the difficulty in locating particular individuals, it was not practical to follow a rigid sampling regime. I attempted to sample each focal subject within a group before beginning a new round of observations, and in the LV group, to alternate males and females as focal subjects. I kept a continuous record of the number of samples obtained for each individual to ensure that sampling was evenly distributed. If a focal subject was lost from view for more than 90 seconds, the session was ended and the data discarded. The nearest three neighbours within ten metres of the focal animal were noted immediately before and after each session. The time that each individual spent foraging and feeding was recorded (see Chapter Two). Agonistic behaviours were scored as 'directed' or 'received', and other participants noted. Behaviours discussed in this chapter are defined in Table 1; a complete ethogram of recorded behaviours is supplied in Appendix C.

Data Analysis

The study yielded a mixture of quantitative data suitable for statistical analyses and qualitative data based on small behavioural samples or *ad lib.* observations. Data were coded and entered onto the computer using PRIMA 1.1 (Primatologist Information Management and Analysis, Copyright 1991 Marc Koehn), a programme specifically designed for this project by Frameworks Management Corp., Victoria, British Columbia. Statistical analyses were carried out using the SPSS and SPSS-PC computer packages. Vigilance behaviour (SCAN) was

Table 3.1: Definitions of behavioural categories.

SCAN: gaze beyond vegetation in immediate vicinity, usually moving eyes and/or head slowly from side to side, and monitor surroundings.

ALARM: an individual gives an alarm vocalisation in response to a potential predator. Scored only if i) a potential predator was seen by the observer or ii) the alarm elicited a response (e.g. scanning and further alarm calls, mobbing) from at least three other group members.

MOB: all or most group members gather near and threaten a potential predator. Includes barking, open-mouthed threats, branch breaking or bouncing, and throwing objects at the predator.

FORAGE: all behaviours concerned with food, including FEED, and manually or visually searching substrates.

FEED: ingest plant or animal food. Includes picking fruit or seeds, capturing and eating prey, and extracting, chewing or licking out embedded invertebrates.

<u>Agonistic Behaviours</u>

AVOID: move away from an approaching individual

BITE OR HIT: Bite or hit another individual.

BRANCH SHAKE OR BOUNCE: Pull rapidly and repeatedly on large branch or small tree trunk. Branch may be broken off and dropped or thrown toward another animal.

CHASE: Chase another individual (excluding play).

COALITION: Two or more individuals join in an agonistic interaction against one or more others (excluding DOUBLE THREAT).

DOUBLE THREAT: Two individuals in bodily contact simultaneously direct OPEN-MOUTHED THREAT to another.

FEAR FACE: Mouth slightly open and lips stretched back, head and/or eyes lowered. Often accompanied by quiet chattering vocalisation and lowered body posture.

OPEN-MOUTHED THREAT: Lips pulled back and canines exposed.

..... **Definitions of behavioural categories** (cont'd).

PUSH AWAY: Push another individual away (excluding play). Includes rejecting an infant attempting to nurse.

SCREAM: Scream at another individual.

SOLICIT AID: During an agonistic encounter, one individual repeatedly glances toward, and may approach or circle, another not directly involved in the agonistic encounter.

STARE: Stare intently at target, eyebrows slightly raised.

SUPPLANT: Approach an individual (usually directing stare or threatface toward it) who responds by leaving, and immediately occupy the space it has vacated.

THREATFACE: Stare with eyebrows raised, mouth slightly opened, lips stretched back as in OPEN-MOUTHED THREAT but canines not fully exposed.

expressed as a percentage of observation time for each focal subject, I used a two-way analysis of variance to test for sex and group differences, with $p < 0.05$ as the criterion for significance. Hourly rates of agonistic behaviours involving males and females respectively were calculated for each individual and divided by the number of potential partners available. Since some males were not present for the entire study period, the number of potential partners in male-female and male-male interactions reflected the percentage of focal samples for which each male was present in the group. The adjusted agonism rates for male and female antagonists respectively were treated as repeated measures in a two-way analysis of variance test for sex and group differences, using $p < 0.05$ as the criterion for significance. Mean hourly rates of female foraging interruptions were calculated for two types of interactions: i) a foraging female is supplanted by or avoids another female, and ii) she is supplanted by or avoids a male. Female foraging success was expressed as the percentage of foraging time spent feeding (Janson 1990b). Rates of proximity were calculated from the proximity scans made at the start and end of each session. Rates of proximity to females were calculated as the total number of females observed within ten metres of the focal animal, divided by the number of samples obtained for the focal animal and by the number of possible female interactants. Proximity to males was calculated similarly, except that male rather than female availability was incorporated in the calculation. To elucidate patterns of association, I calculated the degree of proximity (percentage representation of each partner in the other's proximity scans) within each male-female, female-female, and male-male dyad.

RESULTS

Hypothesis I: Male Benefits to Females

1. <u>Vigilance behaviour</u>

As predicted, males were more vigilant than females. On average, males devoted 8.0% (SE 0.80) of their time to vigilance behaviour [SCAN], significantly more than the 3.2% (SE 0.17) spent by females ($F=41.$[illegible], $p<0.001$). The alpha male was the most vigilant individual in each group.

2. <u>Predator detection and encounters</u>

On a *per capita* basis, males gave more confirmed predator alarms than females (Table 3.2). The focal data yielded too few predator alarms to permit statistical analysis. I made *ad lib.* observations of six snake mobbings (three involving boa constrictors) and several suspected snake mobbings in which I was unable to confirm the target's identity. Typically the entire group participated, with males and females appearing equally active. I was able to discern the initial caller in only two mobbing situations; in both cases, the CP alpha male gave the initial alarm.

Table 3.2. Predator alarms by males and females in each group, including focal and *ad lib.* observations.

	SNAKE	RAPTOR	COYOTE	UNKNOWN	TOTAL	[1] PER CAPITA
LV males (n=4)	2	1	-	1	4	1.14
LV females (n=4)	1	2	-	-	3	0.75
CP males (n=3)	4	2	-	1	7	4.22
CP females (n=4)	1	1	3	2	7	1.75
MALES (n = 7)	6	3	0	2	11	2.15
FEMALES (n = 8)	2	3	3	3	10	1.25

[1] Total alarms by each sex divided by number of individuals of that sex. For males, the index reflects percentage of total observation time that each male was present in group.

3. <u>Intergroup encounters</u>

As predicted, males were involved in slightly more agonistic intergroup encounters than females. However, I observed only six cases, all involving the LV group and a small neighbouring group (group S) in areas of range overlap. Three episodes involved only males, one primarily females, and two included both sexes. Contrary to what was predicted, females involved in intergroup encounters tended to be more aggressive than males. I observed several females fighting, whereas male encounters mainly consisted of prolonged threats and chases. Aggression during intergroup encounters occurred almost exclusively within sex classes.

Hypothesis II: Male costs to females

1. <u>Agonism between and within sexes</u>

As predicted, more agonism occurred between males and females than between females in each group, both in total and during foraging (Figure 3.1; Figure 3.2). There was more agonism and foraging-related agonism in the CP group than in the LV group (F=16.73, p=0.002; F=9.44, p=0.011), and more agonism between CP group females than between LV group females. There was no significant difference in the rate at which males and females participated in agonistic interactions in total or during foraging (F=4.74, p=0.052; F=0.19, p=0.773). The antagonist's sex and the combined effects of the focal animal's sex and its antagonist's sex contributed

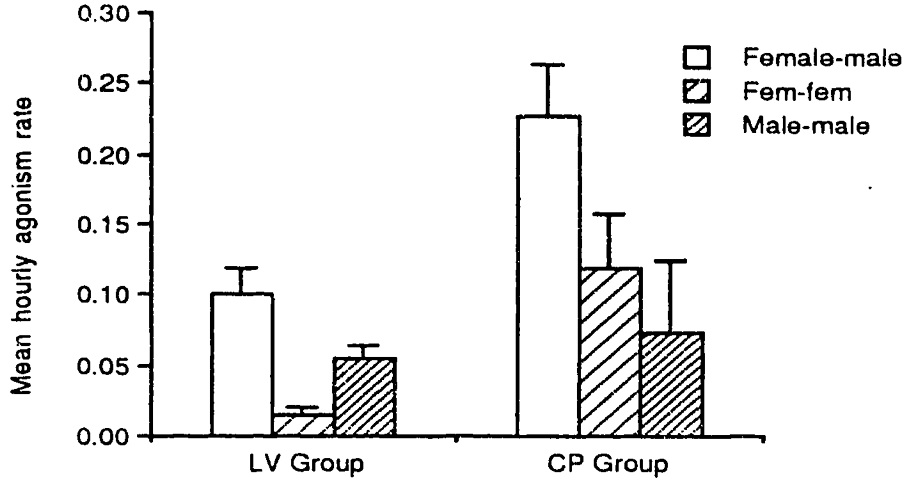


Figure 3.1: Distribution of agonism between and within sex classes expressed as mean hourly rate (and SE) per dyad. Rates adjusted to reflect number of available partners. LV n=4 females, 4 males; CP n=4 females, 3 males.

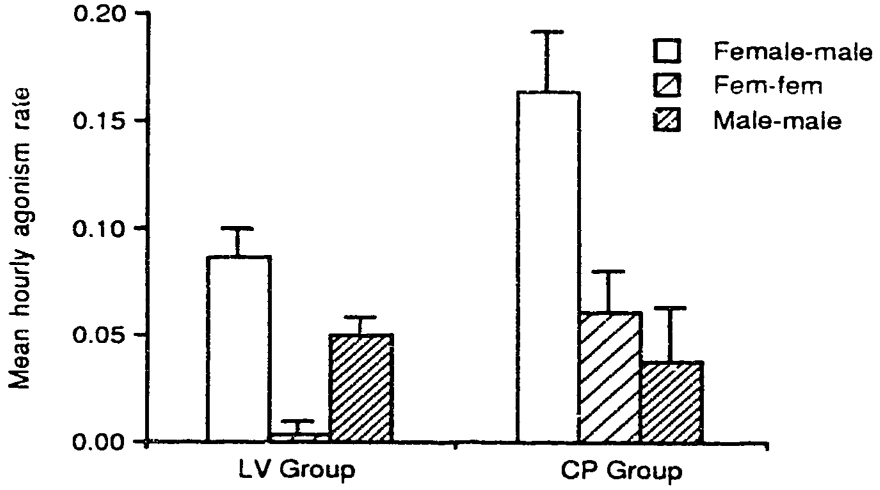


Figure 3.2: Distribution of foraging-related agonism between and within sex classes expressed as mean hourly rate (and SE) per dyad. Rates adjusted to reflect number of available partners. LV n=4 females, 4 males; CP n=4 females, 3 males.

significantly to the variance in total agonism rates (F=9.48, p=0.010; F=8.90, p=0.012). Males and females were equally likely to be antagonists in agonistic foraging interactions (F=2.19, p=0.167), but there was a significant interaction effect between the sex of the focal animal and the sex of its antagonist (F=14.79, p=0.003). The higher rate of agonism between males and females was not a result of increased proximity between the sexes. In both groups, females were in proximity to other females more often than they were in proximity to males (Figure 3.3).

2. Direction of aggressive and submissive signals

Contrary to what was predicted, males and females were equally likely to direct aggressive signals toward each other (Figure 3.4a). However, as predicted, females directed considerably more submissive signals toward males than males directed toward females (Figure 3.4b). Males were not observed to physically attack females, but one male killed a two-day-old CP group infant. Females occasionally formed aggressive coalitions against a male, and two females co-operatively attacked the infanticidal male.

3. Interruptions of female foraging

As predicted, males interrupted female foraging bouts more often than females. Female foraging was 7.5 times more likely to be interrupted by a male than by a female in the LV

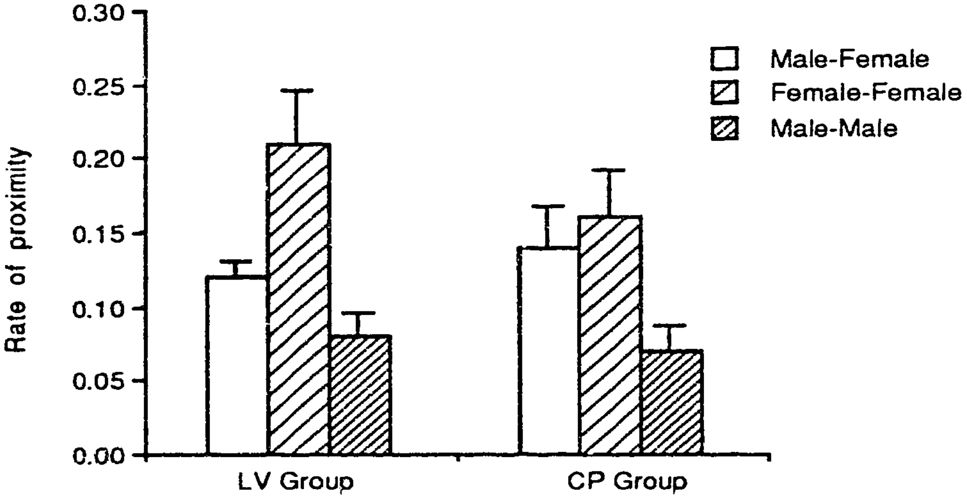


Figure 3.3: Proximity between and within sex classes, expressed as mean rate (and SE) per sample per dyad. n LV = 4 females, 4 males, CP = 4 females, 3 males

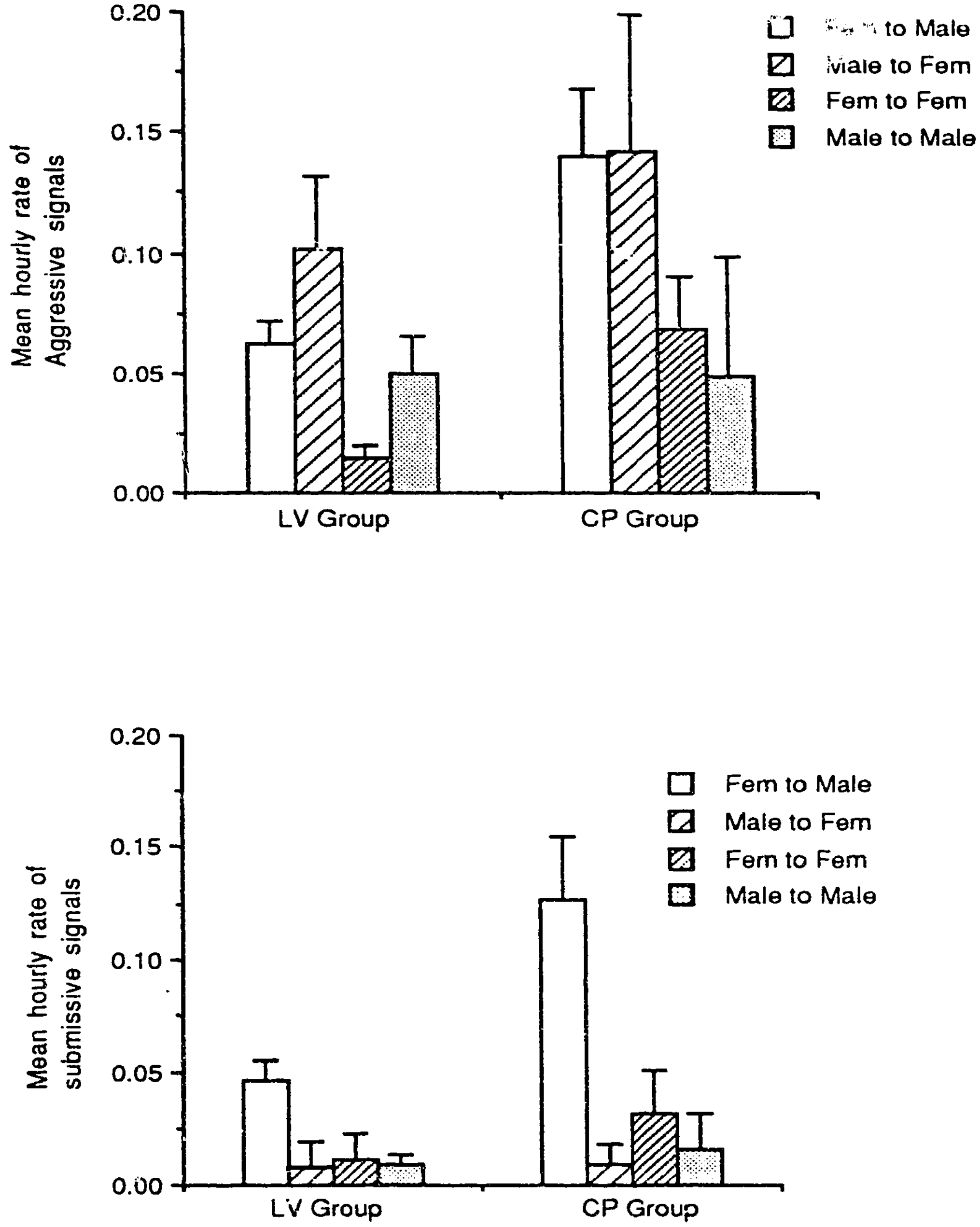


Figure 3.4: Distribution of a) aggressive and b) submissive signals between and within sex classes, expressed as hourly rate per dyad. Rates adjusted to reflect number of available partners. LV n=4 females, 4 males; CP n=4 females, 3 males.

group, and 4.2 times more likely to be interrupted by a male than by a female in the CP group (Figure 3.5).

4. Proximity to others and female foraging success

Contrary to what was predicted, there was no apparent relationship between female foraging success and rate of proximity to males (Figure 3.6).

5. Agonism involving males and female foraging success

As predicted, female foraging success decreased with increased foraging-related agonism involving males (Figure 3.7). There was a weaker negative association between female foraging success and aggression received from males (Figure 3.8).

Hypothesis III: Distribution of male benefits and costs.

1. Patterns of association between females and males

As predicted, some females had strong associations with males, while others did not (Figure 3.9a, 3.9b). There was a marked association between the alpha female and the alpha male in both groups, and between the beta female and the alpha male in the CP group. There was also a moderate association between the lowest ranking LV group male and female. In both groups, the alpha male and female tended to forage together, usually at the centre or leading edge of the group. The patterns of

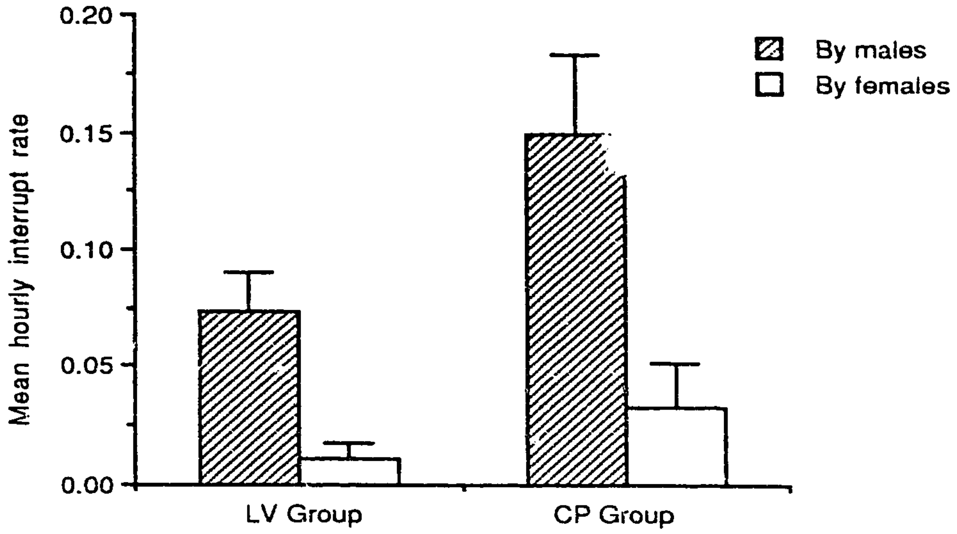


Figure 3.5: Mean hourly rate (and SE) of female foraging interruptions by males and females. Rates adjusted to reflect available interactants of each sex. LV n=4 females, 4 males; CP n=4 females, 3 males. n = 76 foraging interrupts.

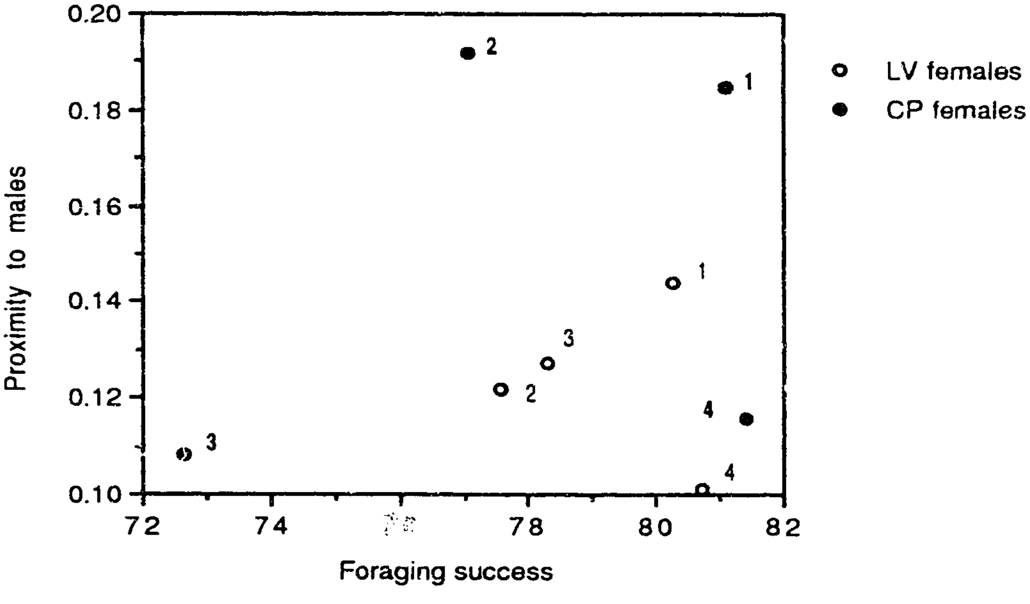


Figure 3.6: Proximity to males (rate per available male per session) and foraging success for females. Numbers indicate female dominance rank

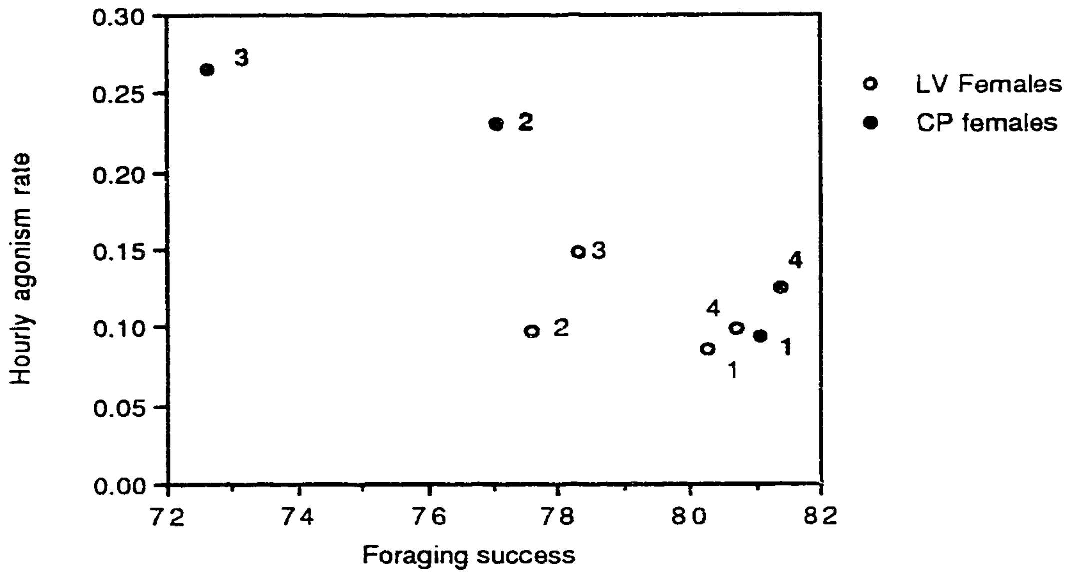


Figure 3.7: Foraging-related agonism involving males (hourly rate per available male) and female foraging success. Numbers indicate female rank.

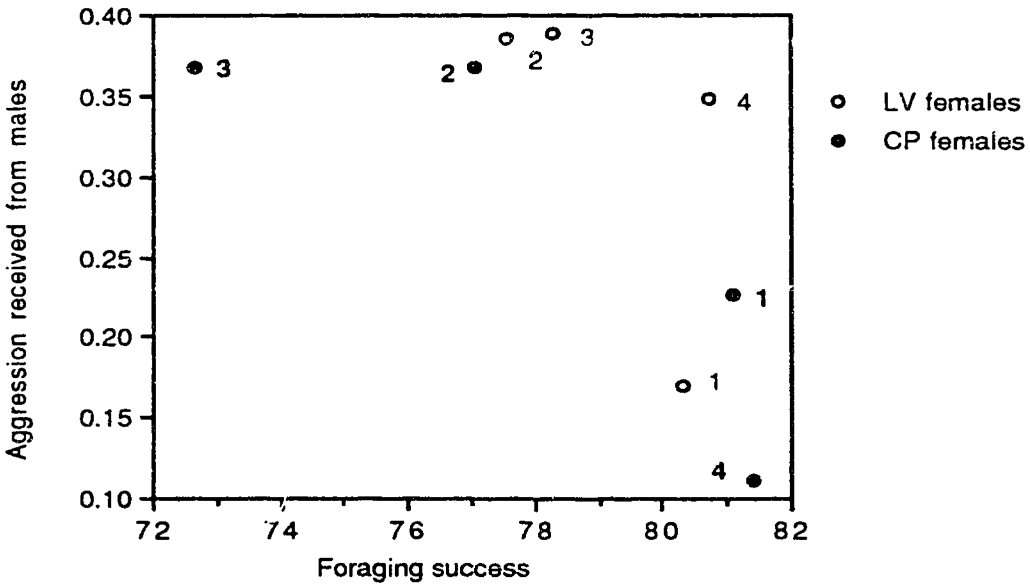
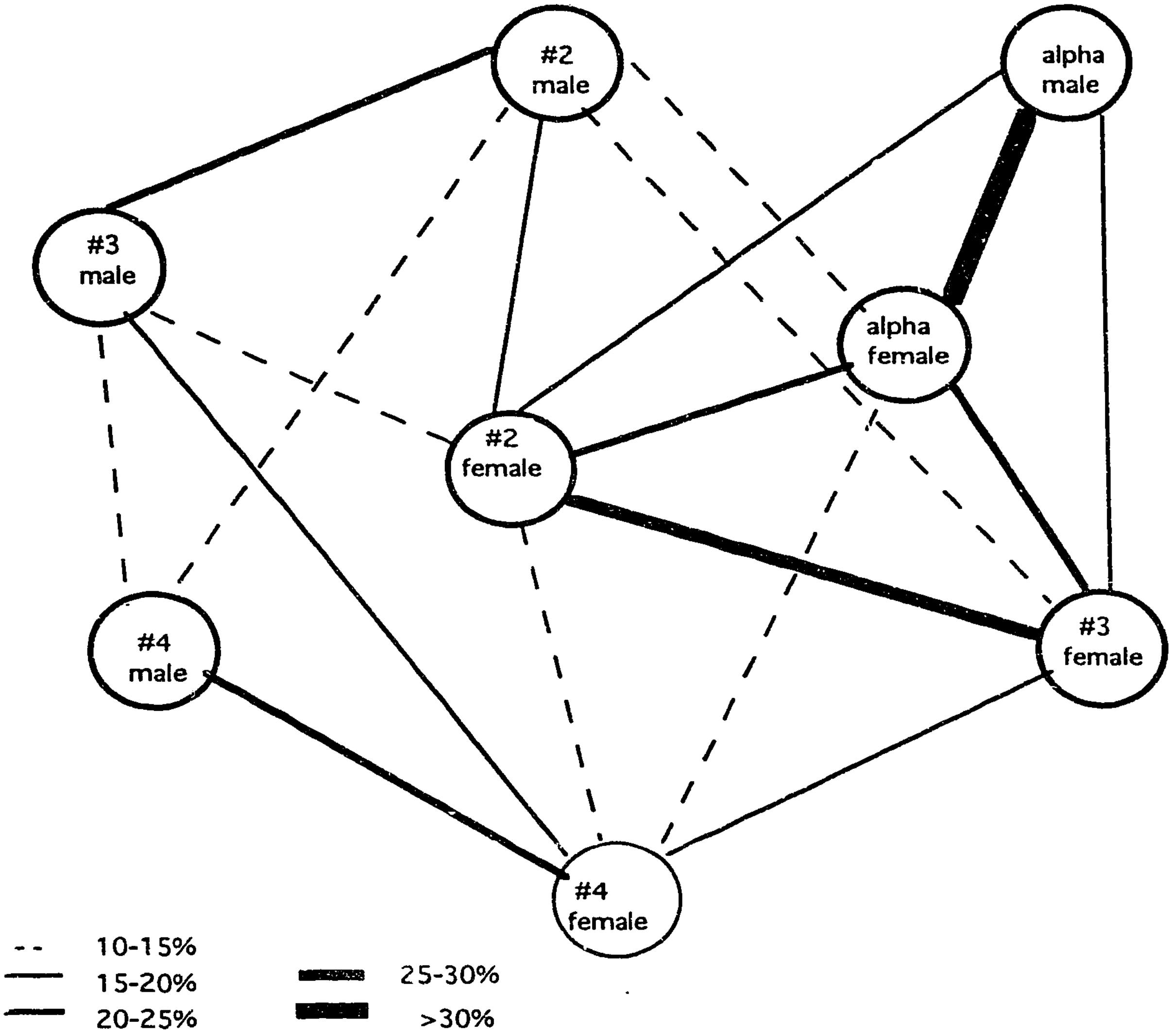


Figure 3.8: Hourly rate of aggression received frcm all males and foraging success for females. Numbers indicate female rank.



ure 3.9a: Patterns of association among LV group adults. Thickness of lines licates percentage representation of each partner in the other's proximity ans, averaged within each dyad, adjusted to reflect the percentage of time that ch male was present in the group. Results exceeding 10% only are included.

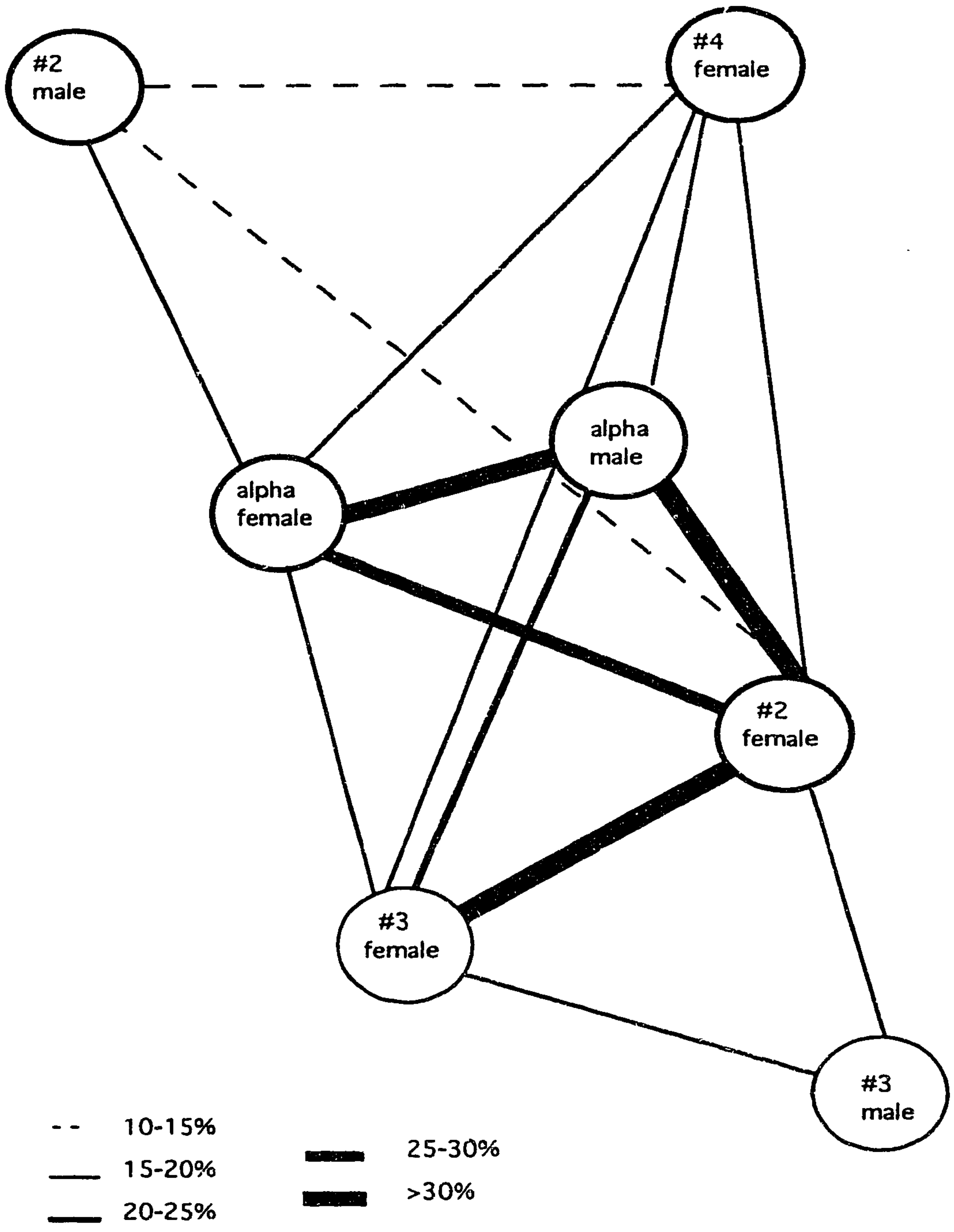


Figure 3.9b: Patterns of association among CP group adults. Lines indicate percentage representation of each partner in the other's proximity scans, averaged within each dyad, adjusted to reflect the percent of time that each male was present in the group. Results exceeding 10% only are included.

proximity in each group suggest a core consisting of the alpha male, alpha female, and mid-ranked females.

2. Male-directed behaviours

The CP group alpha male was the only observed recipient of aid-soliciting behaviour from females. As predicted, the females most often found in proximity to the alpha male were those who solicited his support. The two highest-ranked CP group females independently solicited the alpha male's support during at least five agonistic interactions (primarily against each other). These females also solicited his support in initiating group movement. Females typically initiate group movement by moving in the direction of travel and directing 'twitter' vocalisations toward the group (described as 'bleats' by Boinski, submitted). On several occasions the two highest-ranked CP females simultaneously attempted to initiate movement in different directions. Each female directed increasingly loud twitters toward the alpha male, approached and stared at him, and in one case repeatedly circled him. Eventually the alpha male moved in the direction chosen by one of the females and the group followed.

3. Relationships with males and foraging success

In each group, the females with the greatest foraging success were the alpha female, who had a high rate of proximity to males and a strong association with the alpha male, and the lowest ranked female, who had the lowest rate of proximity to males and the weakest association with the alpha male (Figure 3.6; Figure 3.9). These females shared low rates of foraging-related agonism involving males (Figure 3.7)

4. Distribution of male aggression.

As predicted, male aggression was unequally distributed among females (Figure 3.8). In both groups, most aggression was directed toward mid-ranking females. The alpha female received the least aggression from males in the LV group; the lowest-ranked female received the least aggression in the CP group. Some males directed more aggression toward females than others (Figure 3.10). In the LV group, the beta male (who transferred to a neighbouring group midway through the study) had the highest rate of female-directed aggression. In the CP group, the male who moved from alpha to beta status had the highest rate of female-directed aggression.

DISCUSSION

Male benefits to females

The results of this study support the hypothesis that males offer females a greater benefit than do other females in the form of vigilance behaviour. The finding that males were more vigilant than females is consistent with previous reports for this and other capuchin species (e.g. Fragaszy 1986, 1990; de Ruiter 1986; Robinson 1988; van Schaik and van Noordwijk

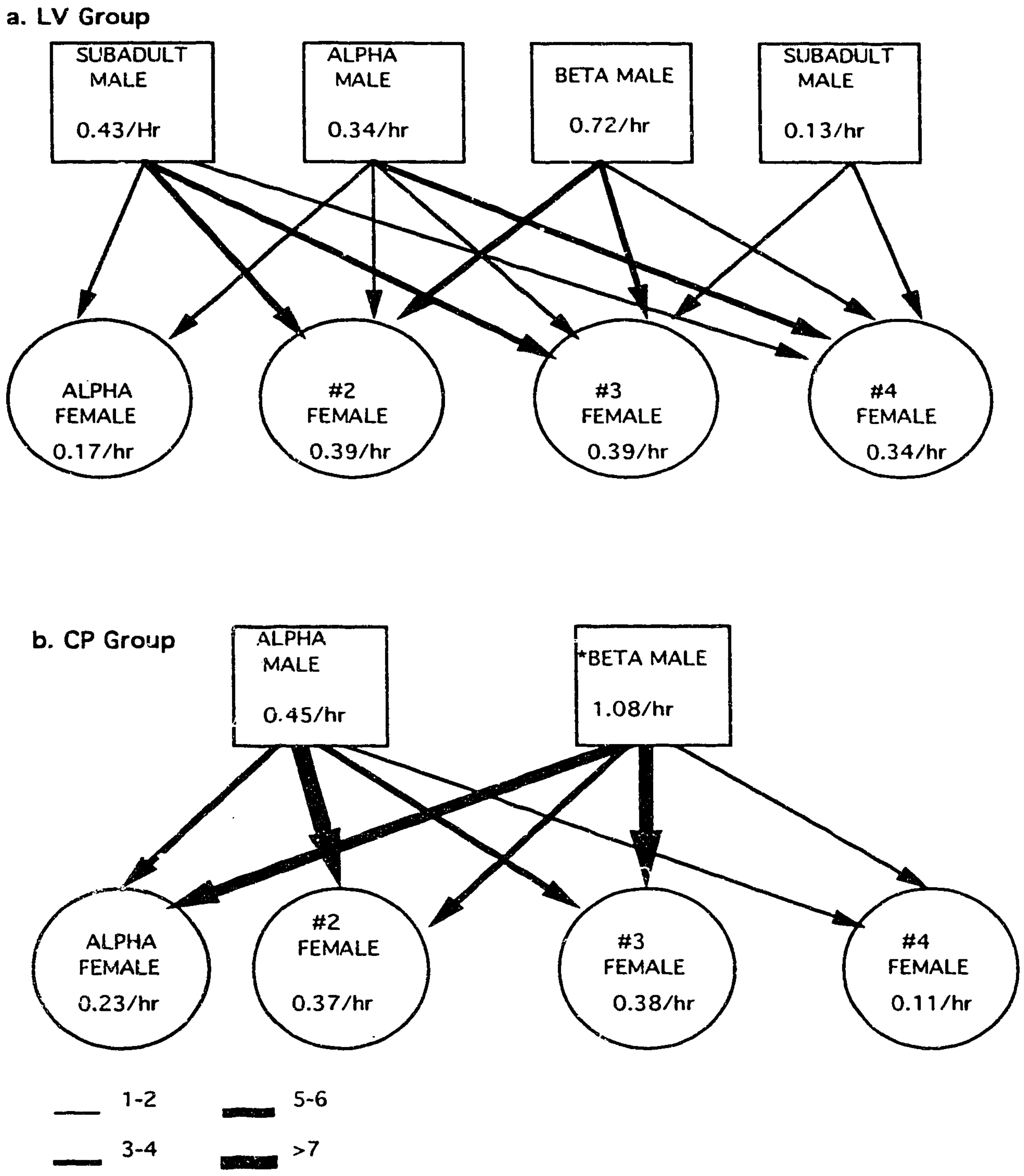


Figure 3.10: Distribution of male aggression among females in a) LV group and b) CP group. Thickness of arrows indicates total number of signals within each dyad. *CP beta male was alpha male at start of study.

1989; Fedigan in press). Male vigilance may have been primarily directed toward detecting other males rather than potential predators, as has been suggested for vervet monkeys (Baldellou and Henzi 1992). However, as these workers noted, the intent of male vigilance behaviour is irrelevant from a female's perspective, provided that it results in her receiving warning of potential predators or other dangers.

It seems likely that more vigilant individuals would be more likely to detect potential predators. Field experiments involving brown and white-fronted capuchins support this conclusion (van Schaik and van Noordwijk 1989). White-faced capuchins typically respond to predators with a distinctive yelping vocalisation or 'alarm call' (Oppenheimer 1982), which may alert other group members. I heard numerous alarm calls during the study (sometimes as many as five in one hour) but because the calls tend to be non-directional, it was difficult to determine the caller's identity, especially when the group was dispersed or visibility was poor. Relatively few alarms were given by focal animals, suggesting that a high percentage originated from juveniles and/or infants. Not all alarm calls were associated with predators: individuals also gave alarm calls when startled by many non-predators, including coatis, deer, peccaries, guans, vultures, and humans. Such calls rarely evoked a group response. The small sample of 'genuine' predator alarms given by adults did suggest that more vigilant individuals - in particular the alpha male of each group -

were most successful in detecting potential predators. However, the only category in which males performed better than females was snakes, which may have reflected the greater proportion of time that males spent on the ground (see chapter two) rather than increased vigilance *per se*.

There was little evidence that males were more active than females in confronting either predators or other capuchin groups. However, the rate of aggressive intergroup encounters in the study groups was uncharacteristically low; in previous years such encounters were recorded far more often, and primarily involved males of opposing groups (Fedigan, in press). In addition, the relationship between the LV and S groups was somewhat unusual. At the start of the study, the LV group males reacted aggressively to the presence of the sole S group male within their range. After this old male disappeared in March, the small S group was led by its alpha female, toward whom LV group females (but not males) responded aggressively. In mid-April an LV group male transferred to the S group, and increasingly led it into the LV range. The LV males appeared to tolerate the group's presence and displayed no aggression toward their former companion, but the presence of the S group alpha female continued to evoke an aggressive response from the LV group females.

Spider monkeys (*Ateles geoffroyi*) at Santa Rosa exploit many of the same foods as capuchins (Chapman 1988) and the two species are thus potential competitors. The LV group was frequently involved in aggressive interactions with spider monkey groups whose ranges overlapped with their own. Both male and female capuchins typically participated, but males - especially the alpha male - were more active and more aggressive in confronting spider monkeys. On one occasion I watched the alpha male come to the defence of a female who was being threatened by two adult female spider monkeys and successfully drive them away. During a prolonged encounter with a group of at least seven adult spider monkeys, a subadult male 'rescued' three infants from the frontline while their mothers participated in barking and threats from the rear of the group. The male made three separate trips, approaching each infant and carrying it on his back to a large tree some 10 m from the group. He then sat with the infants, grooming, cuddling and playing with them, until the encounter had ended. All of the study group males were typically tolerant of infants, occasionally carrying younger individuals or playing with older ones.

Male costs to females

The hypothesis that males impose greater costs on females than do other females was also supported. The study indicates that resident males impose a greater cost on females than do other females in the form of increased intragroup agonism, especially during foraging, feeding interruptions, and harm to infants.

As in Fedigan's (in press) study of capuchins at Santa Rosa, rates of agonism in both study groups were low (334 behaviours in 377 hours), but over 70% of adult agonistic interactions were between males and females. Aggressive signals were more common than submissive signals because aggressive signals frequently elicited an aggressive response. Many agonistic episodes consisted of an exchange of open-mouthed threats. The most common submissive signal was a female avoiding an approaching male, suggesting that females reduced the risk of aggression from a male by removing themselves from his proximity. On the few occasions that a male avoided a female, the response was directed by a subordinate male toward an alpha female. This was consistent with Fedigan's (in press) finding that most females rank below males, but that the alpha female ranks above all but the alpha male. The alpha female may thus be less disadvantaged than other females in agonistic interactions with males, except for those involving the alpha male.

The analyses of variance show that males were not simply more agonistic than females; in fact females were more agonistic than males in social interactions. The significant factor influencing the probability of an agonistic foraging interaction was the sex of both individuals involved; agonism was most likely when one was male and the other female.

Almost 75% of adult agonism occurred in a foraging context. The rate of agonism between males and females increased during foraging, but the rate of agonism between females did not. Agonism between males and females occurred three times more often during foraging than at other times, whereas agonism among females was equally as likely to occur during foraging as at other times. This suggests that the cost of increased agonism associated with resident males was largely manifested as increased feeding competition. Female foraging was more often interrupted by males than by females, and male-related agonism adversely affected female foraging success. As in Janson's (1985, 1990a) studies of *C. apella*, female foraging success was negatively associated with aggression received from males, but the association was weak compared with that between reduced foraging success and increased agonism involving males. I suspect that this was because in my study, females often avoided males during foraging, such that an agonistic signal but no aggression was recorded. Feeding supplants, which were scored as aggressive signals, were considerably less common than avoidance. Since avoidance and supplantation yield similar costs in terms of lost foraging time and lost access to feeding sites, it is not unexpected that male-related agonism proved a better predictor of foraging success than aggression received from males.

There was some evidence that the alpha male was able to monopolise small fruit trees, as Janson (1984, 1986a, 1986b) observed for brown capuchins. For example, in late February a single small fig tree ripened in the CP range. On several occasions I saw the alpha male (JU at that time) chase females and juveniles out of the tree, where he alone remained and fed. There were similar but less striking occurrences in several medium-sized fruit trees, such as *Simaruba glauca* and *Muntingia calabura*. However, monopolisation of fruit trees by a single male was not a common occurrence, and was not observed in the LV group.

The severe cost that males can impose on female reproductive success was demonstrated when a male killed a CP group infant. The infanticide may have been associated with a change in male dominance ranks; the two-day-old infant was killed soon after the group's beta male assumed alpha status. A similar incident has been observed in wedge-capped capuchins (Valderrama *et al*. 1990, case #2). If the CP group male was unrelated to the infant, the killing would be consistent with Hrdy's (1977) hypothesis that infanticide is a male reproductive strategy in which a newly-breeding male kills his predecessor's offspring in order to hasten a female into estrus and inseminate her. However, the paternity of the dead infant was not known. The infanticidal male was a member of the CP group at the time that conception would have occurred, and as matings in white-faced capuchins are not limited to the dominant male (Fedigan in press; pers. obs.) he could thus have killed his own offspring. I did not see him attempt to copulate with the dead infant's mother, and she had disappeared by the following year.

Distribution of benefits and costs among females

The hypothesis that some females receive greater benefits from resident males than others was supported. High-ranking females were able to form strong bonds with the alpha male and subsequently gain his support during agonistic interactions. These females also benefited from the alpha male's support in initiating and leading group movement. The advantage of leading a foraging progression was not immediately apparent, as the monkeys typically spread out once they reached a feeding area, and rarely maintained a linear formation. However, previous studies of other capuchin species suggest that the leading edge of the group is the most advantageous position where foods require only short search and handling time (Robinson 1981; Janson 1990b). Even for foods requiring a long search or handling time, the lead position may still be advantageous for dominants, who are unlikely to be displaced from a feeding site by subordinates moving up from behind (Fragaszy 1986; Janson 1990b). Another advantage of leadership apparent in this study was that the lead animals tended to be the first to enter fruiting trees. As Robinson (1981) observed, fruit trees can be monopolised by those who gain initial access. I frequently observed several individuals (typically the alpha male, alpha female, and one or two infants) feeding on fruit while others foraged nearby. Those nearby repeatedly glanced toward the fruit tree and its occupants, moving in to feed on the remaining fruit as soon as the tree was vacated. As no agonism was involved, this aspect of feeding competition was not reflected in the data.

Low ranking females may have chosen to avoid competition with males - and other females - by foraging on the periphery of the group, as has been reported in both wedge-capped and brown capuchins (Robinson 1981; Janson 1990a). In each of my study groups, the lowest ranked female was noticeably less central than other females, and more likely to undertake solitary foraging trips (pers.obs.). Avoidance of dominant conspecifics may increase foraging success, but there is a trade-off in terms of greater predation risk (Robinson 1981; Janson 1990b). In addition to being more exposed to predators, peripheral individuals receive less benefit from the vigilance of other group members. Thus, by attempting to avoid the costs associated with resident males, low-ranking females may have forfeited the major benefit that these males offered.

My study suggests that there were two means by which a white-faced capuchin female might maximise her foraging success: i) attain high dominance rank and form strong male bonds, or ii) remain low ranking and avoid agonistic encounters with males. Janson (1985, 1990a) made a similar observation for *C. apella*, but identified tolerance by the alpha male as the critical factor for low-ranking females. The *C. apella* alpha male was responsible for most aggression toward females, which was not the case in my study. In addition, the *C. apella* alpha male's ability to limit access

to small fruit trees allowed him to provide a feeding benefit for females and their offspring (Janson 1984, 1986a).
In my study, high-ranking females tended to associate with the alpha male, suggesting that he offered them the greatest potential benefit. The high level of vigilance shown by the alpha male may have been one such benefit. O'Brien (1991) proposed that preferential association with the alpha male by wedge-capped capuchin females reflected a breeding preference. In wedge-capped capuchin groups, the alpha male performs all of the effective breeding (Robinson 1988; O'Brien 1991), which is not true of white-faced capuchins. However, as in wedge-capped capuchins, high ranking white-faced capuchin females may have received a greater share of male benefits than low-ranking females by monopolising access to the alpha male.

Balance of male benefits and costs

Primate social systems are often portrayed as a balance between conflict and co-operation (Crook 1970; Wrangham 1980; Walters and Seyfarth 1986; O'Brien 1991). But is the balance an equal one, or are the options for females more constrained than the options for males? For example, if the costs of resident males outweighed the benefits that they provided, could females choose to exclude males from social groups? White-faced capuchin males are 25-30% larger than females, with larger, stouter canines. The ability of males to inflict severe injuries was observed in this study. I occasionally saw females form successful coalitions against a single male, but it seems unlikely that they could prevail against a number of males. In addition, females may be unable to prevent males from harming their infants. For example, a male killed a clinging infant despite a concerted physical attack by the mother, her juvenile son, and a second female. Continual vigilance against invading males would be costly in terms of energy expenditure and lost foraging or rest time. This, together with the physical difficulty of repelling males, suggests that excluding males from the group is not a viable option for *C. capucinus* females. Thus a mixed-sex social system may persist, even if it is disadvantageous for females. As O'Brien (1991) has suggested, male-directed strategies by individual females may be the 'best' available compromise under these conditions. Many female strategies may be aimed at reducing the probability of male harm to infants, as several researchers have suggested (e.g. Struhsaker and Leland 1987, Smuts 1987; O'Brien 1991, Pereira and Weiss 1991).

Conclusion

This study suggests that for females, resident males provide greater benefits but impose higher costs than other females. Females benefit from the vigilance of resident males, but suffer increased agonism and decreased foraging success in return. Infanticide, although probably rare, is a heavy cost that males can impose on female reproductive success.

The benefits associated with resident males are unequally distributed among females. By forming strong bonds with the alpha male, high ranking females receive greater benefits than low ranking females. Low ranking females may attempt to minimise agonistic encounters and reduced foraging success by avoiding close association with males, but in doing so they may forfeit the benefits of male vigilance. Females may be unable to exclude males from social groups, even if they are disadvantaged by their presence.

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CHAPTER 4
GENERAL DISCUSSION AND CONCLUSIONS

In this thesis, I examine two aspects of life patterns and processes in mixed-sex social groups. First, I compare male and female foraging behaviour, and consider how their differences might best be explained. Second, I examine the effect of resident males on females, and the manner in which females respond. The thesis is set within the conceptual framework that males and females differ in their primary reproductive strategies. Females are considered to maximise reproductive success through food acquisition, whereas males maximise reproductive success through mate acquisition (Trivers 1972; Wrangham 1980, 1983; O'Brien 1991). How do the findings presented here relate to these strategies?

Chapter Two presents evidence that most sex differences in *Cebus capucinus* foraging are best explained by sexual dimorphism. However, one finding seems anomalous: females, despite their smaller size, spend more time foraging than males. Does this reflect a greater preoccupation with food acquisition? One obvious caveat is that proportions of time spent foraging may be an inadequate comparative measure of nutritional intake. A shortcoming of this study is that the actual amount and nutritional composition of foods eaten was not known (cf. Janson 1985). However, comparison of the types of animal foods exploited indicated that males obtained more animal protein per unit foraging time than females. This finding led me to suggest that as in *Cebus olivaceus* (Fragaszy 1986), *C. capucinus* females spend more time foraging than males because they are slower to meet their nutritional requirements. Pregnant and lactating females increased their foraging return by focusing on foods needing little handling time, allowing them to reduce their foraging time and devote more time to rest or social activity. It is problematic to extrapolate from such a small sample of females, but the data from my study suggest that rather than simply attempting to maximise food acquisition, females adjust their foraging strategy in accordance with their changing protein and energy requirements.

What evidence is there that *C. capucinus* males are more concerned than females with mate acquisition? The pattern of male transfer (versus female philopatry) in this species suggests that males seek breeding opportunities outside their natal groups. Most males emigrate at maturity (Robinson and Janson 1987), and males may subsequently transfer to groups offering greater reproductive opportunity. For example, during the present study one adult male transferred from a group containing three other males to one containing none after its single adult male disappeared. Some immigrant males may kill infants in order to hasten females into estrus and inseminate them (Hrdy 1977). We have no direct evidence of such killings at Santa Rosa, but an infant disappeared following the male transfer mentioned above, and the mother had a new infant (almost certainly fathered by the immigrant male) in the following year. A similar infant disappearance after a male takeover occurred several years ago (L.M. Fedigan, pers. comm.). An infanticide followed a change in alpha male status within one of my study groups. Data presented in chapter three suggest that resident males defend their access to breeding partners by directing aggression toward non-group males. The greater vigilance by males, especially the alpha male, may primarily be directed toward detecting non-group males.

In chapter three I consider the extent to which male and female strategies are conflicting and complementary. I suggest that the most pervasive conflict between the sexes is feeding competition, in which males, by virtue of their greater size and dominance status, have an advantage over females. Male and female reproductive strategies heavily conflict when males attempt to increase their reproductive success through infanticide. However, they are complementary to the extent that females benefit from the exclusion of non-group males, either through decreased risk of change in male breeding partners (and possible infanticide) or maintenance of group access to food resources (O'Brien 1991). Male vigilance benefits females by facilitating early detection of predators, and may allow a female to decrease her own vigilance and devote more time to foraging, resting, infant care, or social activity.

In chapter three I also consider female responses to resident males. I suggest that females may be unable to effectively exclude males from social groups, and compromise by following individual male-directed strategies. High-ranking females form alliances with the alpha male and gain his support in both feeding and social competition. Low-ranking females increase their foraging success by avoiding proximity to males, but may forfeit the benefits of male vigilance by foraging on the periphery of the group.

My study suggests that sex differences in primary reproductive strategies are reflected in the foraging and social behaviour of white-faced capuchins. Many further question are generated. For example: was the behaviour of pregnant and lactating females in this study typical of the species, or an idiosyncratic response to local conditions? How does seasonal food availability affect female foraging and reproductive behaviour? How do changes in male group membership affect female reproductive success? The work described in this thesis represents a small contribution to a larger, long-term study of a species which has as yet been little studied outside captivity (see Fedigan, in press).

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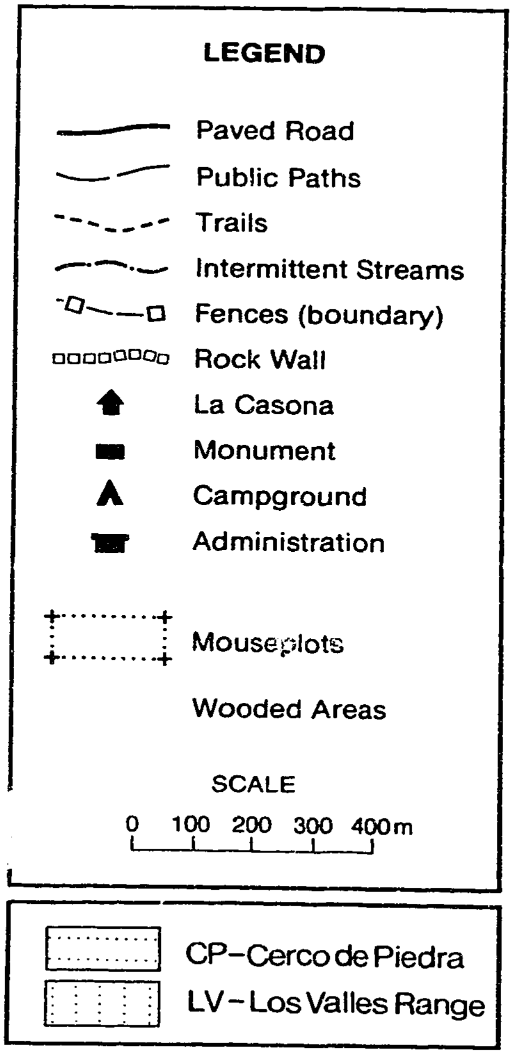
APPENDIX A: Members of two *Cebus Capucinus* study groups. Asterisks indicate focal subjects.

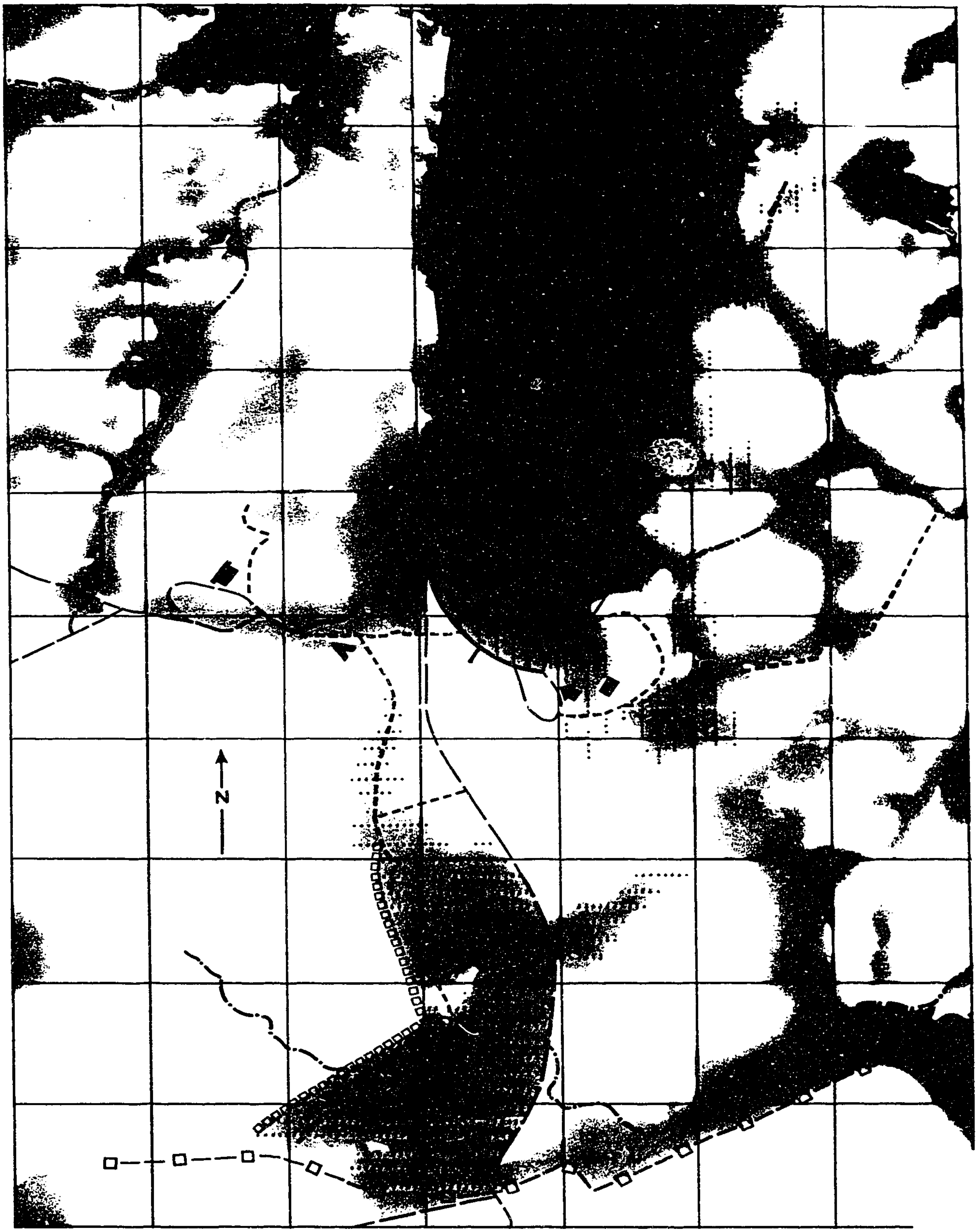
LOS VALLES (LV) GROUP:

BLANQUITA*	Young adult female with independent infant.
BONNIE*	Alpha female; adult with independent infant
BROWSPOT	Large juvenile male Emigrated from group late February 1991.
CHEEKSPOT*	Subadult male
EARS	Juvenile male (BB-88) Immigrated from neighbouring group May 1991
GRINGA*	Adult female with independent infant. New infant born late May 1991.
LEERY*	Adult, alpha male.
MYSTERY	Young adult female, first seen 08/04/91 Immigrated late April after peripheral period
PETER	Small juvenile male
RAMBO	Large juvenile male Emigrated early March 1991.
ROB	Small juvenile (probably female)
SCARS*	Subadult male.
SPIKE	Juvenile male (CH-87). Immigrated from neighbouring group May 1991.
SPLODGE*	Adult female with independent infant. New infant born mid-April 1991.
STEPTOE*	Adult male Emigrated to neighbouring group mid-April 1991.

CERCO DE PIEDRA (CP) GROUP:

BLACKIE*	Subadult male Emigrated? Last seen 22/03/92.
BLANCHE*	Adult female with independent infant
CHOPS*	Adult female
EYES	Juvenile female; inferred daughter of Limp
JUNIOR*	Alpha male at start of study left late March 1991, returned mid May 1991.
LIMP*	Alpha female with independent infant
PATCH*	Adult female with independent infant. Infant born 15-04-91 killed by WINSTON 17-04-91
PEAK	Juvenile male; inferred son of CHOPS
SQUEAKY	Small juvenile male; inferred son of PATCH
TUFT	Juvenile female; inferred daughter of BLANCHE
WINSTON*	Alpha male; supplanted JUNIOR late March 1991.


LEGEND
Paved Road
Public Paths
Trails
Intermittent Streams
Fences (boundary)
Rock Wall
La Casona
Monument
Campground
Administration
Mouseplots
Wooded Areas
SCALE
0
100
200
300
400m
CP–Cerco de Piedra
LV–Los Valles Range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Appendix C: Ethogram used in study of Santa Rosa capuchins

Affiliative Behaviours

ACTIVE PLAY: Play involving chasing and jumping.

DOUBLE PLAY: Two individuals in 'double threat' posture direct playface, pokes, or pounces toward one or more others.

GENTLE PLAY: Includes mouthing, gentle poking, playface, embrace and roll together.

GROOM: Pick through fur of another individual with hands and/or mouth.

HUG: Put arms around and embrace another individual.

IN CONTACT: Sit or lie with body touching that of another individual (excluding grooming or other activity).

PRESENT FOR GROOM: Approach another individual and sit or lie in front of or beside it, inviting grooming.

ROUGH AND TUMBLE PLAY: Includes serial chases, pounces, play hits and bites, forming a 'monkey ball' on ground.

SNIFF: Sniff hand or mouth of another individual.

OTHER AFFILIATIVE BEHAVIOUR: Affiliative behaviours other than those specified above.

Agonistic Behaviours

AVOID: move away from an approaching individual

BITE OR HIT: Bite or hit another individual.

BRANCH BREAK OR BOUNCE: Pull rapidly and repeatedly on large branch or small tree trunk. Branch may be broken off and dropped or thrown toward another animal.

CHASE: Chase another individual (excluding play).

COALITION: Two or more individuals join in an agonistic interaction against one or more others (excluding DOUBLE THREAT)

DOUBLE THREAT: Two individuals in bodily contact - side by side or top of each other - direct OPEN-MOUTHED THREAT to another.

FEAR FACE: Mouth slightly open and lips stretched back, head and/or eyes lowered. Often accompanied by quiet chattering vocalisation and lowered body posture.

OPEN-MOUTHED THREAT: Threat face with canines fully exposed. Usually accompanied by stiff-legged, tense quadrupedal posture and slight piloerection.

PUSH AWAY: Push another individual away (excluding play). Includes 'rejecting' an infant attempting to nurse.

SCREAM: Loud screaming vocalisation

STARE: Stare intently at target, eyebrows slightly raised.

SOLICIT AID: During an agonistic encounter, one individual repeatedly glances toward, and may approach or circle, another not directly involved in the interaction.

SUPPLANT: Approach an individual (usually directing stare or threatface toward it) who responds by leaving, and immediately occupy the space it has vacated.

THREAT FACE: Stare with eyebrows raised, mouth slightly opened, lips stretched back, canines not fully exposed.

OTHER AGONISTIC BEHAVIOUR: Other agonistic behaviours not specified above.

Foraging Behaviours

FEEDING

CATCH AND EAT: catch and eat mobile prey item.

EMBEDDED INVERTEBRATES: Bite and/or dig repeatedly into woody vegetation and pick or lick out encased invertebrates, typically larval forms.

PICK AND EAT: Pick and eat food (fruit, buds, flowers, aggregate emergent caterpillars) directly from vegetation.

PICK, PROCESS AND EAT: Pick food items and modify them before eating. e.g. rub irritating spines from *Slonea terniflora* fruit; bang *Luehea candida* seed case to dislodge seeds; peel or bite open *Acacia collinsi* pods and remove aril.

MANUAL FORAGE

EXPLORE: Reach into and investigate holes, crevices, palm bases, bird nests, or other 'hidden' places.

GRAB AND MISS: Try but fail to catch mobile prey item.

HEAVY FORAGE: Break off large branches, strip bark.

LIGHT FORAGE: Break open and investigate stems, twigs, small branches, or hollow vines; peel back and investigate beneath light surface bark.

PICK AND POKE: manipulate and search through vegetation, including leaf litter or fallen logs.

SAMPLE: Sniff, poke, and/or bite fruit without eating.

VISUAL FORAGE:

Visually inspect adjacent vegetation. Often includes some body movement and turning of head from side to side.

OTHER FORAGE:

DRINK: Drink water

LEAF LICK: Lick moisture from plant stems or leaves

NEST RAID: Prolonged attempts to remove prey (typically coatis) from nest. Includes waiting by nest, attemting to gain access to nest, and confronting defensive adult of prey species.

OTHER FORAGING BEHAVIOUR: Other foraging behaviours not specified above.

Sexual Behaviour

COPULATE: Male mounts female and thrusts repeatedly.

COURTSHIP DANCE: Extension of sexual approach, including same vocalisation and facial expression. Male and female perform complex 'dance', incorporating oblique approaches, follows, parallel progression through canopy, and waits while watching partner. Leading partner (typically the female) frequently stops and looks back over shoulder at follower.

SEXUAL APPROACH: Individual approaches and follows one of the opposite sex, giving characteristic 'warbling-bark' vocalisation. Lips are extended into a pout, cheeks puffed out, and piloerection is often extreme.

Other Behaviours

ALARM: An individual gives an alarm (chracteristic barking vocalisation) in response to a potential predator. Scored only if i) potential predator is seen by the observer or ii) the alarm elicits a response (e.g. scan and further alarm, mob) from at least three group members.

APPROACH: Move within approximately 2 body lengths (1 m) of another individual.

AUTOGROOM: Self-grooming.

FOLLOW: Follow another individual, keeping within 2 body lengths.

FUR RUB: Chew leaves and rub them into own fur and/or that of another individual. Often involves rolling on plant from which leaves taken. Observed only during rain.

INACTIVE: Sit or lie without other visible activity. Includes sleeping.

LEAVE: Move away after having been within 2 body lengths of another individual.

LOST CALL: Long loud call, usually initiated by individual separated from group.

MOB: All or most group members gather near and threaten a potential predator, typically a large snake. Includes barking, open mouthed threats, branch breaking or bouncing, and throwing objects at the predator

NURSE: Female suckles infant.

SCAN: Stare beyond vegetation in immediate vicinity, usually moving eyes and/or head slowly from side to side, and monitor surroundings.

SEARCH: An individual separated from group travels alone, scans, listens, and gives repeated long calls.

STARTLE: Jerk body and abruptly turn and stare toward a disturbance.

TRAVEL: Climb, walk, run, or otherwise move above or on ground for more than 1 m.

TWITTER CALL: Vocalisation typically given in moderately dispersed foraging situations (interpreted as contact calls); loud repeated twitters typically given by an individual (usually female) attempting to initiate group movement.

URINE WASH: Urinate on hand and/or foot and rub on fur.

APPENDIX D: Identified plant foods eaten by *Cebus Capucinus* study group.

Family	Species	Part Eaten
ANACARDIACEAE	*Spondias radlkoferi*	fruit
	Spondias purperea	fruit
	Spondias mombin	fruit
ANNONACEAE	*Annona reticulata*	fruit
	Annona purperea (?)	fruit
ARALIACEAE	*Sciadodendron excelsum*	fruit
BIGNONIACEAE	[various bignones]	seeds
BURSERACEAE	*Bursera simaruba*	fruit
CHRYSOBALANACEAE	*Cochlospermum vitifolium*	flowers
COMBRETACEAE	*Combretum farinosum*	flowers
COMMELINACEAE	*Dichorosandra hexandra*	fruit
ELAEOCARPACEAE	*Muntingia calabura*	fruit
	Slonea terniflora	fruit
ERYTHROXYLACEAE	*Erythroxylon havanense*	fruit
EUPHORBIACEAE	*Sebastiana confusa*	fruit
FABACEAE	*Gricidia sepium*	seeds
	Lonchocarpus sp.	seeds
FLACOURTIACEAE	*Casearia arguta*	fruit
	Zuelania guidonia	fruit
LORANTHACEAE	*Phoradendron quadrangulare*	fruit
MALPIGHIACEAE	*Byrsonima crassifolia*	fruit
MALVACEAE	*Malvaviscus arboreus*	fruit
MIMOSACEAE	*Acacia collinsii*	{aril
	Acacia cornigera	*{thorns
	Enterolobium cyclocarpum	* fruit
	Pithecellobium saman	* fruit

MORACEAE	*Cecropia peltata*	?	fruit
	Ficus sp.		fruit
MYRSINACEAE	*Ardisia revoluta*		fruit
RUBIACEAE	*Alibertia edullis*		fruit
	Genipa americana		fruit
	Calycophyllum candissimum		flowers
	Guettarda macrosperma		fruit
	Psychotria sp.		fruit
	Randia subcordata		fruit
SAPINDACEAE	*Dipterodendron costaricensus*		fruit
SAPOTACEAE	*Manilkara zapota*		fruit
SIMAROUBACEAE	*Simarouba glauca*		fruit
TILIACEAE	*Apeiba tibourbou*	*	fruit
	Luehea candida		seeds
	Luehea speciosa		seeds
ULMACEAE	*Trema micantha*		fruit

* exploited primarily for embedded invertebrates.

APPENDIX E: Detailed results of analyses.

1. Summarised time budgets for adult males and adult females (combined groups). Mean percent of total observed time. An asterisk indicates a level of significance in a two way ANOVA test of $p < 0.05$.

	FEMALES (n=8)	MALES (n=7)	F-value	p-value
Forage	53.1	47.5	4.97	0.046*
Travel	17.3	16.9	0.34	0.856
Rest	15.3	22.0	6.55	0.027*
Scan	3.2	8.0	41.32	<0.001*
Affiliative	7.2	2.7	27.87	<0.001*
Agonistic	1.0	0.6	2.89	0.117
Other	3.0	2.2	1.71	0.217

2. Summarised adult time budgets in two capuchin study groups; percentage of total time observed. An asterisk indicates a level of signficance in a two-way ANOVA of $p < 0.05$.

	LV GROUP (n = 8)	CP GROUP (n = 7)	f-value	p-value
Forage	48.1	53.2	4.20	0.065
Travel	16.1	18.3	7.69	0.181
Rest	19.9	15.6	1.61	0.231
Scan	5.2	5.8	1.59	0.233
Affiliative	7.1	2.8	25.85	<0.001*
Agonistic	0.6	1.1	5.07	0.046*
Other	2.1	3.3	4.29	0.064

3. Comparison of foraging types; mean percent (and SE) of total foraging time. An asterisk indicates a level of significance in a two-way ANOVA test of $p < 0.05$.

	FEEDING	MANUAL[1] FORAGE	VISUAL FORAGE	OTHER FORAGE
LV males (n = 4)	77.1 (1.43)	11.1 (0.44)	10.8 (1.04)	1.0 (0.15)
LV females (n = 4)	79.3 (0.72)	11.0 (0.55)	9.2 (0.53)	0.6 (0.19)
CP males (n = 3)	75.0 (3.60)	14.2 (3.62)	9.6 (1.17)	1.3 (0.48)
CP females (n = 4)	78.0 (2.05)	12.1 (1.10)	8.9 (1.16)	0.9 (0.21)
ALL MALES (n = 7)	76.5 (1.43)	11.6 (1.56)	11.0 (0.95)	1.0 (0.21)
ALL FEMALES (n = 8)	77.6 (1.01)	10.5 (0.72)	11.3 (1.29)	0.8 (0.11)
sex difference				
F-value	1.65	0.44	1.35	2.24
p-value	0.225	0.519	0.270	0.163
LV GROUP (n = 8)	78.3 (0.85)	11.1 (0.33)	10.0 (0.62)	0.8 (0.13)
CP GROUP (n = 7)	76.7 (1.86)	13.00 (1.55)	9.2 (0.78)	1.1 (0.23)
group difference				
F-value	0.67	1.69	0.47	1.20
p-value	0.430	0.223	0.509	0.298

[1] Includes Heavy foraging (strenuous foraging activity such as bark stripping and branch breaking)

4. Comparison of heavy foraging and exploitation of fruit requiring processing prior to eating; mean percent (and SE) of foraging time. An asterisk indicates a level of significance in a two-way ANOVA test of $p < 0.05$.

	HEAVY FORAGING[1]	FRUIT PROCESSING[2]
LV males (n = 4)	2.6 (0.43)	26.1 (3.00)
LV females (n = 4)	0.7 (0.19)	18.2 (2.38)
CP males (n = 3)	5.3 (1.56)	22.6 (1.35)
CP females (n = 4)	0.3 (0.09)	24.7 (0.49)
ALL MALES (n = 7)	3.7 (1.08)	24.6 (1.82)
ALL FEMALES (n = 8)	0.5 (0.10)	21.5 (1.67)
sex difference		
F-value	11.99	1.81
p-value	0.005*	0.205
LV GROUP (n = 8)	1.5 (0.42)	18.2 (0.85)
CP GROUP (n = 7)	2.0 (1.30)	24.7 (1.30)
group difference		
F-value	1.26	0.52
p-value	0.304	0.486

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[1] Physically strenuous foraging activity such as branch stripping and branch breaking.

[2] Includes rubbing and removing spines from *Slonea terniflora*, banging *Luehea candida* or other seed cases to remove seeds, peeling or biting open *Acacia* sp. pods to remove aril.

5. Comparison of diet; mean percent (and SE) of feeding time. An asterisk indicates a level of significance in a two-way ANOVA test of $p < 0.05$.

	ANIMAL FOOD	FRUIT/SEEDS	OTHER PLANT MATERIAL
LV males (n=4)	22.5 (2.48)	75.4 (6.04)	2.0 (1.06)
LV females (n = 4)	25.4 (1.16)	72.3 (1.69)	2.3 (0.69)
CP males (n = 3)	18.0 (7.08)	82.8 (6.27)	0.5 (0.27)
CP females (n = 4)	18.5 (0.58)	81.3 (0.63)	0.2 (0.08)
ALL MALES (n = 7)	20.1 (3.84)	78.6 (4.30)	1.4 (0.66)
ALL FEMALES (n = 8)	21.9 (1.44)	76.8 (1.89)	1.3 (0.50)
sex difference			
F-value	0.39	0.33	0.01
p-value	0.546	0.582	0.937
LV GROUP (n = 8)	24.0 (2.56)	73.9 (2.97)	2.2 (0.59)
CP GROUP (n = 7)	17.7 (2.38)	82.0 (2.42)	0.3 (0.12)
group difference			
F-value	2.89	3.88	6.42
p-value	0.117	0.074	0.028*

6. Comparison of animal food types exploited; mean percent (and SE) of foraging time. An asterisk indicates a level of significance in a two-way ANOVA test of $p < 0.05$.

	EMBEDDED INVERTS[1]	CATERPILLARS	OTHER INVERTS	VERTEBRATES
LV males (n = 4)	2.2 (0.78)	11.4 (0.50)	5.4 (0.50)	1.7 (0.50)
LV females (n = 4)	5.1 (1.19)	9.7 (0.54)	4.3 (0.29)	1.0 (0.36)
CP males (n = 3)	4.4 (1.74)	0.2 (0.05)	5.4 (1.50)	2.1 (1.28)
CP females (n = 4)	9.9 (0.60)	0.4 (0.09)	3.7 (0.30)	0.4 (0.25)
ALL MALES (n = 7)	3.2 (0.84)	6.9 (2.52)	5.4 (0.63)	1.9 (0.65)
ALL FEMALES (n = 8)	7.5 (1.09)	5.0 (1.79)	4.0 (1.80)	0.7 (0.23)
sex difference F-value p-value	 15.02 0.003*	 2.60 0.142	 4.15 0.067	 8.30 0.018*
LV GROUP (n=8)	3.7 (0.85)	10.4 (0.46)	4.8 (0.35)	1.2 (0.[illegible]3)
CP GROUP (n = 7)	7.6 (1.32)	0.3 (0.08)	4.4 (0.68)	1.4 (0.57)
group difference F-value p-value	 10.63 0.008*	 548.17 <0.001*	 0.21 0.657	 2.17 0.174

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[1] invertebrates, primarily larvae, encased in woody material such as stems or hollow twigs.

7. Comparison of capture rates for large and small invertebrates; mean rate (and SE) per hour of foraging time. An asterisk indicates a level of significance in a two-way analysis of variance test of $p < 0.05$

	LARGE[1] INVERTEBRATES	SMALL[2] INVERTEBRATES
LV males (n = 4)	2.9 (0.40)	5.1 (0.25)
LV females (n = 4)	2.2 (0.20)	5.1 (0.21)
CP males (n = 3)	2.4 (0.71)	3.7 (1.22)
CP females (n = 4)	1.4 (0.11)	5.9 (0.18)
ALL MALES (n = 7)	2.7 (0.36)	4.5 (0.55)
ALL FEMALES (n = 8)	1.8 (0.18)	5.5 (0.19)
sex difference		
F-value	5.25	5.06
p-value	0.043*	0.046*
LV GROUP (n = 8)	2.6 (0.25)	5.1 (0.12)
CP GROUP (n = 7)	1.8 (0.34)	4.9 (0.65)
group difference		
F-value	3.07	0.51
p-value	0.108	0.492

[1] items comprising more than one monkey mouthful

[2] items comprising less than one monkey mouthful

8. Comparison of foraging support size use; mean percent (and SE) of foraging time. An asterisk indicates a level of significance in a two-way ANOVA test of $p < 0.05$.

	SMALL[1] SUPPORT	MEDIUM[2] SUPPORT	LARGE[3] SUPPORT	OTHER[4] SUPPORT
LV males	1.4	68.9	14.5	8.1
(n = 4)	(0.71)	(2.25)	(0.93)	(2.13)
LV females	16.6	69.3	9.4	3.3
(n = 4)	(1.04)	(0.24)	(1.00)	(0.78)
CP males	2.8	62.0	14.5	12.2
(n = 3)	(0.98)	(5.92)	(0.10)	(3.02)
CP females	15.2	58.9	9.4	15.9
(n = 4)	(1.46)	(2.07)	(0.25)	(0.55)
ALL MALES	2.0	65.9	14.5	9.8
(n = 7)	(0.60)	(2.90)	(0.50)	(1.81)
ALL FEMALES	15.9	64.1	9.4	9.6
(n = 8)	(1.23)	(2.19)	(0.48)	(2.43)
sex difference				
F-value	156.59	0.25	45.57	0.09
p-value	0.000*	0.630	0.000*	0.773
LV GROUP	9.00	69.1	12.0	5.7
(n = 8)	(2.93)	(1.05)	(1.15)	(1.38)
CP GROUP	9.9	60.2	11.6	14.3
(n = 7)	(2.65)	(2.58)	(1.05)	(1.40)
group difference				
F-value	0.01	9.39	0.03	23.66
p-value	0.926	0.108	0.961	0.001*

[1] terminal twigs, thin vines, fence wire or other substrates grasped with hands or tail, ca. <1 cm. diameter

[2] branches or other substrates requiring some grasping with hands or feet, ca 1-10 cm. diameter

[3] branches, walls, or other substrates on which an individual walks quadrupedally without grasping, ca. > 10 cm diameter

[4] supports adjacent to, above or below, feeding site.

9. Comparison of foraging heights used; mean percent (and SE) of foraging time. An asterisk indicates a level of significance in a two-way ANOVA test of $p < 0.05$.

	HIGH[1]	MEDIUM[2]	LOW[3]	GROUND
LV males	31.7	42.6	18.6	7.1
(n = 4)	(2.56)	(1.54)	(1.58)	(1.29)
LV females	39.5	48.3	11.1	1.2
(n = 4)	(1.58)	(0.62)	(1.08)	(0.46)
CP males	15.3	46.8	29.4	8.5
(n = 3)	(2.70)	(2.67)	(2.92)	(2.60)
CP females	19.0	62.5	17.9	0.6
(n = 4)	(1.30)	(0.31)	(1.16)	(0.31)
ALL MALES	24.7	44.4	23.2	7.7
(n = 7)	(3.73)	(1.76)	(2.59)	(1.23)
ALL FEMALES	29.2	55.4	14.5	0.9
(n = 8)	(3.98)	(2.69)	(1.39)	(0.28)
sex difference				
F-value	7.86	44.45	33.20	30.19
p-value	0.017*	<0.001*	<0.001*	<0.001*
LV GROUP	35.6	46.5	14.8	4.1
(n = 8)	(2.02)	(1.51)	(1.68)	(1.29)
CP GROUP	17.4	55.8	22.8	4.0
(n = 7)	(1.45)	(3.33)	(2.65)	(1.88)
group difference				
F-value	80.82	32.73	28.51	0.13
p-value	<0.001*	<0.001*	<0.001*	0.727

[1] Height > 15m
[2] Height 5-15m
[3] Height <5 m

10. Hourly rate (and SE) and mean percent (and SE) of total observed time spent on the ground during all activities. An asterisk indicates a level of significance in a two-way ANOVA test of $p < 0.05$.

	HOURLY RATE	% TOTAL TIME
LV males (n = 4)	5.3 (1.17)	4.6 (0.95)
LV females (n = 4)	1.1 (0.11)	0.9 (0.23)
CP males (n = 3)	6.1 (1.90)	5.8 (1.95)
CP females (n = 4)	0.7 (0.23)	0.5 (0.24)
ALL MALES (n = 7)	5.7 (0.97)	5.1 (0.93)
ALL FEMALES (n = 8)	0.9 (0.1[illegible])	0.8 (0.16)
sex difference		
F-value	25.35	23.82
p-value	<0.001*	<0.001*
LV GROUP (n = 8)	3.2 (0.98)	2.7 (0.85)
CP GROUP (n = 7)	3.0 (1.31)	2.8 (1.30)
group difference		
F-value	0.04	0.17
p-value	0.853	0.685

11. Comparison of time spent foraging and resting during each month of the study by females who gave birth ("birth females") and other females. Mean percent (and SE) of total observed time. June values incomplete and thus omitted for CP group. Bold type indicates months in which births occurred.

	Feb.	March	April	May	June
LV GROUP:					
Forage:					
Birth females (n = 2)	55.6 (2.45)	46.6 (0.65)	**48.0** (1.05)	**38.9** (3.20)	42.7 (2.70)
Other females (n = 2)	58.4 (2.15)	50.3 (5.20)	56.3 (3.40)	56.6 (2.05)	57.3 (1.75)
Rest:					
Birth females (n = 2)	16.5 (2.80)	21.8 (1.65)	**21.0** (0.80)	**23.5** (3.05)	16.6 (2.25)
Other females (n = 2)	20.5 (2.60)	16.4 (3.45)	7.7 (1.20)	9.5 (3.20)	13.5 (0.10)
CP GROUP:					
Forage:					
Birth female (n = 1)	51.6	56.9	**42.8**	57.0	--
Other females (n = 3)	52.9 (3.29)	58.4 (3.94)	54.8 (3.21)	59.5 (1.97)	--
Rest:					
Birth female (n = 1)	12.9	13.4	**17.3**	14.7	--
Other females (n = 3)	12.6 (1.55)	14.2 (3.58)	14.9 (0.87)	10.5 (3.83)	--

12. Comparison of time spent eating animal foods; time spent eating foods requiring processing; and hourly capture rate of large invertebrates by females and other females. Times are mean percent (and SE) of foraging time; rate is per hour of foraging. Bold type indicates months in which births occurred.

	Feb.	March	April	May	June
LV GROUP:					
Animal Foods					
Birth fem.	3.9	7.8	**9.5**	**19.8**	60.3[a]
(n = 2)	(1.10)	(3.50)	(1.75)	(1.15)	(0.55)
Other fem.	3.2	16.7	6.8	26.9	59.8[a]
(n = 2)	(2.60)	(0.95)	(1.35)	(1.95)	(1.79)
Processed foods					
Birth fem	50.7	13.7	**6.0**	**7.9**	7.0
(n = 2)	(2.94)	(3.55)	(0.91)	(3.19)	(0.71)
Other fem	36.5	32.4	18.6	31.5	12.2
(n = 2)	(12.90)	(2.60)	(4.00)	(1.55)	(0.45)
Capture rate for large invertebrates					
Birth fem	1.32	3.20	**3.24**	**2.34**	0.30
(n = 2)	(1.32)	(0.55)	(0.04)	(0.23)	(0.03)
Other fem	1.37	3.80	1.68	1.09	0.89
(n = 2)	(0.04)	(0.97)	(0.54)	(0.54)	(0.89)
CP GROUP:					
Animal Foods					
Birth fem	19.2	9.9	**8.2**	19.5	--
(n = 1)					
Other fem	16.9	9.8	7.3	19.9	--
(n = 3)	(4.43)	(2.79)	(1.21)	(2.19)	
Processed Foods					
Birth fem	17.9	24.0	**27.2**	36.9	--
(n = 1)					
Other fem	18.8	27.5	30.9	35.7	--
(n = 3)	(3.83)	(4.80)	(2.32)	(0.97)	
Capture rate for large invertebrates					
Birth fem	0.68	1.51	**1.64**	0.88	--
(n = 1)					
Other fem	0.99	1.71	1.50	0.82	--
(n = 3)	(0.29)	(0.41)	(0.18)	(0.02)	--

[a] major component is newly emerged caterpillars

13. Mean hourly rate (and SE) of aggression, submission, and female feeding interrupts per dyad between and within sex classes in each group. Rates adjusted to reflect number of potential interactants and percent of samples for which each male was available.

	[1] LV GROUP	[2] CP GROUP
TOTAL AGONISTIC SIGNALS	n = 83	n = 157
Male - Female	0.10 (0.018)	0.23 (0.037)
Female-Female	0.01 (0.006)	0.12 (0.040)
Male - Male	0.05 (0.010)	0.07 (0.051)
FORAGING-RELATED AGONISM	n = 68	n = 109
Male - Female	0.09 (0.014)	0.16 (0.028)
Female-Female	0.01 (0.006)	0.06 (0.020)
Male - Male	0.05 (0.009)	0.04 (0.025)
TOTAL AGGRESSIVE SIGNALS	n = 69	n = 101
Female to Male	0.06 (0.009)	0.14 (0.028)
Male to Female	0.10 (0.030)	0.14 (0.057)
Female to Female	0.01 (0.006)	0.07 (0.022)
Male to Male	0.05 (0.015)	9.05 (0.049)
TOTAL SUBMISSIVE SIGNALS	n = 23	n = 47
Female to Male	0.05 (0.009)	0.13 (0.032)
Male to Female	0.01 (0.011)	0.01 (0.009)
Female to Female	0.01 (0.011)	0.03 (0.019)
Male to Male	0.01 (0.005)	0.02 (0.016)
FEMALE FEEDING INTERRUPTS	n = 27	n = 49
By Males	0.07 (0.016)	0.15 (0.035)
By Females	0.01 (0.007)	0.03 (0.019)

[1] n = 4 females, 3.5 males (4 males, 1 present 50% of samples)

[2] n = 4 females, 1.7 males (3 males; 1 present 50% of samples and 1 present 17% of samples)

14. Mean hourly rate (and SE) of agonism and foraging-related agonism per dyad between and within sex classes in each group. Rates adjusted to reflect number of potential interactants and percent of samples for which each male was available. An asterisk indicates a level of significance in a two-way ANOVA with repeated measures for antagonist's sex of $p < 0.05$.

	ALL AGONISM Sex of antagonist[1] MALE	 FEMALE	FORAGING-RELATED Sex of antagonist[1] MALE	 FEMALE
LV males (n = 4)	0.05 (0.010)	0.07 (0.023)	0.05 (0.009)	0.06 (0.019)
LV females (n = 4)	0.13 (0.020)	0.02 (0.006)	0.11 (0.014)	0.01 (0.004)
CP males (n = 3)	0.07 (0.051)	0.19 (0.054)	0.04 (0.025)	0.14 (0.049)
CP females (n = 4)	0.25 (0.051)	0.12 (0.040)	0.18 (0.041)	0.06 (0.020)
ALL MALES (n = 7)	0.06 (0.020)	0.12 (0.034)	0.05 (0.011)	0.10 (0.027)
ALL FEMALES (n = 8)	0.19 (0.034)	0.07 (0.027)	0.14 (0.024)	0.03 (0.014)
LV GROUP (n = 8)	0.09 (0.018)	0.04 (0.015)	0.08 (0.013)	0.03 (0.015)
CP GROUP (n = 7)	0.18 (0.049)	0.15 (0.033)	0.12 (0.037)	0.10 (0.027)

ANOVA RESULTS:

Variable	F-value	p-value	F-value	p-value
Between subjects effects:				
Sex	4.74	0.052	0.19	0.773
Group	16.73	0.002*	9.44	0.011*
sex/group	0.03	0.857	0.16	0.701
Within subjects effects:				
Antagonist's sex:	9.48	0.010*	2.19	0.167
sex/antag's sex	8.90	0.012*	14.79	0.003*
group/antag's sex	6.55	0.027*	0.30	0.594

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[1] Treated as repeated measures in ANOVA model:
Measure #1 = Male antagonist; Measure #2 = Female antagonist.

15. Proximity to males and females: mean rate (and SE) per dyad per session. Rates adjusted to reflect number of potential interactants and percent of samples for which each male was available.

	Sex of Individual in Proximity	
	MALE[1]	FEMALE[2]
LV Males (n = 4)	0.08 (0.016)	0.12 (0.020)
LV females (n = 4)	0.12 (0.009)	0.21 (0.036)
CP males (n = 3)	0.07 (0.027)	0.13 (0.034)
CP females (n = 4)	0.15 (0.022)	0.16 (0.031)
ALL MALES (n = 7)	0.08 (0.021)	0.12 (0.017)
ALL FEMALES (n = 8)	0.14 (0.012)	0.18 (0.023)
LV GROUP (n = 8)	0.10 (0.009)	0.16 (0.025)
CP GROUP (n = 7)	0.11 (0.023)	0.15 (0.023)

Total between-sex proximity rate (male-female and female-male):

LV GROUP	0.14 (0.018)
CP GROUP	0.12 (0.010)
Both Groups	0.13 (0.010)

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[1] LV n = 3.5 males (4 males, 1 present 50% of samples)
CP n = 1.7 males (3 males; 1 present 50% of samples and 1 present 17% of samples)

[2] n = 4 females in each group