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Sexual Segregation in Spider Monkeys in Belize

by

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ABSTRACT

Sexual segregation is well documented in a wide range of vertebrates; however, it has not been systematically investigated in any primate species. Based on a 23 month study, I examined temporal variation in sexual segregation in a community of spider monkeys using a statistic that has been applied to other animals and distinguishes active patterns of aggregation and segregation from those predicted by random models. This study revealed that spider monkeys live primarily sex-segregated, but patterns of segregation vary within and between years. Males and females segregate during periods of high food availability and group at levels expected by random association during periods of low food availability. In addition, the sexes differ significantly in activity patterns and diet—factors which have been proposed to explain sexual segregation in other animals. Sexual segregation is not yet identified as a factor underlying fission-fusion dynamics and its occurrence may reveal an important new source of variation in primate and other animal grouping patterns.

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*To my grandmother,
Madelyn Thompson Baker,
who encouraged me to pursue my interests, to travel and learn*

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INTRODUCTION

Sexual Segregation

In many animal species males and females live separately, only associating during the breeding season. Sexual segregation, defined as the separation of males and females socially, spatially, or by habitat (Conradt 1999), has been well documented in a wide range of vertebrates (i.e. bats: Senior *et al.* 2005; whales: Ohsumi 1966; fish: Croft *et al.* 2004; reptiles: Shine *et al.* 2000; and birds: Smallwood 1987) and is common in most ungulates (for review: Main *et al.* 1996; Ruckstuhl and Neuhaus 2000; 2002). However, sexual segregation has not been systematically investigated or quantified in any primate species (Watts 2005).

There is much debate surrounding the definition of what sexual segregation means as it can differ within and between species and can occur under a variety of circumstances—not only between the sexes, but also between age classes (Ruckstuhl 1999; Ruckstuhl and Neuhaus 2005). Authors have defined sexual segregation differently and have used various terms, concepts, and hypotheses to explain similar forms and processes of segregation (Main *et al.* 1996; Ruckstuhl and Neuhaus 2002; Bowyer 2004). In an attempt to unify terminology, Conradt (1999) categorized sexual segregation into three non-exclusive forms: *social segregation*: males and females separate into different social groups; *habitat segregation*: the sexes differ in habitat preferences; and *spatial*

segregation: the sexes differ in spatial distribution. However, the later form of segregation should be used as an auxiliary concept since both social and habitat segregation involve some form of spatial segregation (Conradt 1999; 2005; Ruckstuhl 2007). Social segregation was once thought to be a by-product of sexual differences in habitat use (Geist and Petocz 1977; Clutton-Brock *et al.* 1982; Miquelle *et al.* 1992); however, social and habitat segregation can develop independently (Conradt 1999; 2005). For example, males and females can form separate social groups while using the same area or habitat (Jakimchuk *et al.* 1987; Dubois *et al.* 1993; Putman *et al.* 1993), or differ in habitat preferences, but form mixed-sex groups while in the same habitat (Russo 2002; Conradt 2005).

The large majority of studies on sexual segregation have focused on highly dimorphic ungulate species, such as bighorn sheep, *Ovis Canadensis* (Ruckstuhl 1998; Mooring *et al.* 2003; Neuhaus and Ruckstuhl 2004), red deer, *Cervus elaphus* (Clutton-Brock *et al.* 1982; 1987; Conradt 1998), and Alpine ibex, *Capra ibex* (Villaret and Bon 1995; 1998; Bon *et al.* 2001). Males and females may form separate social groups due to differences in optimal activity budgets (Ruckstuhl 1998; Conradt 1998) or innate preferences to associate with same-sex peers (Bon and Campan 1989; 1996; Bon 1991). Females with young may select habitats safe from predation at the expense of food quality (Main *et al.* 1996; Ruckstuhl and Neuhaus 2000) or, in contrast, select habitats with higher quality food than males because of their smaller size, lower digestive capabilities, and higher nutritional demands of pregnancy and lactation (Main *et al.* 1996; Barboza and Bowyer 2000). Example of the later sexual segregation is also described in

the highly dimorphic African elephant, *Loxodonta africana* (Stokke 2000; 2002). Females, which are half the size of adult males, forage in habitats with a greater diversity of nutritious plants, while bull elephants forage in more woody areas and feed on a lower quality diet (Owen-Smith 1988; Stokke 1999; Stoke and du Toit 2000).

In most species, sexual segregation is highly correlated with dimorphism in body size; the greater the sex differences in size, the greater the degree of segregation (Mysterud 2000; Ruckstuhl and Neuhaus 2000; Lewis *et al.* 2005). Sexual dimorphism in body size may result in sex differences in nutritional demands, foraging behaviour, movement rates, predation risk, and activity patterns (Robbins 1993; Conradt 1998; Ruckstuhl 1998). Sperm whales (*Physeter macrocephalus*), elephant seals (*Mirounga* spp.), beluga whales (*Delphinapterus leucas*), and several other marine mammals are highly sexually dimorphic and exhibit sex differences in migration patterns, foraging and social behaviour, and sometimes diet (Whitehead *et al.* 1991; Stewart 1997; Smith *et al.* 1994; Le Boeuf *et al.* 2000). Male sperm whales, almost two and a half times the size of females, migrate up to 5,000 km away from their tropical breeding grounds, while females form stable matrilineal groups which live year round in tropical waters (Rice 1989; Whitehead *et al.* 1991; Lyroholm *et al.* 1999; Whitehead and Weilgart 2000). In northern elephant seals, males weigh ten times more than females (Deutsch *et al.* 1994), migrate 4,000 km north of their breeding grounds along the continental shelf break of North America, and forage primarily on unidentified bottom-dwelling animals. In contrast, females take longer foraging trips, travel in the open ocean over deep waters, and feed on pelagic prey (Antonelis *et al.* 1994; Slip *et al.* 1994; Stewart 1997; Le Boeuf

et al. 2000). Male beluga whales, roughly one and half times larger than females, spend more time out in the open sea, while females and young aggregate in safer habitats away from killer whales in shallow coastal areas and fresh-water estuaries (Smith *et al.* 1994; Michaud 1999).

Sex differences in habitat use, diet, association and ranging patterns are also described in several species of dolphins (*Tursiops* spp.: Connor *et al.* 1992; *Inia geoffrensis*: Martin and da Silva 2004; *Delphinus delphis*: Young and Cockcroft 1994; *Stenella attenuate*: Wells *et al.* 1987). Indian bottlenose dolphins, *Tursiops truncatus*, live in large, fluid social networks of over 300 members (Connor *et al.* 1992). Females are weakly bonded, range within small, overlapping core areas, and use shallow coastal habitats (Smolker *et al.* 1992; Connor *et al.* 1992; 2000; 2001). In contrast, males range over large areas, form long-term social bonds with male kin, and cooperate against other male alliances for access to estrous females (Connor *et al.* 1992; 2000; 2001 Smolker *et al.* 1992; Connor and Smolker 1995; Krützen *et al.* 2003; 2004). Males also cooperate in aggression directed at estrous females to control, sequester, and coerce them into mating (Connor *et al.* 1992; Scott *et al.* 2005). The strong male alliances and female avoidance of male aggressive behaviour may explain sexual segregation in bottlenose dolphins (Wearmouth and Sims 2008).

The giant petrel (*Macronectes halli*), American kestrel (*Falco sparverius*) and the wandering albatross (*Diomedea exulans*) are also sexually dimorphic and segregate by sex (González-Solís *et al.* 2000; Smallwood 1987; Ardia and Bildstein 1997; 2001). In giant petrels, the most sexually dimorphic seabird, females take longer foraging trips out

in the open sea, while males stay closer to the coast of South Georgia and forage on seal and penguin carcasses (González-Solís *et al.* 2000). Similarly, female albatross migrate further north than males, take longer foraging trips, and feed on a greater diversity of fish species (Weimerskirch *et al.* 1993; Xavier *et al.* 2003). Male kestrels spend more time foraging and prefer closed habitats, while females spend more time preening and select open habitats, such as pastures and open fields (Smallwood 1987).

Sexual segregation is not limited to species with marked sexual dimorphism in body size, but few studies have focused on it in non-dimorphic animals. Most bats are monomorphic, segregate by sex, and exhibit sex differences in thermoregulation requirements, migration patterns, home range size, and/or foraging and roosting behaviour (for review: Altringham and Senior 2005). Females of many temperate bat species roost together in warmer environments to remain homeothermic during pregnancy and lactation, while males roost in colder environments and undergo torpor during cold summer nights (Hamilton and Barclay 1994; Altringham 1996). In the Brazilian free-tailed bat, *Tadarida brasiliensis*, females migrate north to Texas, forming large nursery colonies in caves, while males stay south (Davis *et al.* 1962). The grey-headed flying fox, *Pteropus poliocephalus*, segregate into same-sex ‘camps’ located in different trees or at different levels of the canopy (Nelson 1965). Male big brown bats, *Eptesicus fuscus*, have larger home ranges than females (Wilkinson and Barclay 1997) and female proboscis bats, *Rhynchonycteris naso*, group together and feed in the center of their colony’s home range, while males forage alone along the periphery (Bradbury and Vehrencamp 1976; 1977).

Sexual Segregation in Non-Human Primates

Primates have long been regarded as distinctive among social animals in that males and females live together in cohesive groups year round, even in those species that breed seasonally (Fedigan 1992) or are highly sexually dimorphic (Watts 2005). However, there is considerable variation in the cohesiveness of primate social groups. As pointed out by Watts (2005) in a review of sexual segregation in non-human primates, descriptions of spider monkeys and several other primate species portray social groups in which males and females range and/or associate somewhat separately. Yet few studies have used the term ‘sexually segregated’ and nowhere in the primate literature has sexual segregation been systematically examined. Ramos-Fernandez *et al.* (2009) used an analytical technique to model inter- and intra-sexual association networks in spider monkeys, but no study has explicitly quantified sexual segregation in a primate species—despite its recognition as an important part of the socio-ecology of many animals.

Mandrills (*Mandrillus sphinx*) are apparently sexually segregated outside the breeding season. Adult females and dependent young live in large aggregations (600-800 individuals), called ‘hordes,’ which associate cohesively on a permanent basis (Abernethy *et al.* 2002). Adult males, endowed with larger canines, brighter coloration in the face and hindquarters, and weigh three times that of females (Delson *et al.* 2000; Jolly 2007), range alone for nine months out of the year, only coming back to a horde during the breeding season to compete for estrous females (Abernethy *et al.* 2002).

In the nocturnal grey mouse lemur (*Microcebus murinus*), males and females are primarily monomorphic in body size except during the breeding season when males increase their body mass to outcompete other males for mates (Schmid and Kappeler 1998). Both sexes forage solitarily at night, but form sexually segregated sleeping associations during the day or during hibernation. Females hibernate for approximately six months out of the year, while only some males hibernate and for much shorter periods (Schmid and Kappeler 1998). Related females form stable sleeping associations in tree holes which they cooperatively defend from males and other females of non-kin (Perret 1998; Schmid and Kappeler 1998; Radespiel *et al.* 1998; Radespiel *et al.* 2001). Males often sleep alone or occasionally sleep in nests with other related males (Eberle and Kappeler 2002).

Male squirrel monkeys (*Saimiri* spp.) are roughly 20% larger than females and undergo a ‘fattening period’ in which they gain up to 222 grams (22% of their body mass) just prior to and during the breeding season (Du Mond and Hutchinson 1967). Squirrel monkeys live in mixed-sex groups in which males associate primarily around the periphery of a core group of females and their young. Adult females preferentially associate with one another and often form coalitions against males (Boinski 1987; Lyons *et al.* 1992; Mitchell 1994). Female association and affiliation is thought to increase anti-predator vigilance and strengthen alliances to dominate both males and other females over food resources (Boinski 1987; Mitchell 1994). In *S. boliviensis*, the sexes begin segregating as juveniles by forming same-sex play groups. Once males reach sexual

maturity, they often leave their natal group in bachelor groups which may stay together for several years before immigrating into a mixed-sex group (Mitchell 1994).

Among the least cohesive social primates are chimpanzees (*Pan troglodytes*) and spider monkeys (*Ateles* sp). Both species are large-bodied frugivores that live in large, territorial, multi-male/multi-female communities characterized by male philopatry and female dispersal (Wrangham 1979; Symington 1987; 1990; Di Fiore *et al.* 2009). They are also characterized by high fission-fusion dynamics (Aureli *et al.* 2008) in which related males and unrelated females travel and forage in subgroups of varying size, spatial cohesion, composition, and tenure. All members of a community are rarely, if ever, seen together as a cohesive group. Fission-fusion social organization is thought to mitigate the costs of group living when high-quality food such as fruit is distributed patchily in time and space (Klein and Klein 1977; Wrangham 1980; Symington 1990; Chapman *et al.* 1995). By foraging in smaller subgroups, individuals can reduce feeding competition and time spent traveling between food patches. When overall food availability is higher, spider monkeys and chimpanzees will forage in larger subgroups (Chapman 1990; Chapman *et al.* 1995; Mitani *et al.* 2001; Hashimoto *et al.* 2001; 2003; Shimooka 2003; Itoh and Nishida 2007). Female reproductive state may also influence subgroup size. For example, females with infants are more solitary than cycling females (Chapman 1990; Hashimoto *et al.* 2001).

In chimpanzees, males have longer canines and weigh 5-14% more than females (Stumpf 2007). Although sex differences in ranging and association patterns vary greatly within and across populations, male chimpanzees generally use more of the entire

community home range and have much longer day ranges than anestrus females (Wrangham and Smuts 1980; Goodall 1986). Males form strong alliances and cooperate in territory defence, hunting of prey, and male-male competition for status and access to estrous females (Goodall 1986; Nishida and Hosaka 1996; Wrangham 1999; Watts and Mitani 2001). Female chimpanzees are less social than males and often range alone with their dependent young or in ‘nursery groups’ with other females and their young (Pusey 1980; Wrangham and Smuts 1980; Nishida *et al.* 1985; Goodall 1986; Pepper *et al.* 1999). However, in the Tia forest of western Africa, male and female chimpanzees range and forage more cohesively (Boesch 1996).

Spider Monkey Social Organization and Behaviour

Spider monkeys inhabit tropical forests in southern Mexico, Central and South America. Males and females exhibit relatively low sexual dimorphism in body size (Ford and Davis 1992; Di Fiore and Campbell 2007) (Table 1) and they are not considered seasonal breeders (Campbell and Gibson 2008).

Table 1. Average Weight of Adult Male and Adult Female Spider Monkeys
(From Di Fiore and Campbell 2007)

<i>Ateles</i> Species	Average weight (kg)		Dimorphism*	Sample size	Reference
	Males	Females			
<i>A.geoffroyi</i>	8.2	7.7	1.07	>157	Ford and Davis 1992
<i>A. hybridus</i>	8.3	9.2	0.90	9	Hernandez-Camacho and Defler 1985
<i>A.paniscus</i>	9.1	8.4	1.08	62	Smith and Jungers 1997
	7.3	8.8	0.84	20	Ford and Davis 1992
<i>A.belzebuth</i>	8.3	7.9	1.05	16	Smith and Jungers 1997
	8.5	8.1	1.05	27	Ford and Davis 1992
	8.2	8.3	0.99	7	Karesh <i>et al.</i> 1998
Total Average	8.27	8.34	0.99	>298	
*The ratio of average adult male to adult female body weight					

Like chimpanzees, adult male spider monkeys are more gregarious than females; they form close social bonds, show high rates of affiliative and cooperative behaviour (Fedigan and Baxter 1984; Symington 1988; Chapman 1990; Ramos-Fernandez *et al.* 2009), and form all-male subgroups that are larger on average than female subgroups (5.4 individuals compared to 2.8: Shimooka 2005; Wallace 2008a). Males travel faster than females and cover a greater area of their home range daily (Chapman 1990; Shimooka 2005; Wallace 2008a). Van Roosmalen (1985) and Ramos-Fernandez and Ayala-Orozco (2003) have recorded maximum male day-ranges up to five kilometres. Male spider

monkeys frequently interact affiliatively (i.e. groom, pectoral sniff and embrace, sit in body contact) and associate more with each other than with females or female-female dyads (Fedigan and Baxter 1984; Symington 1990; Ahumada 1992; Slater *et al.* 2009; Ramos-Fernandez *et al.* 2009). Even at an early age, male spider monkeys are drawn to same-sex individuals from all ages. Juvenile males preferentially play with other males (McDaniel 1994; Vick 2008) and often seek close contact and initiate affiliative interaction with adult males (Baxter 1979; Vick 2008). Starting around three-four years of age, maturing males spend increasing amount of time away from their mothers and in close association with community adult males (Vick 2008; Ramos-Fernandez *et al.* 2009). Strong male bonds facilitate cooperation in defending access to females and securing a territory with sufficient food resources to support themselves, community females, and their offspring (Aureli *et al.* 2006; Wallace 2008a). Their minimal home range overlap and intense aggression between neighbouring males suggest strong inter-group competition for mates. Like chimpanzees, adult male spider monkeys engage in inter-group aggression during boundary patrols and ‘raiding parties’ into neighbouring territories (Symington 1990; Chapman *et al.* 1995; Wallace 2008a; Aureli *et al.* 2006).

Aggression between males of the same community is rare (van Roosmalen and Klein 1988; Fedigan and Baxter 1984; Slater *et al.* 2009). However, males routinely direct aggression toward mature females of their own community, regardless of female reproductive status (Klein 1974; Fedigan and Baxter 1984; Campbell 2003; Link *et al.* 2009). Two or three males will form a coalition and single out a female to chase and attack. Even older juvenile males will occasionally join adult males in aggression toward

a female (Vick 2008; personal observation). Although these attacks rarely end in serious injury, female spider monkeys show clear signs of distress (e.g. shrieks/distress calls, fleeing close to the ground). The function of female-directed aggression is unclear, but may act as a form of sexual coercion (Link *et al.* 2009) or as a male strategy to dominate over equally-sized females (Campbell 2003).

Female spider monkeys are less social than males and engage infrequently in affiliative interactions (Fedigan and Baxter 1984; Symington 1990; Chapman 1990; Ahumada 1992; Slater *et al.* 2009). They often travel alone with their dependent young or in small subgroups with other females and range within smaller, overlapping core areas that are roughly 20-30% the size of the community home range (Symington 1988; Fedigan *et al.* 1988; Chapman 1990; Shimooka 2003). Females do not differentiate between female association partners (Ramos-Fernandez *et al.* 2009), there are no clear female dominance hierarchies, and aggression between females is generally low (Asensio *et al.* 2008; Slater *et al.* 2009). However, when it does occur, female-female aggression almost always takes place in a feeding context and usually involves an older, more long-term resident female, or group of two to three females, chasing or physically attacking a younger and/or newly immigrated female (Symington 1987; van Roosmalen and Klein 1988; Asensio *et al.* 2008; Slater *et al.* 2009). Female-female aggression primarily occurring in a feeding context suggests female competition over access to high-quality food resources.

Although female social relationships are not as well known in spider monkeys, it appears that they fit Sterck *et al.*'s (1997) dispersal-egalitarian category and support

Wrangham's (2000) scramble competition hypothesis: weakly bonded females reduce feeding competition by spreading out and avoiding one another (van Schaik and Aureli 2000; Aureli and Schaffner 2008). Since females are widely dispersed, male spider monkeys benefit reproductively by forming strong bonds and cooperating with kin in defending a territory containing the ranges of multiple females (Fedigan and Baxter 1984; Symington 1988; Chapman 1990).

OBJECTIVES

This is the first study to explicitly quantify sexual segregation in a primate species using a test that will allow for cross-species comparisons. Based on data collected over a 23 month study on a community of spider monkeys (*Ateles geoffroyi yucatanensis*) at Runaway Creek Nature Reserve in Belize, I used the Sexual Segregation and Aggregation Statistic (Bonenfant *et al.* 2007) to first determine if, in fact, spider monkeys live in sex-segregated societies and second, determine if segregation patterns vary on a bi-weekly, monthly, or yearly basis. As a third objective, I will investigate the relationship between food availability and segregation patterns given that the size and distribution of fruit patches is recognized as a primary factor influencing spider monkey fission-fusion dynamics (Symington 1987; 1988; Chapman 1990; Shimooka 2003; Wallace 2008b). Fourth, I will examine the distribution of infant births over the course of the study to determine if birth seasonality and the time when infants were likely conceived correlates with sexual segregation patterns. Finally, I compare male and female spider monkey activity budgets and diet since these two factors have been the focus of many studies examining causes of sexual segregation in other animals (birds: González-Solís *et al.* 2000; sharks: Klimely 1987; seals: Stewert 1997; Breed *et al.* 2006; ungulates: Ruckstuhl 1998; Conradt 1998; Clutton-Brock *et al.* 1982).

METHODS

Study Site

Runaway Creek Nature Reserve (RCNR) (Figure 1) is a 2,469 ha private reserve in central Belize ($88^{\circ}35'$ W and $17^{\circ}22'$ N) comprising two main vegetative zones: pine savannah and semi-deciduous, broadleaf tropical forest (Figures 2 and 3), and is part of a much larger area of continuous forest. At 20-120 meters above sea level, RCNR is made up of a series of steep limestone karst hills, low valleys, and seasonal swamps. This area of Belize has two seasons: a dry season from January-May and a wet season from June-December in which it receives an estimated 2,000-2,200 mm of rain annually (Meerman 1999).

Figure 1. Topographic Map of Runaway Creek Nature Reserve

Estimated property boundary lines in solid red, Coastal Road in dotted red line,

Scale 1:50,000m (From Meerman 1999)

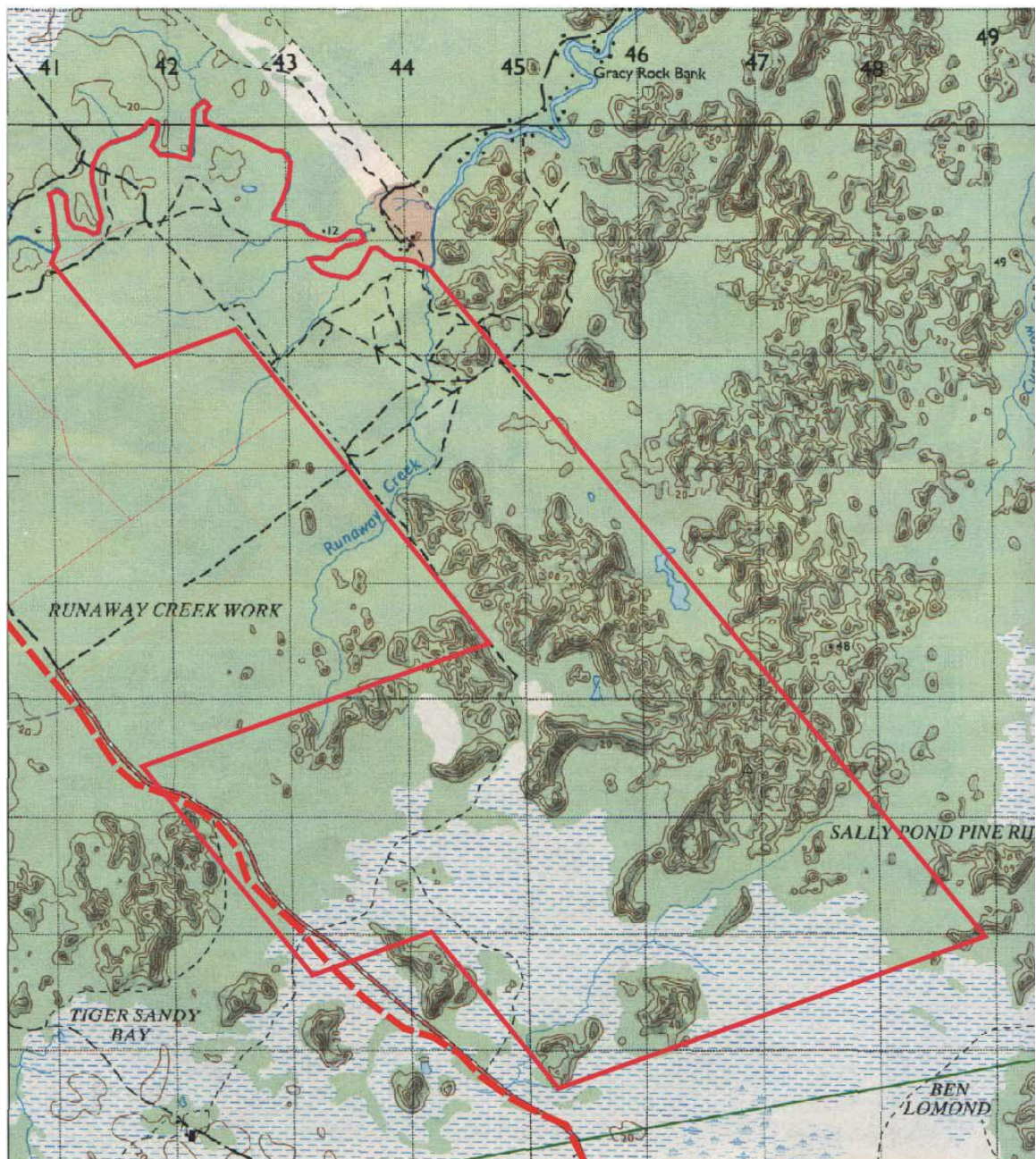


Figure 2. Pine Savannah with Karst Hills in Background



Figure 3. Semi-Deciduous Broadleaf Tropical Forest

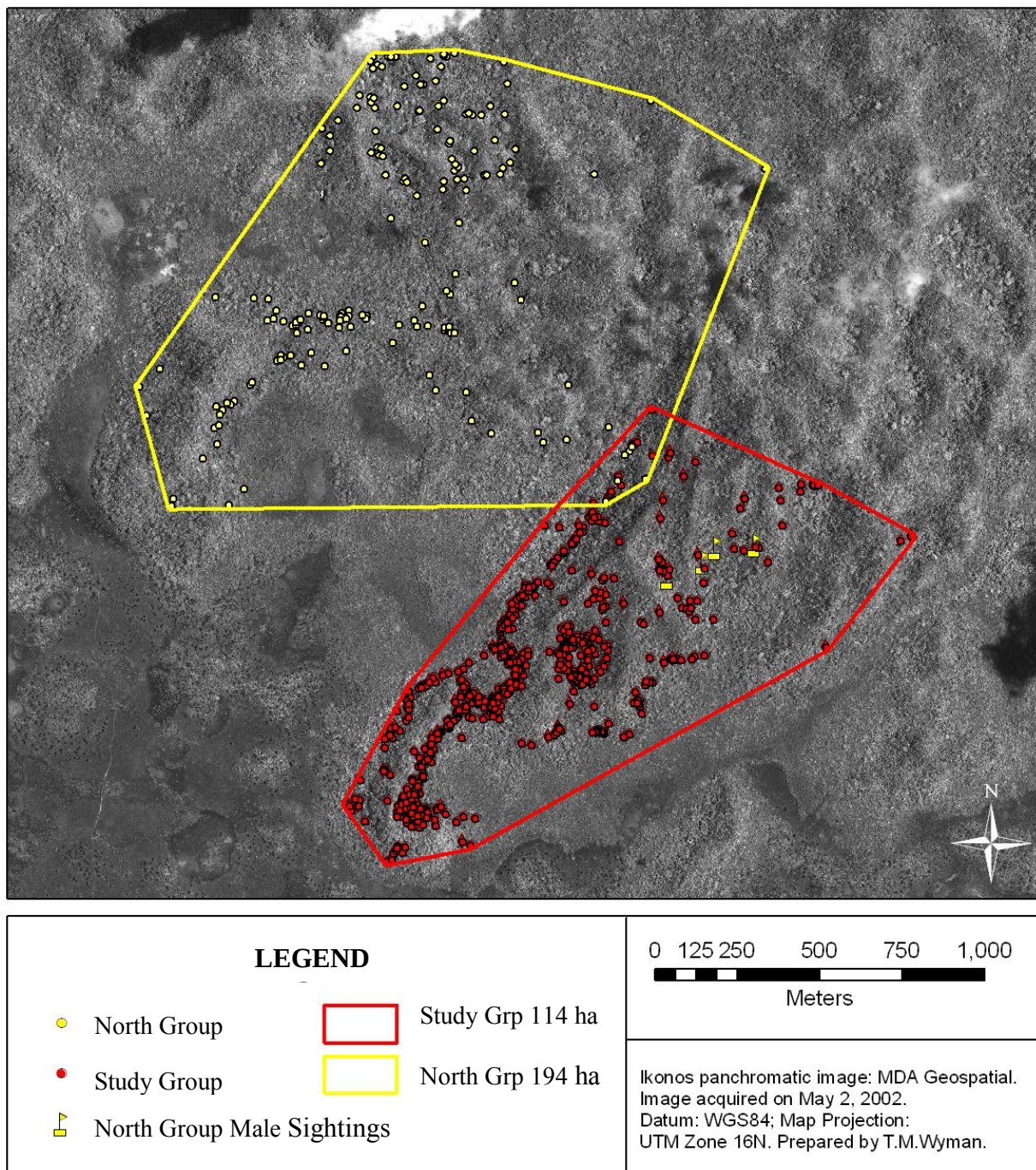


Study Group

The black-handed, or Central American, spider monkey (*Ateles geoffroyi*) ranges from Veracruz in Mexico, through Central America, and along the Choco Region of the Pacific coast to its southern-most distribution in Ecuador (Collins and Dubach 2000; Rylands *et al.* 2006). The Yucatan spider monkey (*Ateles geoffroyi yucatanensis*) is specific to the Yucatan Peninsula of southern Mexico, north-eastern Guatemala, and Belize (Kellogg and Goldman 1944). This subspecies has been studied at Tikal National Park in Guatemala (Coehlo *et al.* 1976; Cant 1977; Baxter 1979; Fedigan and Baxter 1984) and more recently at Punta Laguna Nature Reserve in Mexico (Ramos-Fernandez 2001; Aureli *et al.* 2006; Valero *et al.* 2006; Slater *et al.* 2009). RCNR is the first study site in Belize where data are systematically collected on spider monkey behaviour and ecology.

There are approximately three known communities of spider monkeys within the property boundaries of RCNR, which is connected to a larger population to the east of the reserve. Figure 4 shows the estimated home ranges of two of these communities. Black howler monkeys (*Alouatta pigra*) are also found at RCNR at a lower population density, but are generally more common throughout Belize (Steffens 2008). Large populations of spider monkeys are sighted in the Bladen Nature Reserve in southern Belize and Rio Bravo to the north.

Figure 4. Estimated Spider Monkey Home Ranges at Runaway Creek Nature Reserve.



One community of RCNR spider monkeys has been studied regularly since January 2008. This community, referred to as the “study group,” ranges within an area of approximately 114 hectares (Figure 4) with minimal home range overlap with an adjacent community to the north. At the time of data collection, the study group consisted of 31-35 monkeys with a sex-ratio of approximately 1:4 males to females (Table 2). Over the course of the study, group composition changed slightly. Three females immigrated to the study group and two subadult females disappeared, one of which emigrated to the northern community. Twelve known infants were born (four males, eight females) and one infant female died. All individuals were habituated and individually recognizable by differences in pelage color, facial markings, and skin pigmentation of the anogenital region.

Table 2. Study Group Composition: the number of individuals in each age (A= adult; SA= subadult; J= juvenile; I= infant) and sex class (M= male; F= female) over the course of the study (2008-2009).

Year	Age/sex class								Total
	AM	AF	SAM	SAF	JM	JF	IM	IF	
2008	3	11	2	3	3	2	2	5	31
2009	3	12	2	1	5	4	3	5	35

Behavioural Data Collection

With the help of local field guides Stevan Reneau and David Tzul, I along with Brittany Dean and Kayley Evans, collected data for a total of 23 months (approximately 870 contact hours) starting January 2008 to December 2009 (no data were collected in August 2008). I was present for the first seven months of each year (14 months total), followed by Kayley Evans in fall 2008 (four months), and Brittany Dean in fall 2009 (five months). We collected data using the following protocol which enabled the quantification of sexual segregation as well as the calculation of adult male and adult female activity budgets and diets.

We conducted full or part day follows on spider monkey subgroups for a total of 330 days. A subgroup was defined as all individuals that traveled, foraged, and associated together while maintaining a group spread no greater than 50-meters (distance between the two furthest individuals). Rarely (<1% of observations) were subgroup members spread over an area greater than 50 meters and in such cases, individuals would quickly fission, form separate subgroups, and travel away. It is possible that some subgroup members were not accounted for given the terrain (and thus low visibility) at RCNR, i.e. steep karst hills and small enclosed valleys. However, I feel confident that in at least 98% of subgroups, all individuals within 50 meters accurately represented the subgroup size.

We arrived at the study site at dawn, or occasionally camped in the forest, and located spider monkeys at one of their three main sleeping sites or walked throughout the study area in search of subgroups. When monkeys were encountered, the time and

location (UTM using GPS) were recorded, as well as subgroup size, composition, and identity of recognizable individuals. At 30-minute intervals, we recorded subgroup location and conducted an “instantaneous” scan (maximum five minutes) of all members of the subgroup to determine group size and composition. Males were distinguished from females based on genitalia, and we used the age categories listed in Table 3. For each individual, we recorded their ID, as well as the activity in which it was engaged (feed, travel, inactive, social, or other). If social, the behaviour (i.e. groom, embrace, sit in body contact, sit within one meter) and identity or age-sex class of the interactant was recorded. When a monkey was feeding, we recorded the plant part and species if known, or flagged the tree for later identification with the assistance of a botanist or local vegetation expert.

We stayed with the subgroup all day, or for as long as possible. In the event of a subgroup fission, we stayed with the group containing individuals on which there were less data, or sometimes with the group traveling in an area where we were more likely be able to follow. In an attempt to sample all individuals equally, we entered the forest from different locations and left monkeys who were frequently observed to search for individuals for which we had less data.

Table 3. Spider Monkey Age Categories

Adult	Large, more robust body size; darker faces; sexually mature, i.e. males have fully descended testes and females have given birth to one or more infants (also identified by longer nipples, fuller breasts, and crease/fold under breasts).
Subadult	Slightly smaller/leaner body size (80-90% the size of adults); faces generally appear younger-looking, i.e. more pink around the eyes and mouth.
Juvenile	Travel independently between feeding trees and long distances; may not always travel with mother (approx. 18-24 months to four years)
Infant	Do not travel independently and rely on their mothers to carry them (approx. 0 to 18-24 months of age)

Measure of Sexual Segregation

Following Chapman (1990) and Chapman *et al.* (1995), subgroup size and composition measured during scans at 30-minute intervals were treated as statistically independent. Based on the frequency of arrivals and departures of individuals to and from a sub-group, I calculated the average time interval between any changes to subgroup composition to be 23 minutes. As a result, by using the 30-minute scan interval, the majority of consecutive scans (80%) differed in subgroup composition, and I therefore treated all consecutive subgroup scans as independent, even in the minority of cases where there was no change in subgroup composition. This method also provided a better indication of the duration of time in which two individuals (of the same or opposite sex) were observed together. For example, consider an all-female subgroup which does not change in composition for three hours (six consecutive scans) until a subgroup of males fuse (for one scan) and then quickly fission. By omitting consecutive scans in which subgroups do not change in composition, the relative frequency of mixed-sex subgroups risks being inflated.

Approximately 1,700 subgroup scans were collected over the two year study. Using only the number of adult males and adult females recorded in the scans, I used the Sexual Segregation and Aggregation Statistic (SSAS) (Bonenfant *et al.* 2007) to quantify segregation on a monthly and bi-weekly time scale. SSAS tests three hypotheses: (i) the sexes segregate, (ii) the sexes aggregate, or (iii) the sexes group at levels expected by random association, i.e. males and females do not differentiate between the sexes. This is an appropriate analysis for spider monkeys as it can quantify sexual segregation in less

gregarious species in which solitary individuals are commonly observed. This method has also been used to measure temporal variation in the occurrence of sexual segregation and aggregation in isards (*Rupicapra pyrenaica*), red deer (*Cervus elaphus*), roe deer (*Capreolus capreolus*), and Eurasian wild sheep (*Ovis ammon hodgsoni*) (Bonenfant *et al.* 2007; Singh *et al.* 2010). The following SSAS equation is derived from the chi-square statistic and calculates an index value ranging from 0 (complete aggregation) to 1 (complete segregation):

$$SSAS = 1 - \frac{N}{XY} \sum_{i=1}^k \frac{X_i Y_i}{N_i}$$

where XY is the total number of males and females sampled, k is the total number of subgroups sampled, i is the selected subgroup, N_i is the subgroup size, and $X_i Y_i$ is the number of males and females in the subgroup. Sexual segregation occurs when the average sex ratio for a given time period varies greatly from the community's actual sex ratio of 1:4. Random association between the sexes occurs when the average sex ratio is too close to the community's actual sex ratio and sexual aggregation occurs when the sex ratio is roughly 1:1.

To test the significance of the observed segregation/aggregation patterns, I (with the help of Dr. Christophe Bonenfant) ran a series of permutation tests in program `_R` using the same set of data. This randomization procedure, which tests for independence given the distribution of males and females among subgroups, creates an expected distribution of SSAS under the null hypothesis of random association between the sexes. An empirical distribution of SSAS is simulated to get, at the 5% level, the upper and

lower limits of random association between the sexes. To determine significance, I compared the observed SSAS values with the values generated by the permutation tests. Significant segregation or aggregation occurs when the observed SSAS values fall above the upper limit (segregation) or below the lower (aggregation). Random association occurs when the observed SSAS value falls within the upper and lower limits. Similar to the analytical techniques used by Ramos-Fernandez *et al.* (2009) and Henzi *et al.* (2009), SSAS distinguishes active patterns of aggregation and segregation from those predicted by random models.

Measure of Food Availability

Vegetation data were collected in 2009 only. We sampled a total of 21 40x40m (800m²) vegetation plots within the range of the study group and in all habitat types used by the monkeys: ~~h~~“bajo”/swamp, low valley, karst hill top, ridge side, and transitional forest (to savannah). Within the vegetation plots, we identified and measured the circumference at breast height (CBH) of all trees over 25cm CBH. These data provided a measure of the density and dominance of important spider monkey food tree species. Species dominance was calculated by the following steps:

$$1) \left(\frac{CBH}{2\pi} \right)^2 \times \pi = \text{area}$$

2) Sum of the area for each tree of species A = basal area

$$3) \frac{\text{total basal area of species A}}{\text{total area sampled}} = \text{species dominance}$$

To account for temporal variation in fruit production and provide temporally sensitive food availability scores, we created a “phenology trail” which included 27 feeding tree species, each with approximately five individuals of each tree species (a total of 135 phenology trees). Species chosen for the phenology trail were based on the top fruit species fed on by the spider monkeys at RCNR (not including vines) and constituted a minimum of 1% of their diet (Table 4). Every tree on the phenology trail was checked bi-weekly and scored with an estimate of ripe fruit on the crown as either: 0%, 25%, 50%, 75% or 100%. To provide a bi-weekly food availability score, I averaged the percent fruit coverage for each tree species, multiplied the average score by the dominance of that species in the area, and then summed all the scores for each bi-weekly period.

Table 4. List of Phenology Tree Species and their Represented Percentage in the Spider Monkey Diet

Local Name	Family	Genus	Species	% Diet
1. Fig	Moraceae	<i>Ficus</i>	<i>spp.</i>	23
2. Sapodilla	Sapotaceae	<i>Manilkara</i>	<i>chicle</i>	10
3. Copal	Burseraceae	<i>Protium</i>	<i>copal</i>	9
4. Wild Breadnut	Moraceae	<i>Brosimum</i>	<i>alicastrum</i>	6
5. Wild Cherry	Moraceae	<i>Pseudolmedia</i>	<i>spuria</i>	5
6. Black Poisonwood	Anacardiaceae	<i>Metopium</i>	<i>brownie</i>	5
7. Hog Plum	Anacardiaceae	<i>Spondias</i>	<i>mombin</i>	5
8. Tiger Bayleaf Palm	Arecaceae	<i>Sabal</i>	<i>yapa</i>	5
9. Ironwood	Caesalpinaceae	<i>Dialium</i>	<i>guianense</i>	4
10. Red Ramon	Moraceae	<i>Trophis</i>	<i>racemosa</i>	3
11. Female Bullhoof	Euphorbiaceae	<i>Ampelocera</i>	<i>hottlei</i>	3
12. Warrie Wood	Fabaceae	<i>Caesalpinia</i>	<i>gaumeri</i>	2
13. Cohune Palm	Arecaceae	<i>Attalea</i>	<i>cohune</i>	2
14. Negrito	Simaroubaceae	<i>Simarouba</i>	<i>glauca</i>	2
15. Mountain Moho	Tiliaceae	<i>Luhea</i>	<i>speciosa</i>	1
16. Wild Grape	Polygonaceae	<i>Coccoloba</i>	<i>belizensis</i>	1
17. Grande Betty	Sapindaceae	<i>Cupania</i>	<i>belizensis</i>	1
18. Cecropia	Cecropiaceae	<i>Cecropia</i>	<i>peltata</i>	1
19. Bastard Rosewood	Fabaceae	<i>Swartzia</i>	<i>cubensis</i>	1
20. Male Bullhoof	Euphorbiaceae	<i>Drypetes</i>	<i>browneii</i>	1
21. White My Lady	Apocynaceae	<i>Aspidosperma</i>	<i>megalocarpon</i>	1
22. Red Silion	Sapotaceae	<i>Pouteria</i>	<i>amygdalina</i>	1
23. Black Sapote	Ebeneceae	<i>Diospyros</i>	<i>bumelioides</i>	1
24. Red Bullhorn Acacia	Mimosaceae	<i>Acacia</i>	<i>cookie</i>	1
25. Psuedo Bombax	Bombacaceae	<i>Pseudobombax</i>	<i>ellipicum</i>	1
26. Rubber tree	Moraceae	<i>Castilla</i>	<i>elastic</i>	1
27. Sapodilla (2)	Sapotaceae		<i>spp.</i>	1

Birth Seasonality and Estimated Time of Conception

Due to the highly fluid structure of spider monkey communities, some individuals may not be seen for weeks at a time. For this reason, it is difficult to get exact dates on all infants born into the study group. However, late term pregnancy is unmistakable in spider monkeys, which helps in identifying when a female may soon give birth. For two of the infants, exact birth dates were known after “putting to bed” a pregnant female and noting a newborn attached to her the following morning. For the other infants, birth dates were estimated between the last time the female was seen without an infant (and obviously pregnant) and the first time she was seen with an infant (Table 5). Consistent with that reported by Symington (1988) and Klein (1972) newborn infants were identified by their sparse pelage, almost entirely pink faces, pinkish palms of hands and feet, and limp hanging tails which have limited grasping ability. They also ride ventrally for the first few months after birth, staying close to the mother’s breast and nursing frequently. Spider monkeys have approximately a seven to seven and a half month gestation period (Eisenberg 1973; Milton 1981), so I estimated time of conception approximately seven months prior to the birth of an infant.

Table 5. Infant Birth Dates and Estimated Time of Conceptions

# of Infants	Birth Date	Time of Conception
2	Dec 15-31, 2007	May 15-31, 2007
1	Jan 1-15, 2008	Jun 1-15, 2007
1	Apr 18, 2008	Sep 18, 2007
1	May 5-20, 2008	Oct 5-20, 2007
1	Sep 1-7, 2008	Feb 1-7, 2008
1	Dec 1-15, 2008	May 1-15, 2008
2	Jan 1-7, 2009	Jun 1-7, 2008
1	Apr 1-14, 2009	Sep 1-14, 2008
1	May 13, 2009	Oct 13, 2008
1	Oct 1-7, 2009	Mar 1-7, 2009

Data Analysis

In addition to SSAS, I used two other analyses: logistic regression and chi-square test. For 2009, the year fruit phenology was recorded, I used a simple logistic regression (equation below) to determine if food availability predicted whether males and females would segregate on a bi-weekly time scale.

$$\ln\left(\frac{p}{p-1}\right) = \mu + \beta X_1 + \beta X_2$$

‘_Segregated’ vs. ‘_non-segregated’ was treated as the binary variable with food availability scores as the explanatory variable. Likewise, a simple logistic regression was used to determine if the sexes segregate or not based on the number of births, as well as the number of conceptions for a given time period.

Frequency of occurrences of behaviours recorded in subgroup scans were used to calculate adult male and adult female activity budgets. Behaviours were categorized into

one of the following five activities: feed, travel, inactive, social (allogroom, pectoral sniff and embrace, sit in body contact, and sexual and aggressive interactions) or other (place sniff, chest rub and other scent marking behaviour). Frequency of occurrences of these behavioural categories for males and females were put into a two by five contingency table and analyzed using a chi-square test. Similarly, male and female dietary profiles were calculated from frequency of plant parts fed on during subgroup scans. Plant parts were categorized as: ripe fruit, unripe fruit, flowers (including flower buds), or leaves (young leaves or leaf buds) and also compared using a chi-square test.

RESULTS

Monthly Variation in Sexual Segregation

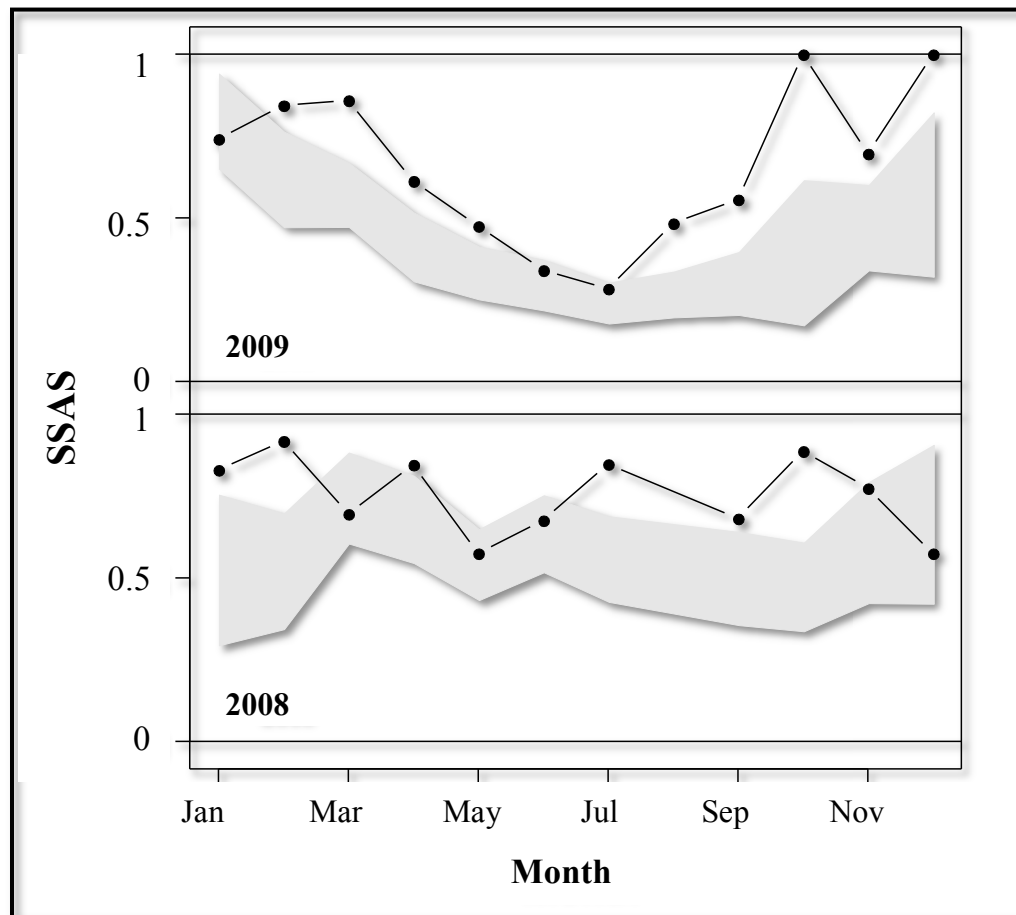
Spider monkeys live primarily in sex-segregated societies. Based on the monthly SSAS analysis, significant aggregation never occurred in this community and males and females were significantly segregated in 15 out of the 23 months (65% of all months). For the remaining eight months, males and females grouped at levels predicted by random association. However, segregation varied monthly and differed between the two study years (Table 6 and Figure 5). Males and females were significantly segregated during nine out of the 12 months in 2009 (75% of months), in contrast to six out of the 11 months in 2008 (55% of months). Although the sexes were segregated more often in 2009 than in 2008, the timing of segregation was fairly consistent between the two years. Males and females segregated primarily during February-April and August-November. The sexes appear to associate at random seasonally: twice a year in May-June and December-January. However, males and females associated at random earlier in 2008 than 2009.

Table 6. Observed Monthly SSAS Values Showing the Upper and Lower Limits of Random Association between the Sexes.

Values shaded in blue indicate months where male and female spider monkeys were significantly segregated. Segregation or aggregation occurs when the observed SSAS values fall above the upper limit (segregation) or below the lower (aggregation). Random association occurs when the observed value falls within the upper and lower limits.

Month	2008			2009		
	observed	lower	upper	observed	lower	upper
Jan	0.83	0.30	0.76	0.74	0.65	0.94
Feb	0.92	0.35	0.70	0.84	0.48	0.77
Mar	0.70	0.61	0.87	0.86	0.47	0.68
Apr	0.85	0.55	0.82	0.61	0.32	0.51
May	0.58	0.43	0.64	0.48	0.25	0.42
Jun	0.68	0.51	0.76	0.34	0.22	0.37
Jul	0.85	0.43	0.68	0.28	0.18	0.30
Aug	NA	NA	NA	0.48	0.19	0.33
Sep	0.68	0.36	0.65	0.56	0.20	0.39
Oct	0.89	0.34	0.61	1.00	0.17	0.62
Nov	0.77	0.42	0.84	0.70	0.34	0.59
Dec	0.58	0.42	0.82	1.00	0.38	0.82

Figure 5. Monthly Variation in Sexual Segregation in Spider Monkeys. Significant segregation occurs when the observed SSAS values fall above the gray shaded area. Black dots = observed SSAS values. Grey shading = the limits of SSAS values expected under random association between the sexes.



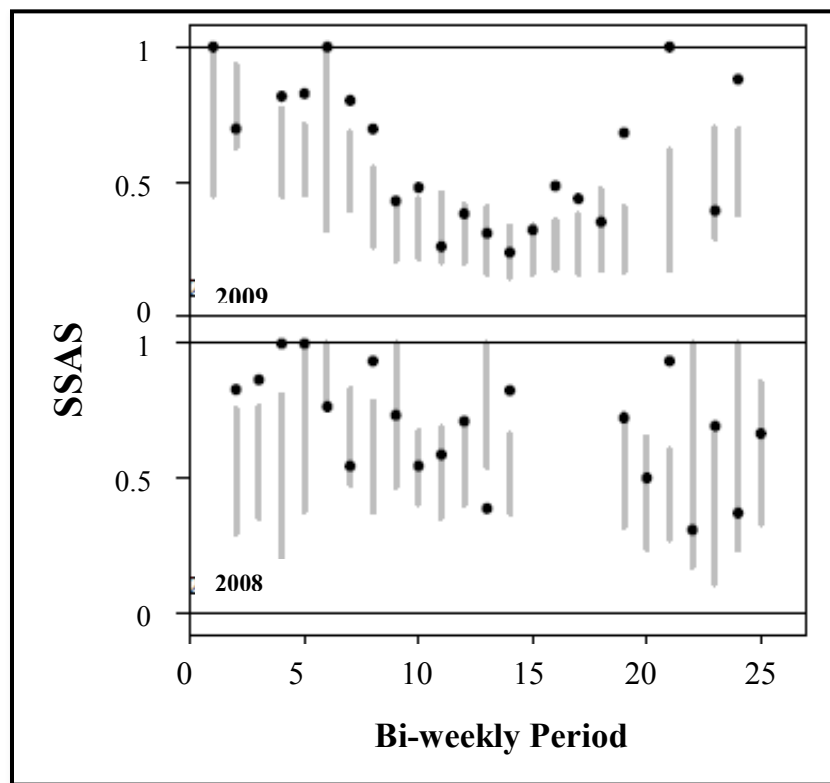
Bi-weekly Variation in Sexual Segregation

I had data for 41 bi-weekly periods and in 18 of those, (44% of periods), the sexes were significantly segregated (Table 7 and Figure 6). In 2008, sexual segregation occurred in eight out of 19 bi-weekly time periods (42% of all periods) and ten out of 22 in 2009 (45% of all periods). In one time period only were the sexes significantly aggregated: the first bi-weekly period in July 2008.

Table 7. Observed Bi-Weekly SSAS Values Showing the Upper and Lower Limits of Random Association Between the Sexes. Values shaded in blue indicate periods where male and female spider monkeys were significantly segregated and the pink shading indicates the period when the sexes were significantly aggregated. ‘_NA’= periods of no data collection and ‘_x’ = periods where no males were sighted and therefore, SSAS cannot distinguish between sexual segregation, aggregation, or random association.

Month	2008			2009		
	observed	lower	upper	observed	lower	upper
Jan	x	x	x	1	0.45	1
	0.83	0.3	0.76	0.7	0.63	0.93
Feb	0.87	0.35	0.77	x	x	x
	1	0.15	0.81	0.82	0.45	0.77
Mar	1	0.38	1	0.83	0.45	0.71
	0.77	0.77	1	1	0.32	1
Apr	0.55	0.48	0.83	0.8	0.4	0.68
	0.94	0.38	0.79	0.7	0.26	0.55
May	0.74	0.47	1	0.43	0.21	0.43
	0.55	0.41	0.68	0.48	0.22	0.44
Jun	0.59	0.36	0.69	0.26	0.2	0.46
	0.71	0.41	0.69	0.38	0.2	0.42
Jul	0.39	0.54	1	0.31	0.16	0.41
	0.83	0.37	0.67	0.24	0.15	0.34
Aug	NA	NA	NA	0.32	0.16	0.34
	NA	NA	NA	0.48	0.18	0.36
Sep	x	x	x	0.44	0.16	0.38
	x	x	x	0.35	0.17	0.47
Oct	0.73	0.32	0.74	0.68	0.17	0.4
	0.5	0.24	0.65	x	x	x
Nov	0.94	0.27	0.61	1	0.17	0.62
	0.31	0.17	1	x	x	x
Dec	0.69	0.11	0.67	0.39	0.29	0.7
	0.37	0.24	1	0.89	0.38	0.69

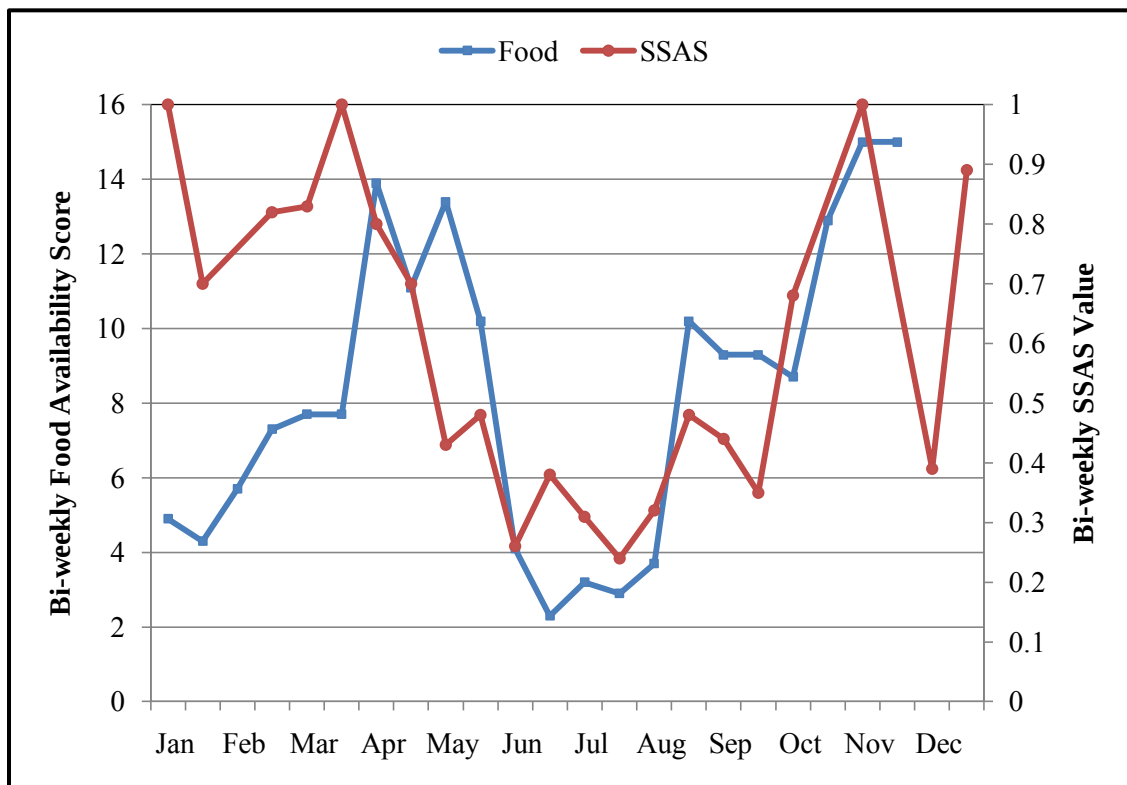
Figure 6. Bi-Weekly Variation in Sexual Segregation in Spider Monkeys. Significant segregation occurs when the observed SSAS value falls above the grey bar. Significant aggregation occurs when the observed SSAS value falls below the grey bar. Black dot = observed SSAS value, grey bar = range at which the sexes associate at levels expected by random



Bi-weekly Variation in Food Availability and SSAS in 2009

I examined the relationship between bi-weekly food availability scores and sexual segregation since temporal variation in fruit availability and distribution are thought to be primary factors influencing spider monkey grouping patterns (Chapman 1990; Symington 1990; Chapman *et al.* 1995; Shimooka 2003; Wallace 2008b). In 2009, the year fruit phenology was recorded, food availability was highest in April-May and August-November and lowest January, June and July.

Figure 7. Bi-weekly Food Availability Scores and SSAS Values in 2009



Using a simple logistic regression analysis with *_segreated'* vs. *_non-segregated'* as the binary variable and bi-weekly food availability scores as the explanatory variable, I found a higher probability that the sexes would segregate when food availability was high ($p = 0.033$) (Figure 7 and Table 8). Food availability correctly predicted whether males and females would segregate in 76.5% of all cases (Table 9). In general, sexual segregation occurred when food availability was above a score of six and the sexes grouped at levels expected by random association when food availability was below a score of six. The formula for predicting sexual segregation was:

$$p = \frac{e^{-3.241+0.400FOOD}}{1 + e^{-3.241+0.400FOOD}}$$

where p = probability, e = exponential, and $FOOD$ = bi-weekly food availability score.

Table 8. Analysis Results For Simple Logistic Regression: Food Availability as a Predictor For Sexual Segregation in Spider Monkeys

		B	S.E.	Wald	df	Sig.	Exp(B)	95% C.I. for EXP(B)	
								Lower	Upper
Step 1 ^a	food	.400	.187	4.555	1	.033	1.492	1.033	2.154
	Constant	-3.241	1.584	4.185	1	.041	.039		

a. Variable(s) entered on step 1: food.

Table 9. Simple Logistic Regression Classification Table^a

			Predicted		
			Segregated		Percentage Correct
			0	1	
Step 1	Segregated	0	7	2	77.8
		1	2	6	75.0
Overall Percentage					76.5

a. The cut value is .500

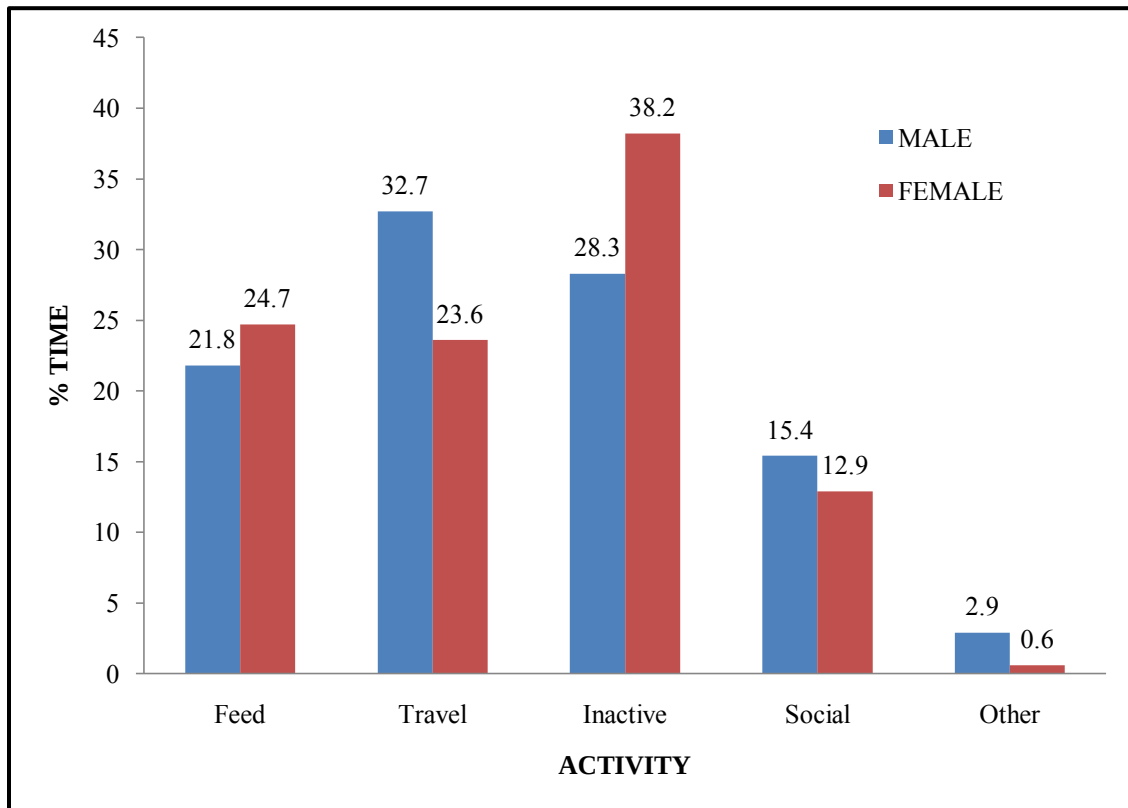
Birth Seasonality, Time of Conception, and SSAS

Twelve infants were born over the course of the study. In the two years combined, six infants were born in December-January, four in April-May, and two in September-October. Therefore, with a gestation period of approximately seven to seven and a half months (Eisenberg 1973; Milton 1981), six infants were likely conceived in May-June, four in October-September, and two in February-March. A simple logistic regression was used to determine whether males and females would segregate or not based on the number of births and the number of estimated conceptions during a bi-weekly time period. There was no significant relationship for either the number of births ($p = 0.781$) or conceptions ($p = 0.073$).

Sexual Differences in Activity Budgets and Diet

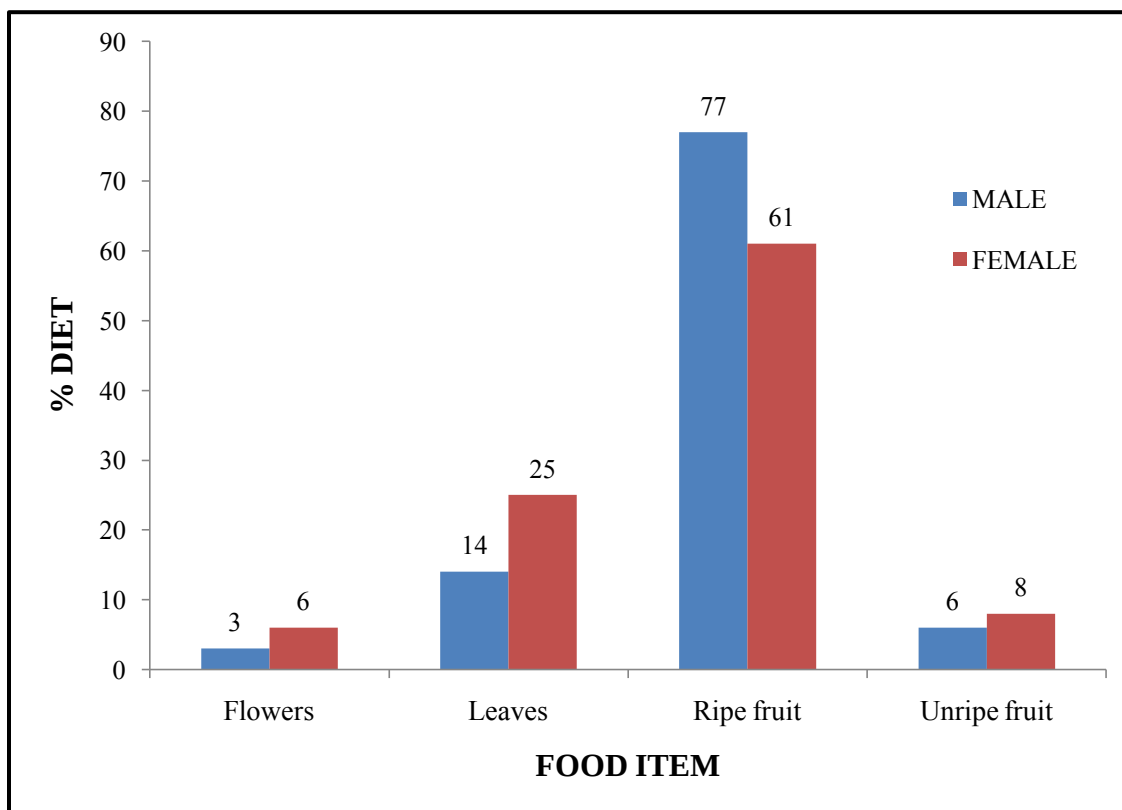
Similar to spider monkeys studied at other sites (Symington 1987; 1988; Chapman *et al.* 1995; Ramos-Fernandez 2001), the study group spent 24.2% of time feeding, 36.2% inactive, 25.3% traveling, 13.3% social, and 1.1% engaged in ‘other’ activities such as place sniffing, chest rubbing, and other scent marking behaviours. However, males and females differed significantly in activity budgets ($\chi^2 = 92.56$ df = 4 $p = < 0.001$) (Figure 8). Males spent more time traveling, socializing, and engaging in other activities (N = 662), while females spent more time feeding and being inactive (N = 3025).

Figure 8. Comparison between Adult Male and Adult Female Activity Budgets



The spider monkeys fed on approximately 90 species of trees, vines, and other epiphytic plants with fruit constituting 71% of their diet, followed by 22% immature leaves, 6% flowers, and < 1% other (i.e. insects, algae/moss, soil, limestone, and undetermined food items). Adult males (N = 160) and females (N = 743) also differed in diet ($\chi^2 = 21.5$ df = 3 $p = < 0.001$) (Figure 9). Both sexes fed primarily on ripe fruit, but females included more flowers, leaves, and unripe fruit in their diet than did males.

Figure 9. Comparison between Adult Male and Adult Female Diets



DISCUSSION

Primates are thought to be unique among social animals in that the sexes live cohesively year round. However, spider monkeys have been described as living in social groups in which males and females range and associate separately (Fedigan and Baxter 1984; Symington 1989; Chapman 1990; Shimooka 2003; 2005; Ramos-Fernandez *et al.* 2009). Spider monkeys might actually live in sexually segregated societies—a possibility which has not been systematically examined. This is the first study to explicitly quantify sexual segregation in a primate species using a statistic that has been applied to other species and distinguishes active patterns of aggregation and segregation from those that would be predicted by random association. The objectives of this study were to determine if, in fact, spider monkeys are sexually segregated, and to determine if segregation patterns varied on a monthly or bi-weekly basis. I then determined if temporal variation in sexual segregation was driven by food availability and/or birth seasonality and the probable time of infant conceptions. I also examined sex differences in activity budgets and diet since these two factors have been suggested to explain sexual segregation in other animals (birds: González-Solís *et al.* 2000; sharks: Klimely 1987; seals: Stewart 1997; Breed *et al.* 2006; ungulates: Ruckstuhl 1998; Conradt 1998; Clutton-Brock *et al.* 1982).

This study revealed that spider monkeys live primarily in sex-segregated societies, but patterns of sexual segregation vary greatly within and between years. Based on the monthly SSAS analysis, significant aggregation never occurred in this community and males and females segregated for the majority of months in both study years.

However, the sexes were more segregated in 2009 than 2008 (nine out of the 12 months in 2009 versus six out of the 11 months in 2008). In the remaining months, the sexes grouped at levels expected by random association. On a bi-weekly basis, sexual segregation was less common, but it generally occurred at the same time of the year as observed at a monthly time scale. Out of 41 bi-weekly periods, significant aggregation only occurred once in the first two weeks of July 2008. Although sexual segregation differed within and between the two study years, it appears to follow a general pattern: males and females segregate for the majority of the year, except during the very beginning and end of the rainy season when food availability is low.

Why Do Spider Monkeys Segregate By Sex?

Several hypotheses have been proposed to explain the causes and adaptive advantages of habitat and social segregation in animals, particularly ungulates. Although these hypotheses derive from extensive research on large-bodied herbivores with marked sexual dimorphism in body size, their principle underlying mechanisms can be applied to a wider range of vertebrates with little to no sexual dimorphism. Males and females may segregate due to sex differences in optimal activity budgets (Ruckstuhl 1998; Conradt 1998), forage-selection (Main *et al.* 1996; Barboza and Bowyer 2000), feeding competition (Clutton-Brock *et al.* 1987), inter-sexual aggression (Weckerly *et al.* 2004), or social preferences to interact with same-sex individuals (Bon and Campan 1989; Bon 1991; Ruckstuhl and Neuhaus 2000). However, these hypotheses may not be mutually

exclusive and a combination of related factors contributes to sexual segregation in spider monkeys.

The activity budget hypothesis predicts that sexual dimorphism in body size will lead to differences in movement rates and foraging behaviour that require the sexes to segregate in order to meet optimal activity budgets (Ruckstuhl 1998; Conradt 1998). Despite low levels of sexual dimorphism, I have shown that male and female spider monkeys differed significantly in activity budgets. Due to high inter-group competition for mates and the dispersed distribution of females over a large home range, males must travel faster and farther than females to cover a large area on a daily basis. They also engage in higher rates of affiliative behaviour in order to facilitate their cooperation in territory defence and prevent incursions by neighbouring males. In contrast, females spend more time feeding and resting, which reflects the high nutritional and energy demands of pregnancy and lactation. Due to differences in time spent traveling, resting, foraging, and socializing, male and female spider monkeys may segregate in order to achieve optimal activity budgets and therefore, increase reproductive success.

The forage-selection hypothesis (Main *et al.* 1996; Barboza and Bowyer 2000) predicts that males and females segregate in response to differences in dietary requirements. This hypothesis derives from the Jarman-Bell principle (Bell 1971; Jarman 1974), and it has been proposed specifically to address sexual segregation in large-bodied herbivores that exhibit marked sexual dimorphism in body size (Beier 1987; Pérez-Barberia and Gordon 1999; Barboza and Bowyer 2000; 2001). Although both sexes feed primarily on ripe fruit, results from my study demonstrate that female spider monkeys

include more *unripe* fruit, flowers, and leaves in their diet than do males. Like females in other sexually segregated species (i.e. ungulates: Clutton-Brock *et al.* 1987; African elephants: Stokke 1999; wandering albatross: Xavier *et al.* 2003; dolphins: Young and Cockcroft 1994), a more varied diet may provide a greater diversity of nutrients necessary for pregnancy and lactation. A larger percentage of ripe fruit in the male diet may reflect the high energy demands of their daily activities (i.e. fast travel, long day ranges, territory defence) vis-à-vis the activity demands of females. In addition, because males range within a much larger area on a daily basis, they may come across more fruiting trees than what would be available in the smaller female ranges.

The different, but overlapping dietary profiles of male and female spider monkeys may also be a result of inter-sexual feeding competition. Sexual segregation is predicted to occur when one sex out-competes the other (directly or indirectly) for preferred feeding sites (Clutton-Brock *et al.* 1987; Ruckstuhl 2007). In species that rely more heavily on high-quality, temporally and spatially distributed food patches, direct contest competition is predicted to occur, which may result in the submission and/or displacement of one sex (females) by another (males) in feeding contests. In spider monkeys at RCNR, 66% of all female-directed male aggression occurred in a feeding context (N=58), suggesting the occurrence of inter-sexual feeding competition. When adult or subadult males entered a fruiting tree, particularly small fruit patches, they sometimes chased females out of the tree. More commonly, a female would leave a fruiting tree as males arrived; only returning to feed once the males had traveled off. A male would also direct aggression toward a female if she came too close while he was

feeding. In a study by Slater *et al.* (2009), females, but not males, spent significantly less time feeding in a mixed-sex subgroup than in a same-sex subgroup, which provides further evidence for male displacement of females in a feeding context. Inter-sexual feeding competition may contribute to sexual segregation in spider monkeys if males dominate females in direct contest over preferred fruit patches. A male's ability to displace females from ripe fruit patches may also explain the larger percentage of ripe fruit in the male diet, and the greater quantities of unripe fruit in the female diet.

It is possible, then that females are actively avoiding aggressive males. The social-avoidance hypothesis predicts that sexual segregation would occur if females avoided males because of increased aggression in mixed-sex groups (Weckerly *et al.* 2004). In spider monkeys, males are more aggressive and routinely direct aggression to community females (Klein 1974; Fedigan and Baxter 1984; Campbell 2003; Link *et al.* 2009). Consistent with that described in other spider monkey populations, female-directed male aggression at RCNR primarily occurred when a small subgroup of females and their young were either foraging or resting in a tree. A subgroup of two to five adult and/or subadult males would approach by quickening their pace, while growling and piloerected, and charge towards the females and young. As the females and young screamed and quickly dispersed, the males would single out a female to chase. The distressed female usually fled close to the ground, while the males hovered above her, growling and showing their teeth. Her dependent young, often left behind from the start of the chase, usually screamed and gave high-pitched whistles (cry vocalizations) until the attack ended. Sometimes an older juvenile would try to come to its mother's aid by

chasing and lunging at the males. This chaotic scene usually lasted just a few seconds, but occasionally the males continued to chase, lunge, and grab at the female, sometimes inflicting scratches or minor wounds. Although these ritualized attacks rarely ended in serious injury, it was clearly stressful for females and their associated young. Regardless of its function, female-directed male aggression may contribute to sexual segregation in spider monkeys. Females may avoid traveling, foraging, or fusing with subgroups of males.

Other social factors may also contribute to segregation between male and female spider monkeys. Regardless of differences in body size, the social-preference hypothesis predicts that sexual segregation occurs due to the innate preferences of juveniles to interact with same sex peers that persist into adulthood (Bon 1991; Bon and Campan 1996; Ruckstuhl and Neuhaus 2000). Social attraction to individuals of the same sex has been argued to facilitate social learning and aid in the development of sex-specific skills for reproductive success later in life (Appleby 1982; 1983; Bon 1991; Villaret and Bon 1995; 1998). In spider monkeys, a higher frequency of same-sex affiliative interactions appears to start as early as juvenescence. In the studies by McDaniel (1994) and Vick (2008), juvenile males were more social than juvenile females, directed affiliative interactions primarily toward other males (of all ages), and engaged in more aggressive interactions directed toward females. Similarly, juvenile females appeared to associate more often with other females. Vick (2008) further described how juvenile males sought out affiliative interactions with adult males and occasionally traveled with them along territory boundaries. Similar juvenile male behaviour is observed at RCNR. As juveniles,

male social preferences could facilitate strong male alliances and aid in the development of important fighting skills for territory defence later in life.

Why Would the Sexes Associate?

When fruit is abundant and spatially distributed in clumped patches of varying size, spider monkeys can disperse over their large home range and feed at different feeding sites. Males and females can segregate and pursue different reproductive agendas. However, when food availability is low and fruiting trees are scarce, males and females are limited in their choice of food patches and forced to coincide at the few available fruiting trees. In 2009, the year fruit phenology was recorded, males and females did not segregate during the food scarce months of January, June, and July. During this time, the spider monkeys formed larger subgroups on average (8.1 vs. 5.5) and fed primarily on the fruit and leaf buds of fig trees (*Ficus* spp.). At RCNR, fig trees present large food patches, but occur at relatively low densities. Chimpanzees (*Pan troglodytes*) and orangutans (*Pongo pygmaeus*) also form larger parties when feeding in scarce fig trees (Hashimoto *et al.* 2001; Sugardjito *et al.* 1987) and female chacma baboons (*Papio hamadryas ursinus*) studied by Henzi *et al.* (2009), aggregate in more cohesive social groups when food availability is low. When ecological conditions are optimal, spider monkeys will segregate by sex. However, when limited in their choice of feeding sites, males and females will group at levels expected by random association and feed at the same fruiting trees.

Another factor that may influence mixed-sex association patterns is the presence of estrous females. In chimpanzees, the number of males in a subgroup positively correlates with the presence of estrous females (Riss and Busse 1977; Boesch 1996; Matsumoto-Oda *et al.* 1998; Matsumoto-Oda 1999; Wrangham, 2000). My data show that in January, June and July, there may have been more females in estrous than in the other months of the year, but in spider monkeys, it is difficult to determine the number of estrous females at any given time. Females vary greatly in inter-birth intervals (Symington 1988; Vick 2008) and they do not exhibit sexual swellings or other visual signals that advertize their reproductive status (Campbell 2004). In addition, spider monkeys are secretive in their mating behaviour (Symington 1987; Campbell 2004; Campbell and Gibson 2008) and researchers rarely witness copulations. Wallace (1998) observed a total of two copulations in over 2,700 contact hours and Ramos-Fernandez (2001) observed five in 1,896 hours. Female hormonal analyses taken from fecal samples may be necessary to determine the number of estrous females.

Spider monkeys are non-seasonal breeders (Campbell and Gibson 2008), but data from several long-term studies suggest peaks in the number of births during certain months of the year (Klein 1972; Milton 1981; Symington 1987; Chapman and Chapman 1990; Campbell 2004). It is too early to draw any conclusions about whether or not spider monkeys at RCNR experience birth seasonality. However, based on the 12 infants born over the course of the study, half were born in late December and early January. With a gestation period of approximately seven months (Eisenberg 1973; Milton 1981), these infants would have been conceived in June— a period in both study years in which males

and females were *not* segregated. Although results from my study show no relationship between mixed-sex associations and the time when infants were conceived, the P value does approach significance ($P = .078$). It is possible that more long-term data and a larger sample size may reveal how the presence of estrous females influences sexual segregation and male-female association patterns.

Another factor that may contribute to inter-sexual association is that male spider monkeys at RCNR show a strong interest in infants, particularly newborns less than six months of age (personal observation). Adult and subadult males commonly sit by the side of a mother to smell, touch, and exchange pectoral sniffs with her infant. Males show persistent interest in handling infants by presenting their chest for the infant to climb on to, just as a mother would do to retrieve her infant. Occasionally, if the mother permits, the male will carry the infant while the mother follows close behind. Over the course of the study, I witnessed 59 infant handling bouts in which 81% ($N=48$) were performed by adult and subadult males (unpublished data). As all infants born in a male philopatric community are presumed to share some degree of paternal kinship, male infant handling may be a function of kinship-based affiliation or tolerance. More long term data are needed to determine if male attraction to infants influences inter-sexual association patterns.

Sexual Segregation, Spider Monkeys and Fission-Fusion Dynamics

Sexual segregation has been described, but never quantified, in some primate species, and most of the hypotheses presented above addressing its occurrence derive from studies of other mammalian taxa, and especially ungulates. Primates, however, present a unique challenge to these hypotheses because of the range and variability of social grouping patterns exhibited both within and between species. For the most part, primate males and females associate year-round, but there is tremendous variation in the extent to which the sexes are cohesive in their associations with each other. In particular, species such as spider monkeys and chimpanzees display a relatively uncommon grouping pattern that is characterized by high fission-fusion dynamics (Aureli *et al.* 2008), and the demands that such dynamics impose on the relative fitness interests of each sex may only partially overlap. As a result, observed sexual segregation in spider monkeys might reflect the different strategies of males and females for optimizing fitness interests within their species-specific socio-ecological milieu.

At a most basic physiological level, high fission-fusion dynamics may lead to sexual differences in activity budgets, requiring males and females to segregate in order to meet different reproductive agendas. When food availability is high and spatially distributed in patches of varying size, female spider monkeys can reduce feeding competition over high-quality food patches by spreading out and avoiding each other. The dispersed distribution of females creates a unique challenge for community males, especially given -or in fact resulting in- their large home range size. In addition, the minimal range overlap between communities and the aggressive interactions observed

between neighbouring males suggest strong inter-community competition for mates. As the philopatric sex, male spider monkeys can gain direct, as well as inclusive fitness advantages, by cooperating with kin in defending a large area of high-quality food resources that contain the ranges of multiple females. By preventing incursions by inter-group males, community males can monopolize mating access to females within their home range. To do so, they must travel further and faster than females, cover a large area on a daily basis, and cooperate in border patrols and territory defence during inter-group encounters. High rates of affiliative interactions between community males will assure their strong bonds and facilitate cooperation. The more cooperative the males, the more successful they will be in protecting and maintaining a large home range and securing exclusive access to dispersed females.

The variation and flexibility documented in primate and other animal grouping patterns, i.e. group size, composition, and spatial cohesion, has led to a renewed interest in the *range of fission-fusion dynamics* that may exist within and between species, and the conditions that produce them (Aureli *et al.* 2008). Strier (2009) argues the importance of cross-site comparisons in contributing to our understanding of the social, ecological and even physical dimensions that might shape social relationships. In addition to spider monkeys and chimpanzees, several other mammalian species are characterized by relatively high fission-fusion dynamics and various forms of sexual segregation. These include dolphins (Connor *et al.* 2000), elephants (Wittemyer *et al.* 2005), spotted hyenas (Holekamp *et al.* 1997), bighorn sheep (Ruckstuhl 1998), bats (Kerth and König 1999), and even humans (Marlowe 2005). If sexual segregation is a quantifiable characteristic

that is particular to species with high fission-fusion dynamics, then variation in the degree of sexual segregation may represent another fundamental dimension of fission-fusion dynamics that has important implications for understanding social relationships in these and other species. As a first step in investigating how sexual segregation relates to fission-fusion dynamics, SSAS could be used to quantify and compare sexual segregation in other species characterized by high fission-fusion dynamics.

DIRECTIONS FOR FUTURE RESEARCH

Although sexual segregation is widespread in the animal kingdom, it remains unclear what factors, or combination of factors, contribute to the separation of males and females. To further elucidate the causes and adaptive advantages of sexual segregation, Ruckstuhl and Neuhaus (2000) emphasize the importance of focusing future research on a diversity of social-living species with varying degrees of sexual segregation and sexual dimorphism. Spider monkeys may be particularly intriguing to the study of sexual segregation given that they are not considered seasonal breeders, they live primarily sex-segregated, and males and females are relatively monomorphic in body size. This means either that existing predictions for the conditions under which sexual segregation is likely to occur are incomplete, or that spider monkeys are anomalous and therefore present an additional dimension to the study of factors that contribute to sexual segregation.

As a future study, I hope to continue investigating sexual segregation in spider monkeys by collecting more long term socio-ecological data, testing the various hypotheses proposed to explain social and habitat segregation, and by examining the relationship between sexual segregation/aggregation and fission-fusion dynamics, reproductive behaviour, inter and intra-sexual sociality, and the degree of relatedness within and between community members. Sexual segregation in spider monkeys may have important implications for our understanding of fission-fusion dynamics, primate (and other animal) sociality, and the ecology of the sexes.

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