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The Effects of a Hurricane and Fire on Feeding Ecology, Activity Budget, and Social Patterns of Spider Monkeys (*Ateles geoffroyi*) in Central Belize.

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The Effects of a Hurricane and Fire on Feeding Ecology, Activity Budget, and Social
Patterns of Spider Monkeys (Ateles geoffroyi) in Central Belize.

by

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ABSTRACT

Studying the effects of hurricanes on primate populations provides valuable insight into species adaptability and their resiliency to major climatic events. On October 25, 2010 Hurricane Richard hit a spider monkey research site in Belize and was followed by a extensive forest fire 6 months later. Utilizing this rare opportunity and 44 months of data, this study examined activity, diet, and grouping patterns in a group of spider monkeys in multiple time period comparisons. The monkeys showed behavioural, dietary, and grouping flexibility in the aftermath of the storm and fire. Although spider monkeys are generally considered to be ripe fruit specialists, they showed increased folivory after the hurricane. In the shorter term, the monkeys travelled less and spent more time foraging, however that trend did not hold. Subgrouping patterns were not consistent across all time periods examined; however in some comparisons, daily subgroups were more spatially cohesive with fewer changes in membership after the disturbances. Aggression rates significantly decreased after the hurricane, presumably due to an increase in the consumption of evenly distributed, non-defensible leaves. Dietary, behavioural, and grouping flexibility are critical to mitigating the after-effects of major habitat disturbances. However, the coping mechanisms vary when examining different time periods and negative consequences may not present themselves in shorter-term studies.

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LIST OF TABLES

Table 1. Study Group Composition as of August 2013.....	22
Table 2. Summary of Results	45

LIST OF FIGURES

Figure 1. Photos of Before and After Hurricane Richard.....	9
Figure 2. Average Precipitation and Temperatures.....	21
Figure 3. 8 Weeks Before and After: Activity	29
Figure 4. 8 Weeks Before and After: Diet.....	29
Figure 5a. 8 Weeks Before and After: Subgroup Size.....	30
Figure 5b. 8 Weeks Before and After: Subgroup Spatial Cohesion	30
Figure 6a. 8 Weeks Before and After: Subgroup Fluidity	31
Figure 6b. 8 Weeks Before and After: Aggression.....	31
Figure 7. 22 Months Before and After: Activity	31
Figure 8. 22 Months Before and After: Diet	32
Figure 9a. 22 Months Before and After: Subgroup Size.....	33
Figure 9b. 22 Months Before and After: Subgroup Spatial Cohesion.....	33
Figure 10a. 22 Months Before and After: Subgroup Fluidity.....	33
Figure 10b. 22 Months Before and After: Aggression.....	33
Figure 11. Hurricane, Fire and In-Between: Activity	34
Figure 12. Hurricane, Fire and In-Between: Diet.....	36
Figure 13a. Hurricane, Fire and In-Between: Subgroup Size	37
Figure 13b. Hurricane, Fire and In-Between: Subgroup Spatial Cohesion.....	37
Figure 14a. Hurricane, Fire and In-Between: Subgroup Fluidity	38
Figure 14b. Hurricane, Fire and In-Between: Aggression	38
Figure 15. Rainy Seasons: Activity.....	39
Figure 16. Rainy Seasons: Diet	40
Figure 17a. Rainy Seasons: Subgroup Size.....	41
Figure 17b. Rainy Seasons: Subgroup Spatial Cohesion.....	41
Figure 18a. Rainy Seasons: Subgroup Fluidity.....	42
Figure 18b. Rainy Seasons: Aggression.....	42
Figure 19. Rainy Seasons: Activity	43
Figure 20. Rainy Seasons: Diet	43
Figure 21a. Rainy Seasons: Subgroup Size.....	44
Figure 21b. Rainy Seasons: Subgroup Spatial Cohesion.....	44
Figure 22a. Rainy Seasons: Subgroup Fluidity.....	45

Figure 22b. Rainy Seasons: Aggression.....	45
Figure 23. Photo of Woodrose Vine Growth	53

TABLE OF CONTENTS

ABSTRACT	ii
ACKNOWLEDGEMENTS:	iii
LIST OF TABLES	iv
LIST OF FIGURES	v
TABLE OF CONTENTS	vii
CHAPTER ONE: INTRODUCTION	8
1.1.1. Overview	8
1.1.2. Natural Disturbances	11
1.1.3. Natural Disturbances and Primates	14
1.1.4. Spider monkeys	17
CHAPTER TWO: METHODS	20
2.2.1. Study Site	20
2.2.2 Study Group	21
2.2.3 Behavioural Data Collection	23
2.2.4 Analysis	24
CHAPTER THREE: RESULTS	28
3.1. Review of hurricane and fire	28
3.2. 8-week and 22-month comparison results.....	28
3.2.1. 8-week comparison	28
3.2.2. 22-month comparison.....	31
3.3 Hurricane, fire and in-between results	34
3.4. Rainy and dry seasons before and after results	38
3.4.1. Rainy season comparison	38
3.4.2. Dry season comparison	42
CHAPTER FOUR: OVERALL DISCUSSION	46
5.1.1. Summary of results.....	46
5.1.2. Discussion of study	46
5.1.3. Future directions of research	56
REFERENCES CITED	57
Appendix 1	65
Appendix 2	66
Appendix 3	70

CHAPTER ONE: INTRODUCTION

1.1.1. Overview

The opportunity to study the effects of natural disturbances on a population of primates presented itself when a hurricane and fire hit a spider monkey research site in Belize. On October 25, 2010 Hurricane Richard made landfall in Central Belize and travelled inland, hitting Runaway Creek Nature Reserve (RCNR) before dissipating a few hours later. Six months later, a forest fire caused significant damage to the study site. Behavioural data has been collected continuously on spider monkeys at RCNR since 2008; and without interruption following both the hurricane and fire. As a result, long-term data exist for comparing pre- and post- disturbance data on feeding ecology, behaviour, and grouping patterns of this population.

In this thesis I take advantage of the opportunities provided by Hurricane Richard October of 2010 and the subsequent forest fires of April and May 2011 to describe changes in spider monkey behaviour at Runaway Creek Nature Reserve, Belize that may have resulted from these disturbances. An aerial photo of a core area of the study group's range before and after Hurricane Richard helps to convey the extent of the damage (Figure 1). Studies of the effects of severe weather events and other forms of disturbance suffer the limitations of most observational field research in that it is difficult to draw firm conclusions about cause and effect; however descriptions of behaviours before and after can move our understanding of primate response to these events forward. In this thesis I investigate spider monkey diet, activity, grouping patterns (subgroup size, spatial cohesion, fluidity), and rates of aggression across different time periods in an attempt to reveal behavioural responses to

such events. I approached the question by considering three different categorizations of the independent variable (time relative to the hurricane and fire) in relation to the behavioural variables identified above. I acknowledge that the disturbances produced changes to the forest and food supply are almost certainly involved in whatever behavioural changes are observed, however analysis of the vegetation is underway by other members of the research team and beyond the scope of this Master's thesis. Where possible I acknowledge unpublished data and otherwise incorporate likely ecological intermediaries in my interpretation of the behavioural changes observed.



Fig. 1: A depression in the karst hills and common spider monkey sleeping site at RCNR before and after Hurricane Richard. Before photo was taken during the dry seasons on March 25, 2008. After photo was taken during the rainy season on November 12, 2010. Photo credit: K.S. Hartwell.

The three different (but interrelated) approaches that I took are as follows:

1. 8-week and 22-month comparison: many studies of the effects of severe weather or climatic events do not have access to pre-disturbance data, and if they do, analysis may only reflect those that occur immediately, in a relatively short time frame. Thus my first set of analyses compares before and after the storm by first investigating the behavioural variables in the 8-weeks immediately before and after the hurricane, and then in the 22 months before and 22 months after (without respect to the fire). This

longer term time frame helps with the problem of regular seasonal differences being conflated with those resulting from a disturbance event. It also allows me to distinguish between short and longer term changes, and to begin to observe behavioural recovery.

2. Hurricane, fire, and in-between: in an attempt to focus in more on the effects of the two separate events, I compare the behaviour of the spider monkeys 6 months before Hurricane Richard to the 6 months between the hurricane and fire, and to the 6 months after the fire of the spring of 2011.
3. Rainy and dry seasons before and after: while the 22 months before and 22 months after comparison (above) is long enough to have included and controlled for seasonal variation, I also undertook a comparison of the wet season before the events with the first wet season after, and of the dry season before the events with the dry season after.

Chapter two of this thesis describes the data collection that allowed me to measure diet, activity, grouping patterns (subgroup size, spatial cohesion, fluidity), and rates of aggression across different time periods. As well, it explains the different analyses involved in the three different approaches outlined above. Chapter three begins with a presentation of the timeline of events, and then a qualitative description of the circumstances in the forest after the hurricane and during and after the fire, followed by the results of the three different temporal breakdowns used in the quantitative analyses. Chapter four brings together the

results of all of the behavioural comparisons across all time frame analyses in an attempt to summarize and clarify the results, and discuss what they might tell us about spider monkey behavioural responses to severe events such as hurricanes and fires.

1.1.2. Natural Disturbances

Natural disturbances can cause immediate damage to ecosystems as well as long-term, indirect effects. Large-scale climatic patterns, especially the El Niño Southern Oscillation (ENSO), generate tropical storms and severe drought periods (“Tropical Cyclone Climatology,” 2013). Major storms can cause immediate and drastic alterations to forests in their path, while other disturbances such as droughts and slow burning forest fires can be equally destructive but are generally more seasonally predictable and have more gradual onsets. Irrespective of the type of disturbance, long after the event, these occurrences have the potential to alter tropical forests and affect the animals living in them.

Fluctuations in weather are a regular aspect of seasonal forests, especially those in the tropics. Most tropical forests experience seasonal periods defined by levels of rainfall: a dry season with little to no precipitation and a wet or rainy season with increased precipitation and humidity. During the dry season, vegetation endures water stress that can lead to higher levels of leaf fall (Wright and Cornejo 1990), increased mortality in some species (Condit 1998), and altered distribution of tree species and diversity (Slik 2004). In years when the normal dry season lengthens into an extended drought, severe water stress may result. Droughts can have a severe and prolonged effect on the forest in a number of ways including limiting fruit production, alteration of vegetation structure, and influencing plant species composition (Bunker and Carson 2005; Condit 1998). During dry seasons and droughts, animals living in the forests are also then exposed to more stressful conditions and resource

scarcity (Bunker and Carson 2005; Wright and Cornejo 1990; Hemingway and Bynum 2005).

The occurrence of both natural and human generated forest fires during the dry season is common due to exceedingly flammable conditions. Fires not only kill the living plants in the area but also limit the growth of secondary succession species and promote the growth of pioneer species (Woods 1989). Thus, a forest fire causes both immediate damage and long-term changes to the vegetation,. The original forest is altered not only by the loss of trees, but also the species composition of the forest, especially when fires are frequent. Post-fire, seedling regeneration is dominated by fire specialist, pioneer species. Pioneer species can only generate when there are gaps in the canopy, which allow sunlight to reach the ground, a limiting resource in thick forests (Whitmore 1989; Whitmore and Swaine 1996). The new and abundant pioneer species are often non-native, invasive species that thrive when competition is minimized and sunlight is maximized (Woods 1989). Fire damage is particularly severe and extensive when the forest has recently suffered another disturbance, such as a storm or drought (Woods 1989; Whigham *et al.* 1991), leaving the vegetation to recover from immediate damage, but also to compete with new invasive species.

Weather events can produce significant habitat disturbances as well, and the amount of damage rises with the intensity of the storm. The National Oceanic and Atmospheric Administration (NOAA) uses “tropical storm” as the general term for storm systems that originate in maritime tropical air masses. Tropical storm nomenclature varies based on the geographic location of origin: hurricanes originate in the North Atlantic and Northeast Pacific oceans; typhoon refers to storms formed in the Northwest Pacific; and tropical

cyclones to storms in the Indian Ocean, Australia, and Southwest Pacific. The formation of tropical storms occurs due to a disturbance caused by combination of high sea surface temperatures, rising moisture, convection, and prevailing winds. These storms gain energy as warm water vapor is pulled up and moves over the water but lose energy upon hitting cold water or land. They are carried from their oceanic origin to land by prevailing air currents. Because storms lose strength quickly over land, coastal regions tend to suffer the most damage (“Tropical Cyclone Climatology,” 2013).

Hurricanes form in an area of the Atlantic Ocean called the hurricane belt, which includes the Caribbean Sea and the Gulf of Mexico. They are ranked by intensity on the Saffir-Simpson wind scale, one being the lowest and five being the highest. A level one hurricane is categorized as such when winds are sustained at over 119 kilometres per hour (km/h) and the category of the storm increases to level five hurricane when it has sustained winds of over 252 km/h. In the Atlantic region, which consists of the Atlantic Ocean, Caribbean Sea, and Gulf of Mexico, hurricane season is from June 1st to November 30th with some yearly variation and a peak occurring from late August to the end of September (“Tropical Cyclone Climatology,” 2013).

Depending on their strength, tropical storms can have dramatic effects on forests with the most common damage being defoliation, followed by branch snapping and uprooting of trees (Brokaw and Walker 1991). Storms with high winds cause more damage on windward-facing slopes than those facing to leeward because those areas lack any shelter from the wind and take the brunt of the storm (Brokaw and Walker 1991; Metcalfe *et al.* 2008). Deep valleys, such as those created by karst hills, have more protection than ridge tops or open areas; consequently, a large region can vary in topography over smaller scale areas. Areas

with more dynamic and variable topography may fare better with more patchy damage and some unaffected areas. After a storm, secondary damage is common from falling trees including more de-limbing, crushing of the understory, and reduced canopy cover. This further alters the forest structure and food supply. Fruit trees are particularly vulnerable to storm damage and often abandon fruit and flower production in favour of leaf bud production (Barone 1998; Vandermeer *et al.* 1998). Although usually a latent response, new leaf production, recruitment, and growth increase exponentially after storms (Brokaw and Walker 1991). This boost in foliage production is due to gaps in the canopy and the subsequent increase of sunlight throughout the under story (Fernandez & Fetcher 1991; Burslem *et al.* 2001).

1.1.3. Natural Disturbances and Primates

Natural disturbances, including droughts, fires, and tropical storms, can cause immediate primate mortalities and affect primates through changes in the food supply or forest structure. Important food sources may be scarce in the period of time following a disturbance due to forest damage and slow recovery. Primates utilize various coping mechanisms such as altering diet and behaviour in response to natural disturbances and damaged forests. Although rare, demographic studies on primate populations have provided information on the effectiveness of such responses to disturbances including drought, fire, and tropical storms (Pavelka and Chapman 2006, Ratsimbazafy 2002, O'Brien 2003, Lewis and Rakontondranaivo 2011, Gould *et al.* 1999, and O'Brien *et al.* 2003).

Primates living in seasonal tropical forests normally experience environmental extremes, especially in the dry seasons. Limited resources, high temperatures, and water stress in the dry season has been correlated with changes in primate diet, behaviour, and

grouping patterns. For example, dry seasons in tropical forests have been correlated with limited resource production (Bunker and Carson 2005; Murphy and Lugo 1995; Wright and Cornejo 1990), including a lack of fleshy ripe fruits (Asensio *et al.* 2009; Zimmerman *et al.* 2007), which can result in higher stress levels for primates (Cavigelli 1999). In addition, higher temperatures and lower rainfall levels during dry seasons have been associated with decreases in energetically expensive activities and corresponding increases in time spent resting (Gonzalez-Zamora *et al.* 2011; Korstjens *et al.* 2010). When a dry season extends into a drought, resources continue to become even more limited beyond the dry season. After a two-year long drought in Madagascar, ring tailed lemurs showed an immediate population decrease and high levels of mortality in subsequent seasons. The authors hypothesized that these high mortality rates were due to a lack of food resources and related physiological stress (Gould *et al.* 1999).

Forest fire damage can cause a decrease in primate food supply, including both leaves and fruit (O'Brien *et al.* 2003, Berenstein 1986). A fire in Borneo decreased siamang fruit resources, lower infant and juvenile survival rates which resulted in smaller groups (O'Brien *et al.* 2003). In a study of long-tailed macaques that experienced a fire following a drought, Berenstein (1986) attributed the macaques' lack of any population mortalities to dietary flexibility. The macaques diet switched from preferred fruits, seeds, and flowers to less preferred herbaceous food sources following the disturbances (Berenstein 1986).

The survival prospects of a primate population after a storm or hurricane has been directly related to the change in food availability and in some cases, fruit availability (Schaffner *et al.* 2012; Pavelka and Behie 2003). A decrease in preferred food supply can cause a dietary shift to less preferred foods (Schaffner *et al.* 2012; Tsuji and Takatsuki 2008),

which can include exotic or rare resources (LaFleur and Gould 2009; Ratsimbazafy *et al.* 2002; 2007). As a result of a cyclone, langurs and macaques in Sri Lanka over-browsed and killed off an already limited food source (Dittus 1985). The lack of preferred food sources can cause a nutritional deficit with long term effects on the genetic diversity of a population (Louis *et al.* 2005) or a cessation of births following the storm (Pavelka and Chapman 2006; Vasey and Bergerson 2009). Further studies have linked increased stress from nutrient deficiency to population losses (Behie and Pavelka 2012 a, b). On the other hand, Lewis and Rakotondranaivo (2001) found that a group of folivorous lemurs were largely unaffected by the effects of a storm in both body condition and reproduction. The authors proposed this was because lemurs already regularly experience extreme dry seasons and are well adapted to deal with periods of limited resources and environmental stress.

Many primate populations affected by tropical storms have responded by changing activity and grouping patterns. Following a disturbance, some species limit energetically expensive activities, such as travelling and social behaviours, and spend more time resting (Pavelka *et al.* 2003; Tsuji and Takatsuki 2008; Ratsimbazafy *et al.* 2002; Schaffner *et al.* 2012). Reducing group size or solitary ranging may be a method to decrease feeding competition in a storm-damaged forest. For example, Dittus (1988) associated the permanent fission of macaque groups to changes in food availability caused by cyclone damage. Due to a major population loss after a major hurricane, howler monkeys in Belize were found in smaller groups, including unimale groups and solitary individuals (Pavelka *et al.* 2007). After a cyclone caused a decrease in ripe fruit, black and white ruffed lemurs were found foraging alone more often (Ratsimbazafy *et al.* 2002). Following two hurricanes in Mexico, a group of spider monkeys coped with increased feeding competition by forming smaller

subgroups with fewer changes in subgroup composition throughout the day (Schaffner *et al.* 2012).

1.1.4. Spider monkeys

Spider monkeys are large-bodied and highly frugivorous, their diet consisting of 55% to 90% fruit (Di Fiore *et al.* 2008). They specialize in fleshy, ripe fruits but they will also consume other plant parts, including leaves, flowers, and seeds (DiFiore *et al.* 2008; Kinzey 1997). Although a portion of their diet can include leaves, their digestive systems may not cope well with long periods of intensive folivory (Milton 1981). Ripe fruits are a seasonal resource located in patches that can be far apart, resulting in large home range requirements, significant daily travel costs (Ramos-Fernandez and Ayala-Orozoco 2003), and established arboreal travel routes (DiFiore and Suarez 2007).

Spider monkeys live in large mutli-male/multi-female groups that are characterized by male philopatry and female dispersal (Symington 1987; 1990; DiFiore *et al.* 2009). They are one of the least cohesive social primates, in which the larger group of related males and non-related females travel and forage in smaller subgroups that vary in size, composition, and tenure (Aureli *et al.* 2008). The entire group is rarely seen all together, although individuals form larger subgroups at night (Chapman 1989) and adjust group size to food availability (Asensio *et al.* 2009; Chapman 1990; Chapman *et al.* 1995; Shimooka 2003). Fissioning and fusing throughout the day into temporary smaller subgroups may reduce intragroup feeding competition on a high-quality food source that is patchily distributed in space and time (Klein and Klein 1997; Wrangham 1980; Symington 1990; Chapman *et al.* 1995).

Long-term studies describe spider monkeys as ranging in sexually segregated groups (Fedigan and Baxter 1984; Klein and Klein 1977; Symington 1987; Chapman 1988). Recently, a study at Runaway Creek Nature Reserve (RCNR) applied a sex segregation statistic used for other animal species and confirmed that spider monkeys are sex segregated (Hartwell 2010). Adult males are usually more gregarious than females, forming closer bonds and showing cooperative behaviour (Fedigan and Baxter 1984; Symington 1988). Females are less bonded, have weak patterns of association and no clear dominance hierarchy (Chapman 1990; Symington 1990; Ramos-Fernandez *et al.* 2009). Similar to male chimpanzees, spider monkey males patrol territory borders apparently to defend access to females and food resources (Shimooka 2003; Aureli *et al.* 2008; Link *et al.* 2009). On average, males form larger subgroups than females (Shimooka 2005; Wallace 2008) and tend to travel farther and faster throughout their range (Chapman 1990).

Males and female spider monkeys vary in their agonistic behaviour. Agonism has been associated with subgroup fusions, occurring shortly after two subgroups come together (Aureli and Schaffner 2007). Males may direct aggression towards females within the same group with non-contact chases, displacements, or non-contact physical aggression (Slater *et al.* 2009). Female directed aggression (FDA) can occur in a feeding context (Van Roosmalen and Klein 1988) but is believed to be a form of either sexual coercion (Campbell 2003) or indirect sexual coercion via social control (Link *et al.* 2009). Intrasexual aggression, especially between males, is rare (Van Roosmalen and Klein 1998; Fedigan and Baxter 1984; Slater *et al.* 2009). Lethal intragroup aggression between males has been observed in a small number of cases and is attributed to unusual demographic circumstances (Campbell 2006; Valero 2006). Males more commonly cooperate in territorial defenses that can lead to high-

intensity intergroup encounters (Aureli et al 2006). Female-female aggression, when it does occur, usually takes place in a feeding context and involves long-term resident female(s) attacking a younger or newly immigrated female (Symington 1987; Van Roosmalen and Klein 1988; Asensio *et al.* 2008; Slater *et al.* 2009).

Spider monkeys are particularly interesting for studying the effects of a natural disturbance because although they are commonly considered a sensitive species, they display high levels of fission-fusion dynamics and grouping flexibility in response to varying resources. They may be able to compensate for a decrease in fruit availability, changes in forest canopy, or associated stress by altering grouping patterns. Although spider monkeys may respond to habitat disturbances by altering grouping patterns, it may be difficult to distinguish grouping responses to a disturbance in species with higher levels of fission fusion dynamics from normal fluctuations in subgroup size, density, and composition. In this study, I analyzed not only short term changes before and after a hurricane and fire but long term changes to control for normal seasonal variation.

CHAPTER TWO: METHODS

2.2.1. Study Site

Runaway Creek Nature Reserve (RCNR) is a 2,469 ha private reserve in central Belize (88°35' W and 17°22'N), owned by the Foundation for Wildlife Conservation, under the management of the local NGO Birds Without Borders (*Aves Sin Fronteras*). RCNR is comprised of two main vegetative zones: pine savannah and low broadleaf tropical forest. The forest landscape is dominated by limestone karst hills, some over 100 meters high. The average slope of the hills ranges from 15 to 50 degrees with some vertical cliff faces. Sections of the savanna and valleys between the hills flood during the rainy season creating swamp conditions. RCNR is part of a larger continuous forest and the Central Belize Biological Corridor, connecting the Manatee Forest Reserve to the Rio Bravo. Forested wildlife corridors are important because many birds and mammals are less inclined to travel through open spaces, where they are much more vulnerable (Arroyo-Rodriguez and Mandujano 2009). Biological corridors are also important for maintaining long-term conservation of biodiversity (Miller *et al.* 2001).

This area of Belize has a dry season from January to May and a wet, hurricane season from June to December. RCNR receives an estimated 2,000-2,200 mm of rain annually (Meerman 1999). Most rainfall in Belize comes from tropical systems or from “northers”, cold air systems from North America. Figure 2 shows the average precipitation and temperatures by each month from a weather station approximately 50 kilometers from the field site. Central Belize was hit by unnamed hurricanes in 1921, 1934, and Hurricane Hattie in 1961 (Meerman 1999).

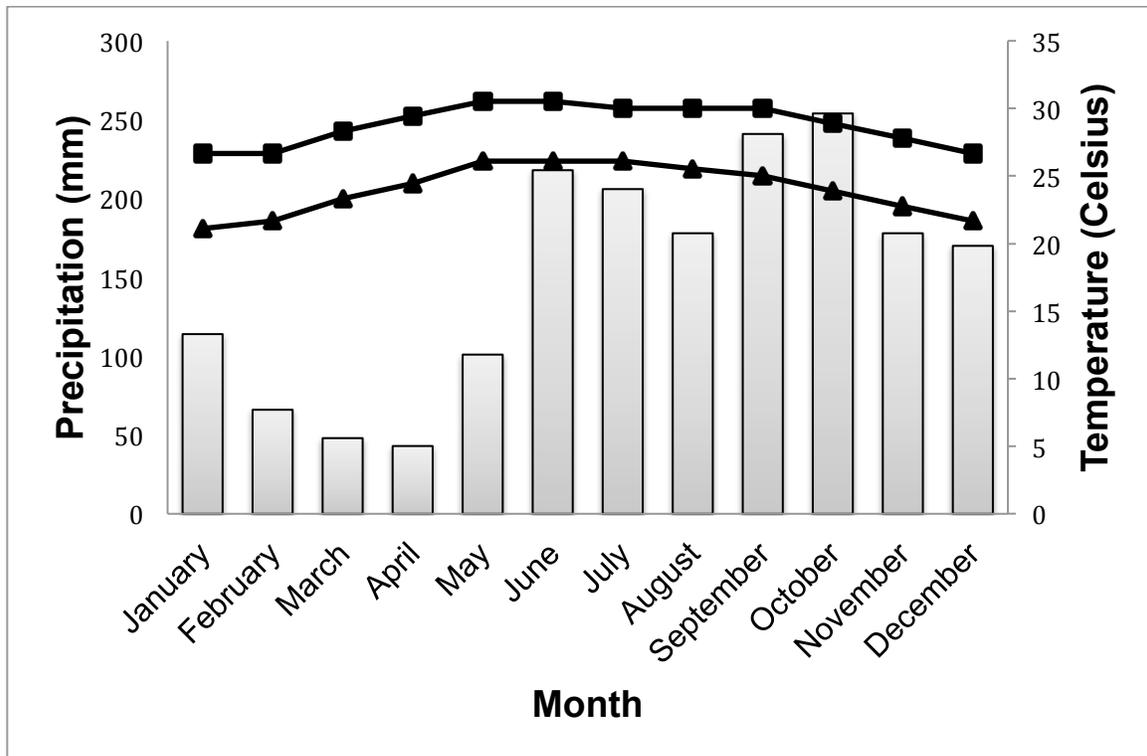


Fig. 2: Monthly average precipitation, and minimum and maximum temperatures near Runaway Creek, Belize. Data taken from the Philip S.W. Goldson International Airport weather station. Data compiled from 1994 to 2010 and retrieved from Weather Underground (wunderground.com).

2.2.2 Study Group

The black-handed spider monkey (*Ateles geoffroyi*) ranges throughout Central America and western South America down to Ecuador (Rylands *et al.* 1997). *Ateles geoffroyi* is also commonly referred to as the Central American spider monkey, one of four *Ateles* species and numerous subspecies (Collins and Dubach 2000; Nieves *et al.* 2005). The Yucatan spider monkey (*Ateles geoffroyi yucatanensis*) is found in the Yucatan Peninsula of southern Mexico, northeastern Guatemala, and throughout Belize (Kellogg and Goldman 1944). The Yucatan spider monkey has been studied at Tikal National Park in Guatemala (Coelho *et al.* 1976; Baxter 1979; Fedigan and Baxter 1984; Estrada *et al.* 2004), Punta

Laguna National Reserve in Mexico (Ramos-Fernandez 2001; Aureli *et al.* 2006; Valero *et al.* 2006; Slater *et al.* 2009; Chaves *et al.* 2011a,b; Schaffner *et al.* 2012) and at Runaway Creek Nature Reserve in Belize. In Belize, large populations of spider monkeys are sighted in the Maya Mountains of the Bladen Nature Reserve in the south and in the Rio Bravo Conservation Area in Orange Walk to the north (Waters and Ulloa 2007; Hartwell 2010).

The University of Calgary study focuses on two spider monkey groups at RCNR. The majority of the pre-hurricane data collection has been on the primary study group (F-group) in a home range of approximately 134 ha. Throughout the period of data collection, the study group consisted of 31-37 individuals (Table 1). Over the course of the study, group composition changed due to births, disappearances, immigrations, emigrations, and deaths. Individuals are recognized by differences in pelage colour, facial markings, or skin pigmentation of the anogenital region.

Table 1. Runaway Creek Nature Reserve 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 (2008-2012).

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
2010	5	13	2	2	2	6	4	3	37
2011	5	13	2	2	5	6	2	1	36
August 2012	7	11	1	2	3	5	5	0	35

2.2.3 Behavioural Data Collection

Spider monkey research has been on going at RCNR since February 2008. For this study, I used behavioural data gathered from January 2009 to August 2012. I arrived in Belize on October 25, 2010, the day after Hurricane Richard, to work as a research assistant. I contributed to the collection of immediate post-hurricane data from October 2010 to January 2011 and returned to gather more data in 2011 and 2012. My analysis is based on 22 months pre-hurricane and 22 months post-hurricane data. Data collection protocol has been standardized since the beginning of the study, so pre- and post- hurricane data are directly comparable.

Data collection procedures for this project allowed for measurement of all of the variables in this study. Five days per week, members of the research team conducted full or part day follows on spider monkey subgroups. A subgroup was defined using a chain rule (Ramos-Fernandez 2005), in which all individuals that associated together while maintaining a distance no greater than 50 meters from another monkey are included in the subgroup. A subgroup fission was recorded when an individual moved further than 50 meters from another and a fusion was recorded when an individual moved within 50 meters of another subgroup member. Daily follows began either at dawn when the monkeys were still at their sleeping sites or at midday and continued until dusk when the monkeys bed down for the night. We accessed different areas of the range to find different subgroups and individuals.

When we encountered a subgroup, we conducted a subgroup that scan included: time, location (in UTM's using GPS), subgroup size and composition, group spread, identity of recognizable individuals (age/sex class for those we cannot identify), and the activity of each individual (feeding, resting, traveling, social, other). If an individual was feeding, we

recorded the plant species and plant part. If the plant species was unknown, we tagged the tree or plant for later identification with the assistance of local vegetation experts. If the behaviour was social, we recorded the specific behaviour (groom, embrace, sit in body contact, play, etc.) and the identity of the other individual. See ethogram in Appendix 2 for all behaviours recorded. Scans were repeated every 30 minutes as long as we were able to maintain contact with the subgroup. The scan samples provided data on activity, diet, subgroup size and spatial cohesion.

When we located a subgroup that included individuals on which we had abundant data, we would leave to find a less familiar subgroup: otherwise, we would stay with the subgroup all day or until we could no longer follow them. Maintaining visual contact with a subgroup can be difficult due to the presence of steep cliffs and ridges at RCNR combined with the spider monkeys' rapid travel speed. When a subgroup follow ended, we recorded the time, location, and whether we lost or left them. In the event of a subgroup fission, we stayed with the group containing individuals on which we had less data.

We described all observed occurrences of agonistic interactions and any other rare or unusual events. While following a subgroup, we recorded all fission-fusion events, noting the individual(s) arriving or leaving. Throughout data collection, we worked in a team of at least two researchers. One researcher was the primary observer and dictated behavioural data to the other researcher who assisted in observation and recording of the data.

2.2.4 Analysis

From the scan data, I calculated individual activity budgets, diet, subgroup size, and subgroup spatial cohesion. Activity budget was calculated as the proportion of scans in each

category (feeding, travel, inactive, or social) divided by the total number of scans. Diet was calculated as the proportion of feeding scans spent foraging on each plant part (ripe fruit, unripe fruit, leaves, or flowers) divided by the total number of feeding scans. Daily subgroup size was calculated as the mean number of individuals, excluding dependent infants, present in all scans for every day. Subgroup spatial cohesion was calculated as the mean subgroup size, divided by the mean subgroup area, in square meters, for that day. Subgroup area was calculated using the distance, in meters, of the two outermost individuals in the subgroup as the group spread measurement, which was used as the diameter for the group area.

Using 'all observed occurrence' data I calculated subgroup fluidity and rate of aggression. Subgroup fluidity was defined as the number of fission and fusion events divided by total contact time for each day. Rate of aggression was calculated as the total number of agonistic events (open mouth threats, lunges, charges, inter- and intra-sexual aggression events, displacements, and avoidances) divided by the total contact time for each day.

I used different statistical tests for the three approaches:

1. 8-week and 22-month comparison

I used paired t-tests to compare the activity and diet of individual monkeys 8 weeks before and 8 weeks after Hurricane Richard. For subgroup size, cohesion, fluidity, and aggression I used independent t-tests using daily averages as the unit of analysis. For the 22-month before and after comparison I used an ANOVA to test if the variance of means were greater between the two time periods than within them. For this, monthly averages

were used as the unit of analysis. Given the high level of fission-fusion dynamics, we did not see some group members for extended periods of time. In addition, there were several births, deaths, and changes in age classes throughout the course of the study. Therefore, the sample size is not consistent across the statistical analyses. In cases where sample sizes were not equal, I used Levene's tests to confirm homogeneity of variances. When the ANOVA data violated the assumption of the homogeneity of variance, I used a Welch's ANOVA. When ANOVA data violated the assumption of sphericity, I applied the Huynh-Feldtor or Greenhouse-Geisser correction.

2. Hurricane, fire, and in-between

I compared activity, diet and grouping patterns for six months before Hurricane Richard (time period 1), six months in-between the storm and fire (time period 2), and six months after the peak of the fire (time period 3). I compared the activity and diet of individual monkeys in the three time periods. For subgroup size, cohesion, fluidity, and aggression rates I used daily averages as the unit of analysis. ANOVA tests were used to determine if the variance of means were significantly greater between the three time periods than within them. I performed repeated measures ANOVA tests to compare the activity and diet of individual monkeys activity budget and diet comparisons. I used one-way ANOVA tests for three variables of subgroups: size, spatial cohesion, and fluidity. Finally, because data violated the assumption of homogeneity, I used Welch's ANOVA tests on aggression rates. Sample size was not consistent across the statistical analyses due to changes in population demography and the nature of spider monkey grouping patterns. When the data violated the assumption of sphericity, I applied the Huynh-

Feldtor or Greenhouse-Geisser correction. For all tests, I accepted a p value of 0.05 as significant.

3. Rainy and dry seasons before and after

I compared of activity, diet and grouping patterns for both the rainy seasons and dry seasons before and after the hurricane and fire. The rainy seasons analyzed were June to December of 2009 and 2011. Hurricane Richard occurred between these time periods, in the rainy season of 2010. The rainy season of 2011 brought the precipitation that extinguished the forest fire. The dry seasons analyzed were January to May of 2010 and 2012, and the forest fire occurred between these two, during the dry season of 2011. See Appendix 1 for a timeline including the hurricane, fire, and seasons. I used t-tests in each comparison and with the individual monkey as the unit of analysis. I used paired t-tests to compare the activity and diet of individual monkeys in the seasons before and after Hurricane Richard. For subgroup size, cohesion, fluidity, and aggression I used independent t-tests with daily averages as the unit of analysis. Given the high level of fission-fusion dynamics, we did not see some group members for extended periods of time. In addition, there were several births, deaths, and changes in age classes throughout the course of the study. Sample size is not consistent across the statistical analyses due to highly fluid subgroups and changes in the overall group composition over the study period. In cases where sample sizes were not equal, I used Levene's tests to confirm homogeneity of variances.

CHAPTER THREE: RESULTS

3.1. Review of hurricane and fire

Hurricane Richard hit Runaway Creek Nature Reserve (RCNR), located approximately 30 kilometers from the coast in Central Belize, on October 25, 2010, causing damage to the forest structure and resources. Immediately following the storm, researcher access to the study site was compromised due to downed trees and obstructed trails. The spider monkey research team made a concerted effort to open trails up in the days following the storm and resume behavioural data collection as soon as possible. One consequence of the hurricane was increased deadfall on the forest floor and therefore more flammable conditions in the dry season that followed the hurricane season of 2010. Accordingly, a fire that began in the pine savannah bordering the hills of the forest spread throughout the study site. The fire started in April 2011, peaked in early May, and continued to burn for nearly two months.

3.2. 8-week and 22-month comparison results

3.2.1. 8-week comparison

In the 8 weeks after the hurricane there was a significant increase in the proportion of time spent feeding (Fig. 3; paired t-test: $t=-2.134$, $df=20$; $p=0.031$) and a significant decrease in the proportion of time spent travelling (Fig. 3; paired t-test: $t=2.264$, $df=20$; $p=0.035$).

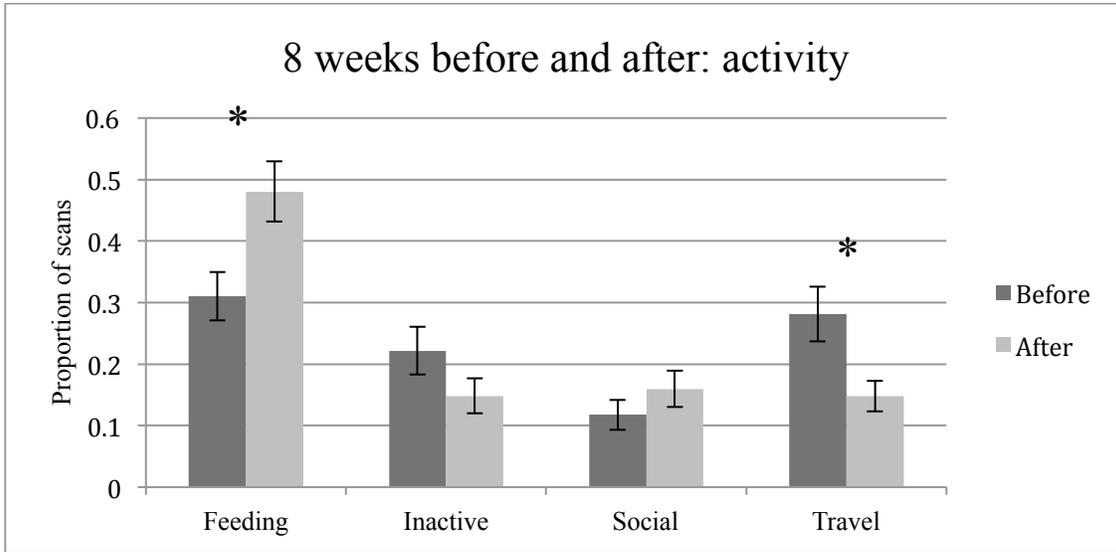


Fig. 3 Mean (\pm SE) proportions of scans in different activities 8 weeks before and after Hurricane Richard (paired *t*-tests). * $p < 0.05$.

In terms of diet (Fig. 4), there was a post-hurricane increase in feeding on leaves (paired *t*-test: $t = -3.435$; $df = 28$; $p = 0.002$) and unripe fruit (paired *t*-test: $t = -5.709$; $df = 28$ $p < 0.0005$), and consumption of ripe fruit decreased (paired *t*-test: $t = 12.510$; $df = 28$; $p < 0.0005$).

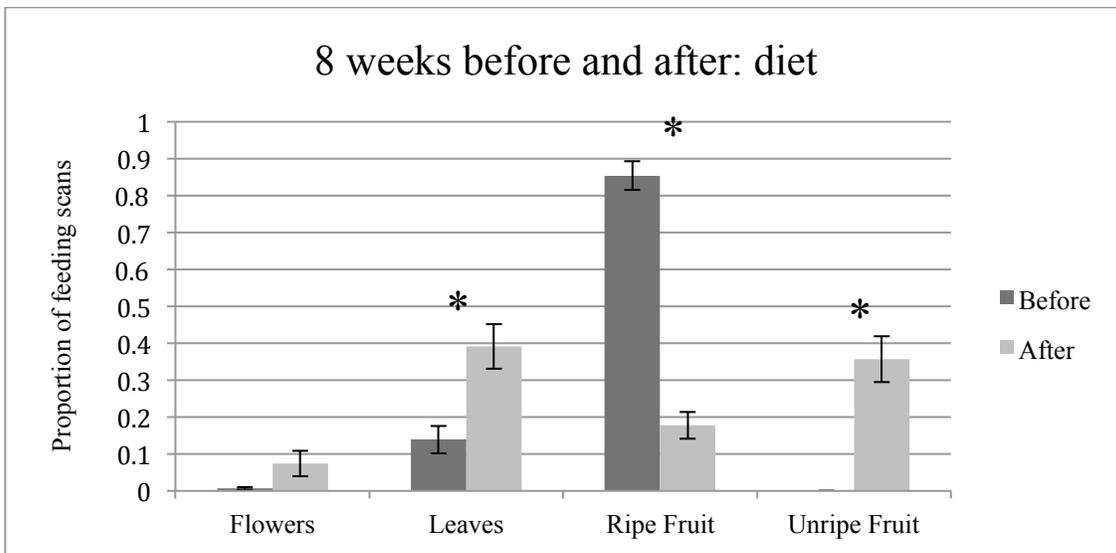


Fig. 4 Mean (\pm SE) proportions of feeding scans for different food types 8 weeks before and after Hurricane Richard (paired *t*-tests). * $p < 0.05$.

Subgroup size did not vary pre and post hurricane (Fig. 5a) nor did daily subgroup density (spatial cohesion) (Fig. 5b) in the 8 weeks after the storm compared with 8 weeks before.

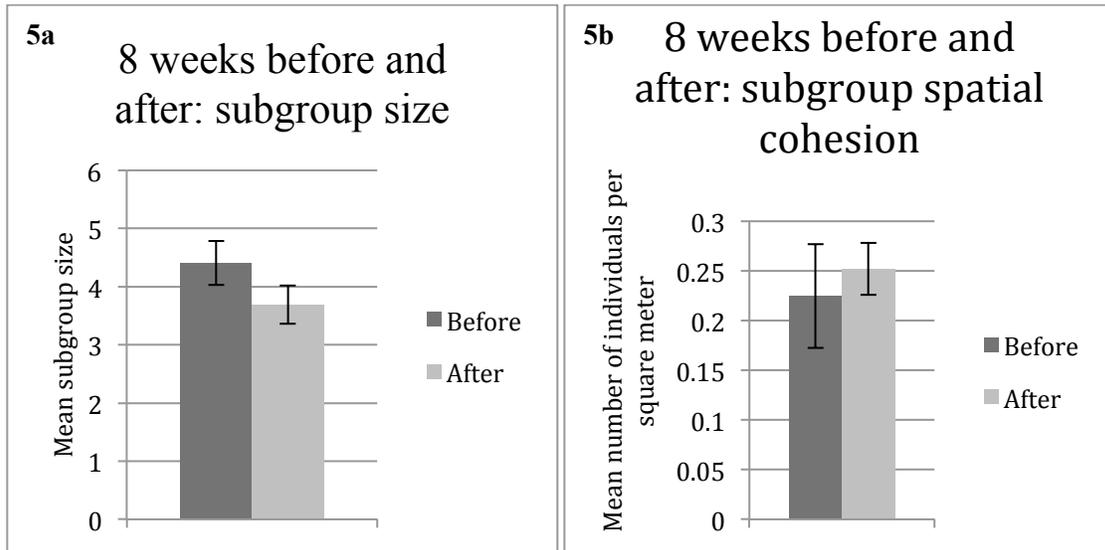


Fig. 5a Mean (\pm SE) daily subgroup size compared 8 weeks before and after Hurricane Richard (independent t -test). **Fig. 5b** Mean (\pm SE) number of individuals per square meter of subgroup area compared 8 weeks before and after Hurricane Richard (independent t -test).

The 8-week comparison of fission and fusion rates indicated that subgroup fluidity was significantly lower after the storm (Fig. 6a; independent t -test: $t=3.566$; $df=51$; $p=0.001$). Subgroups were more stable, with fewer changes in membership, consistent with travelling less and eating a uniformly distributed food. No aggression events were recorded by the research team in the 8 weeks after Hurricane Richard. The rate of aggression was significantly lower post hurricane (Fig. 6b; independent t -test: $t=2.205$; $df=22.000$; $p=0.038$).

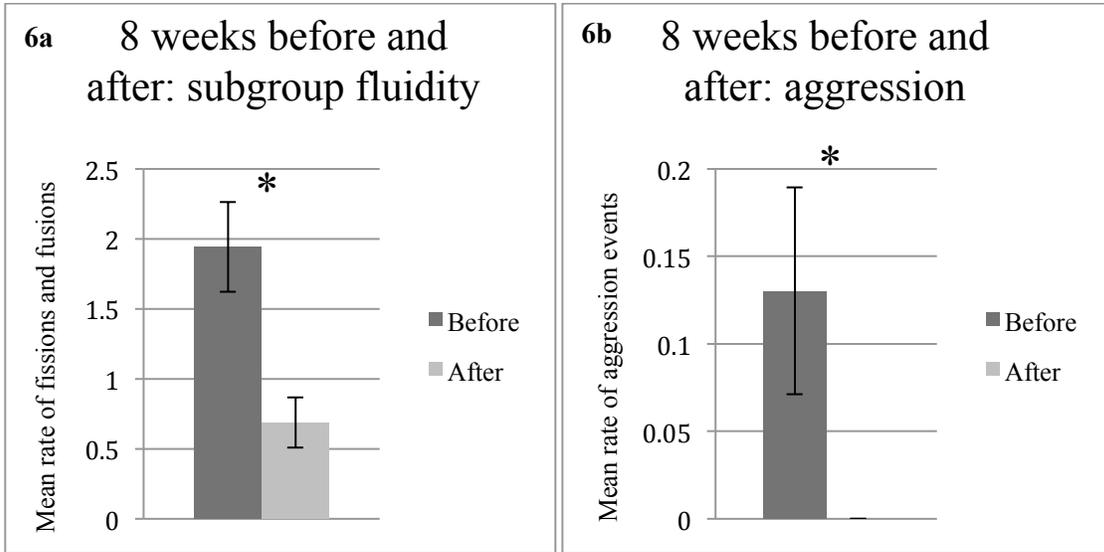


Fig. 6a Mean (\pm SE) rate of fission and fusion events per hour of contact time compared 8-weeks before and after Hurricane Richard (independent *t*-test). * $p < 0.05$. **Fig. 6b** Mean (\pm SE) rate of aggression per hour of contact time compared 8-weeks before and after Hurricane Richard (independent *t*-test).

2.3.2. 22-month comparison

Time spent feeding was significantly lower in the 22 months post hurricane (one-way ANOVA: $F=4.933$, $df=43$, $p=0.032$).

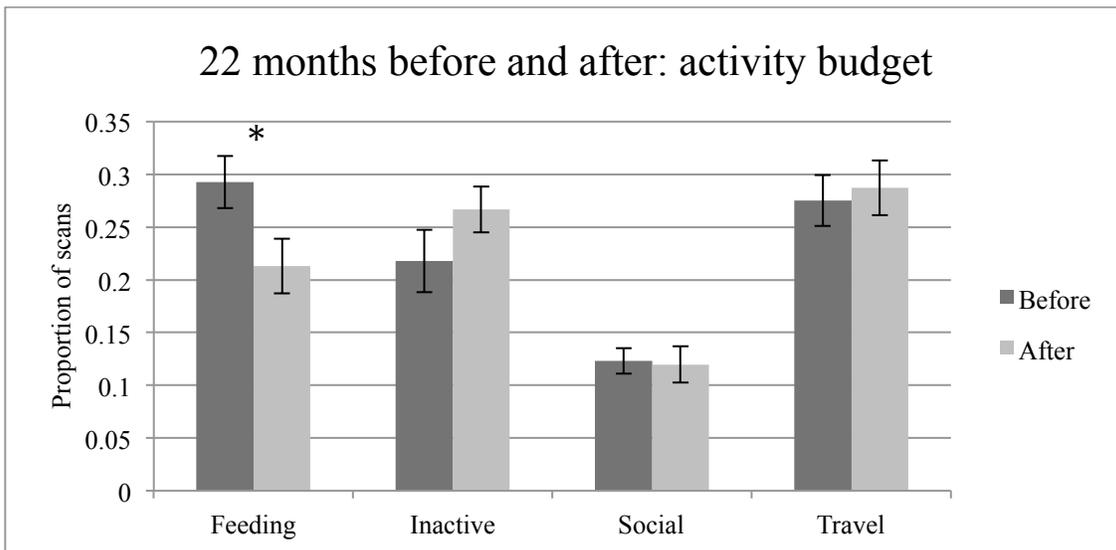


Fig. 7 Mean (\pm SE) proportions of scans in different activities 22 months before and after Hurricane Richard (one way ANOVA). * p <0.05.

The changes in diet revealed in the short term comparison were also found in the 22 month comparison (Fig. 8). Time spent feeding on leaves and unripe fruit was significantly higher 22 months after the hurricane than before (leaves: one-way ANOVA: $F=19.521$, $df=43$, $p<0.0005$; unripe fruit: Welch's ANOVA: $F(1, 23.624)=9.453$, $p=0.005$) There was a corresponding decrease in the consumption of ripe fruit in the 22 months post-storm when compared to 22 months pre-storm (one-way ANOVA: $F=19.768$, $df=43$, $p<0.0005$).

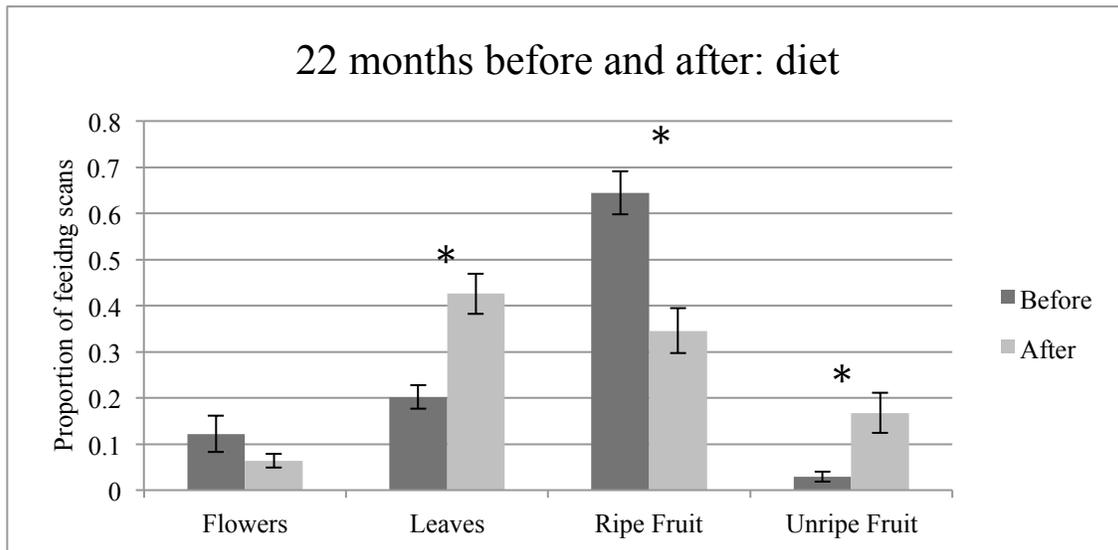


Fig. 8 Mean (\pm SE) proportions of feeding scans for different food types 22 months before and after Hurricane Richard (one way and Welch's ANOVA). * p <0.05.

There was no significant difference in average subgroup size in the 22 months pre and post hurricane (Fig. 9a). Subgroup density (spatial cohesion) significantly increased after the hurricane (Fig. 9b; Welch's ANOVA: $F(1, 34.623)=6.083$, $p=0.019$).

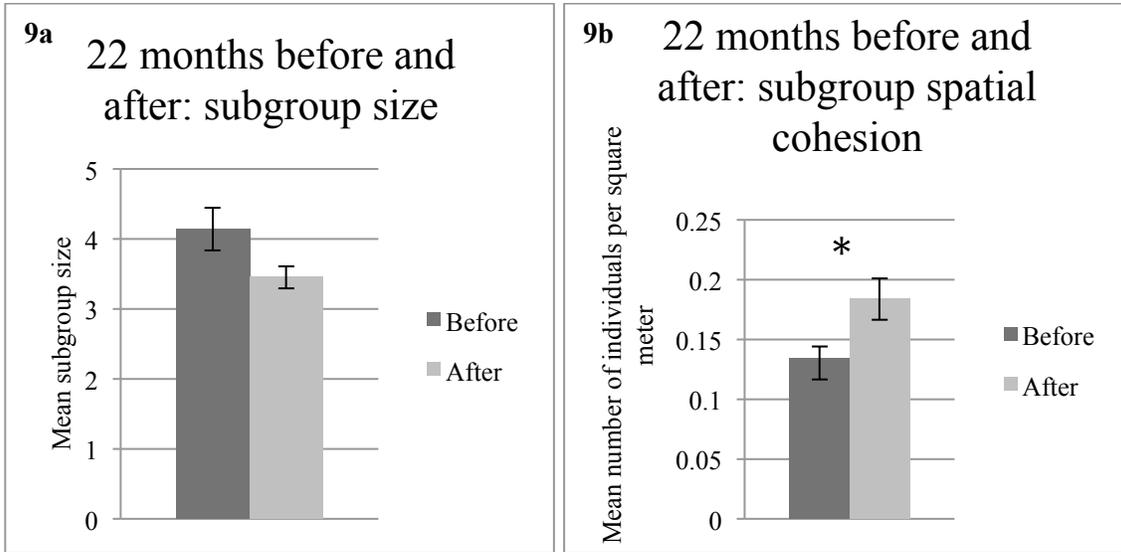


Fig. 9a Mean (\pm SE) subgroup size compared 22 months before and after Hurricane Richard (Welch's ANOVA). **Fig. 9b** Mean (\pm SE) number of individuals per square meter of subgroup area compared 22 months before and after Hurricane Richard (Welch's ANOVA). * p <0.05.

Subgroup fluidity did not differ pre and post hurricane (Fig. 10a). Hourly rates of aggression bouts were lower in the 22 months after Hurricane Richard than the 22 months leading up to the disturbance (Fig. 10b; one-way ANOVA: $F=10.044$ $df=44$, $p=0.003$).

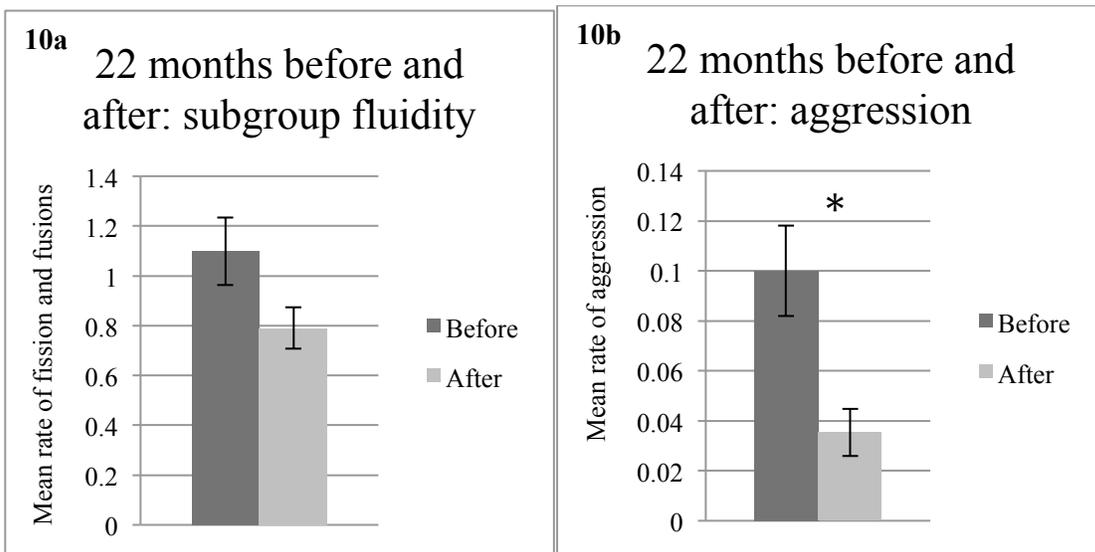


Fig. 10a Mean (\pm SE) rate of fission and fusion events per hour of contact time compared 22 months before and after Hurricane Richard (Welch's ANOVA). **Fig. 10b** Mean (\pm SE) rate of aggression per hour of contact time compared 22 weeks before and after Hurricane Richard (one-way ANOVA). * p =0.05.

3.3 Hurricane, fire and in-between results

The analysis of the 6-month time periods 1, 2, and 3 showed significant changes in activity budgets between each period (Fig. 11). Feeding significantly increased in time period 2 compared to period 1 (repeated measures ANOVA: $F(2, 44)=11.661, p=0.014$) but decreased after the fire (repeated measures ANOVA: $F(2, 44)=11.661, p=0.001$). The proportion of time spent inactive significantly increased from both periods 1 and 2 to the 6 months after the fire (period 3) (repeated measures ANOVA: $F(2, 44)=23.816, p<0.0005$).

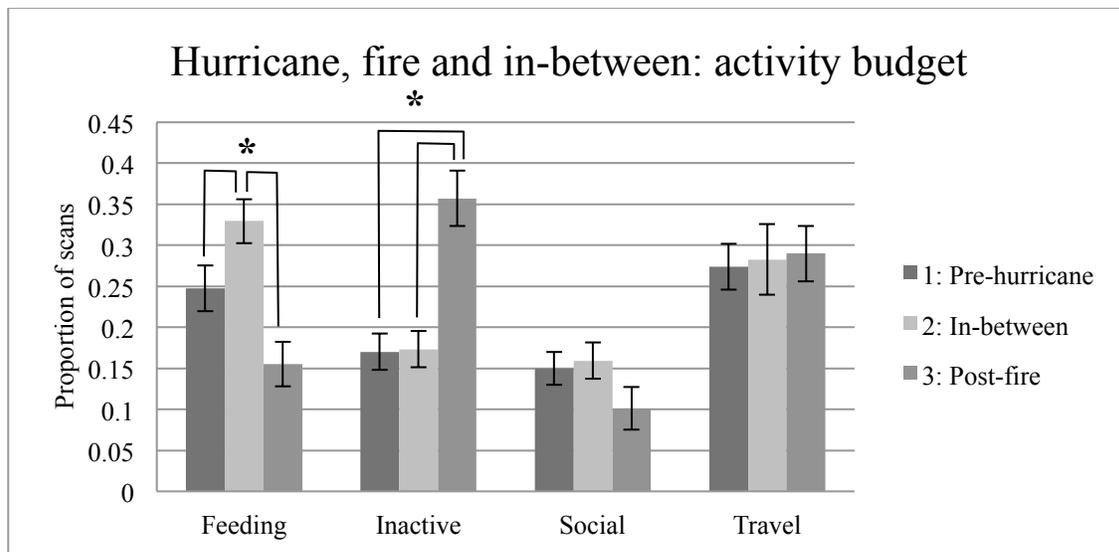


Fig. 11 Mean (\pm SE) proportion of scans in different activities 6 months before Hurricane Richard, in-between the hurricane and fire, and 6 months after the fire (ANOVA with repeated measures). * $p<0.05$.

Across the 18 months of the study that included the hurricane and fire, leaf consumption gradually increased (Fig. 12). It increased significantly from period 1 (pre-hurricane) and period 2 (in between) (repeated measures ANOVA: $F(2, 58)=13.763, p=0.001$) as well as from period 2 (in between) and period 3 (post-fire) (repeated measures

ANOVA: $F(2, 58)=13.763, p<0.0005$). Ripe fruit consumption decreased after the hurricane but recovered somewhat after the fire, although not to nearly as high as pre-hurricane levels. The analysis shows that the monkeys ripe fruit consumption decreased from time period 1 to 2 (repeated measures ANOVA: $F(2,58)=49.129, p<0.0005$) as well as in from time period 1 to 3 (repeated measures ANOVA: $F(2,58)=49.129, p<0.0005$). The consumption of unripe fruit increased after the hurricane (period 2) and fell back after the fire (period 3). When I compared the consumption of unripe fruit across periods, there were significant differences in all three comparisons (repeated measures ANOVA with Huynh-Feldt correction: $F(1.748, 50.705)= 21.654; p<0.0005$). Post hoc tests revealed a significant increase from time period 1 to period 2 ($p<0.0005$), a decrease from period 2 to period 3 ($p=0.006$), and a significant increase comparing period 1 and period 3 ($p=0.008$). Flower consumption was significant in the overall comparison (repeated measures ANOVA with Greenhouse-Geisser correction: $F(1.184, 34.347)= 4.898, p=0.028$) but there were no specific differences in the Bonferroni post hoc test between any of the time periods.

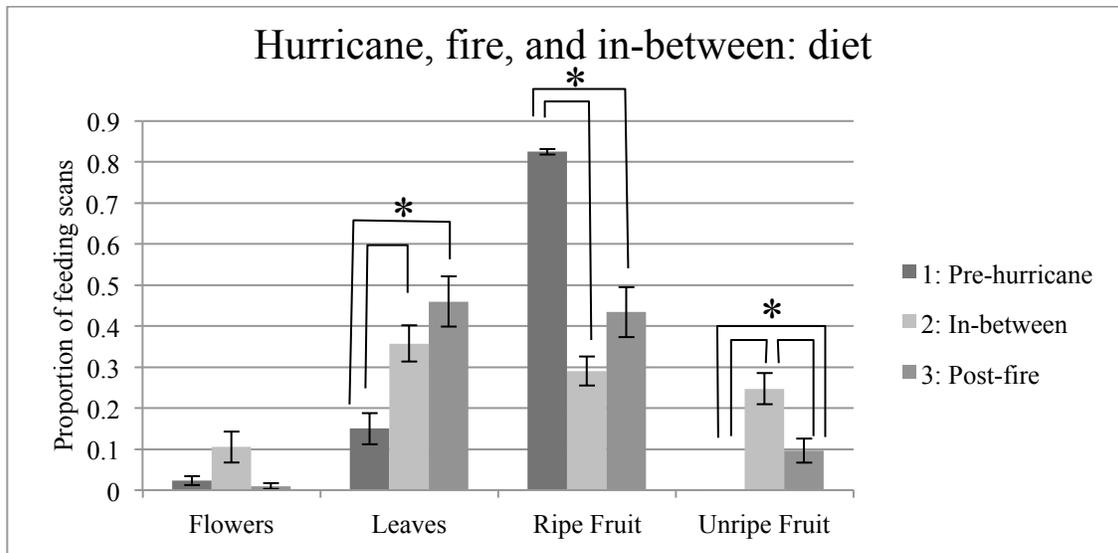


Fig. 12 Mean (\pm SE) proportion of feeding scans for different food types 6 months before Hurricane Richard, in-between the hurricane and fire, and 6 months after the fire (ANOVA with repeated measures). * $p < 0.05$.

The only difference found when comparing average daily subgroup size was that groups were significantly smaller in the period between the two events (period 2) when compared to period 1 (Fig. 13a: one-way ANOVA with Bonferroni post-hoc test: $F(2, 190) = 6.793, p = 0.001$). Subgroup spatial cohesion was higher in the six months between the hurricane and fire (one-way ANOVA: $F(2, 191) = 10.030, p < 0.0005$). Specifically, average subgroup density per day was higher in time period 2 than in period 1 (Bonferroni post-hoc test: $p = 0.003$) and period 3 (Bonferroni post-hoc test: $p < 0.0005$). These grouping pattern results revealed that after the storm, subgroups were smaller and more cohesive but after the fire they returned to larger groups that were less cohesive.

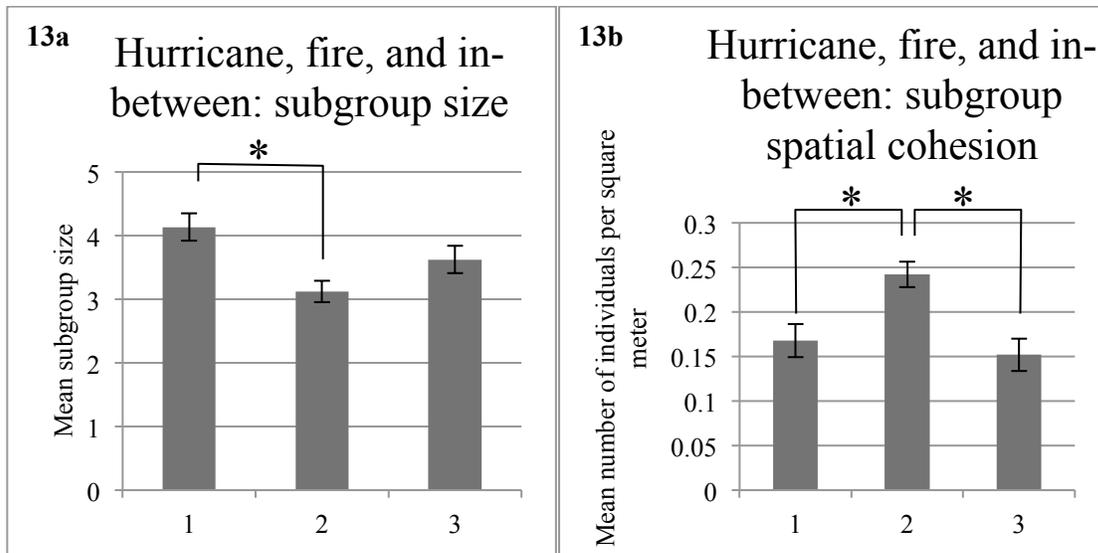


Fig. 13a Mean (\pm SE) daily subgroup size 6 months before Hurricane Richard, 6 months in-between the hurricane and fire, and 6 months after the fire (one-way ANOVA). * $p < 0.05$. **Fig. 13b** Mean (\pm SE) number of individuals per square meter of subgroup area 6 months before Hurricane Richard, 6 months in-between the hurricane and fire, and 6 months after the fire (one-way ANOVA).

Rates of fissions and fusions decreased in period 2 from levels in period 1 (Welch's ANOVA: $F(2, 121.111) = 7.038$, $p = 0.001$). For the hurricane and fire comparisons, the rate of aggression decreased in each period from the pre-hurricane period to the six months in-between (Welch's ANOVA: $F(2, 118.890) = 5.584$, $p = 0.001$). Aggression continued to decrease after the hurricane and fire.

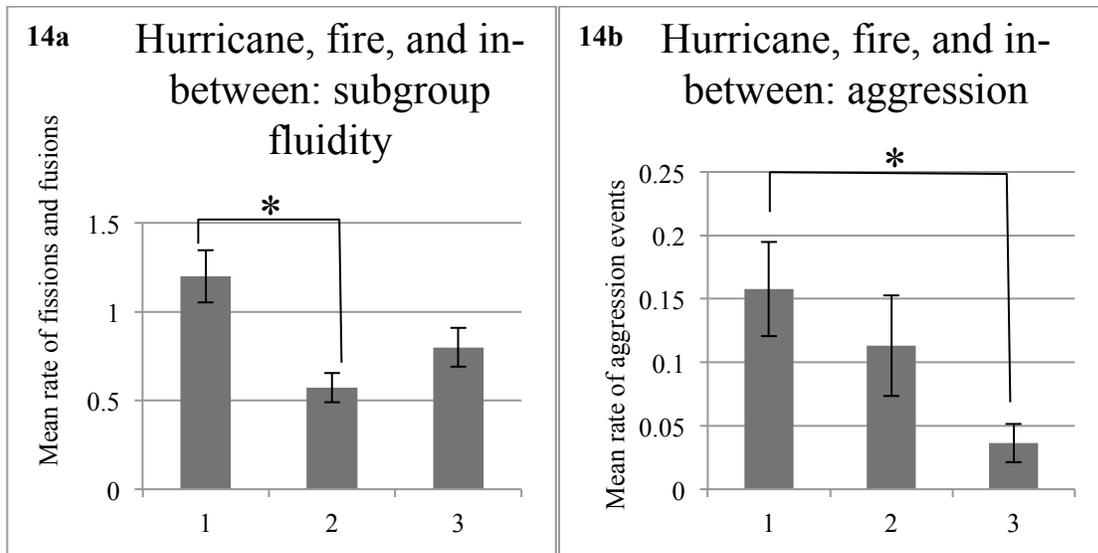


Fig. 14a Mean (\pm SE) rate of fission and fusion events per contact hour 6 months before Hurricane Richard, 6 months in-between the hurricane and fire, and 6 months after the fire (one way ANOVA). **Fig. 14b** Mean (\pm SE) rate of aggression per hour of contact time 6 months before Hurricane Richard, 6 months in-between the hurricane and fire, and 6 months after the fire (Welch's ANOVA). * $p < 0.05$.

3.4. Rainy and dry seasons before and after results

3.4.1. Rainy season comparison

The rainy season comparison revealed that activity budgets showed no significant differences between the rainy seasons of 2009 and 2011 (Fig. 15).

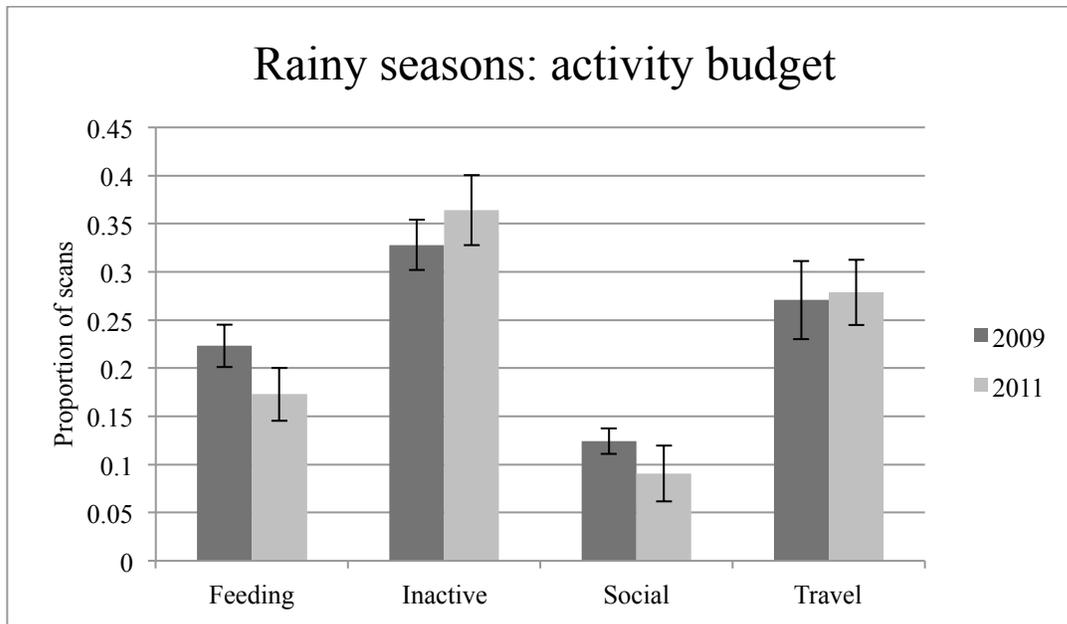


Fig. 15 Mean (\pm SE) proportions of scans in different activities between the rainy seasons before (2009) and after (2011) Hurricane Richard and the subsequent fire (paired t -tests).

The comparison of feeding scans (Fig. 16) revealed an increase in the proportion of leaves (paired t -test: $t=-3.550$; $df=27$; $p=0.001$) and unripe fruit (paired t -test: $t=-2.468$; $df=27$; $p=0.020$) in the post hurricane and fire rainy season. Ripe fruit consumption decreased when comparing the rainy seasons of 2009 and 2011 (paired t -test: $t=4.679$; $df=27$; $p<0.0005$).

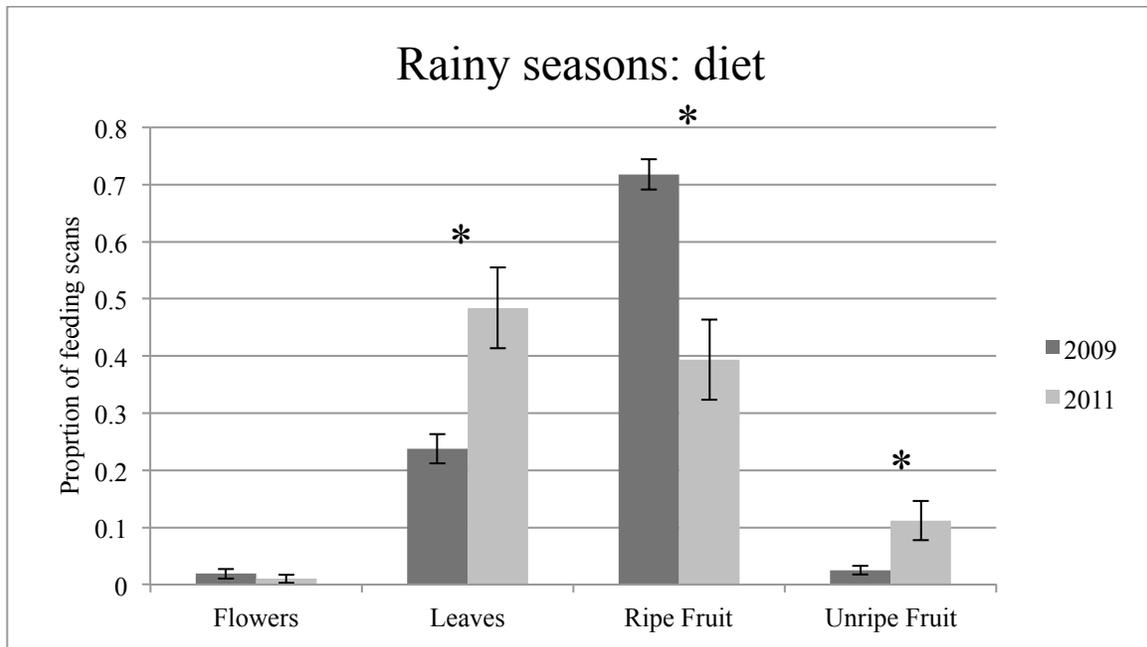


Fig. 16 Mean (\pm SE) proportions of feeding scans for different food types between the rainy seasons before (2009) and after (2011) Hurricane Richard (paired t -tests). * $p < 0.05$.

Mean subgroup size was significantly smaller (Fig. 17a: independent t -test: $t=5.639$; $df=127.967$; $p < 0.0005$) and more spatially cohesive (Fig. 17b: independent t -test: $t=-2.902$; $df=56.624$; $p=0.005$) in the rainy season of 2011 when compared with the rainy season of 2009. In other words, after the disturbances, number of individuals found in a subgroup was smaller and the subgroups were more spatially cohesive.

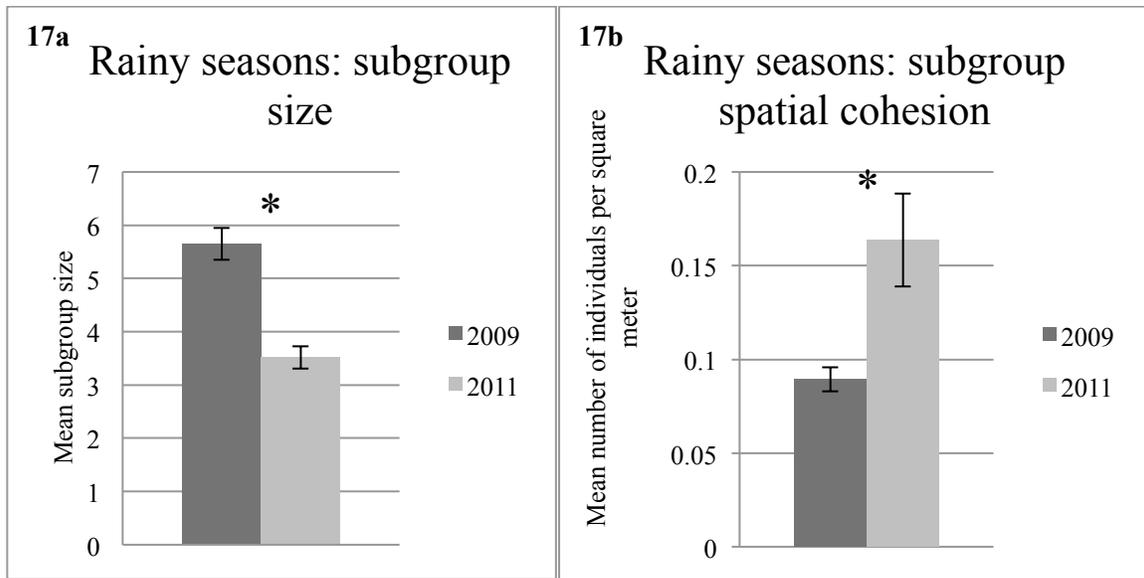


Fig. 17a Mean (\pm SE) daily subgroup size compared between the rainy seasons before (2009) and after (2011) Hurricane Richard (independent t -tests). $*p < 0.05$. **Fig. 17b** Mean (\pm SE) number of individuals per square meter of subgroup area compared between the rainy season before (2009) and after (2011) Hurricane Richard (independent t -tests). $*p < 0.05$.

The rainy season comparison showed significantly fewer fissions and fusions per hour (Fig. 18a: independent t -test: $t=3.483$; $df=107.846$; $p=0.001$) in the 2011 rainy season after the events. Between rainy seasons, there were fewer aggression events per hour of observation in 2011 than in 2009 (Fig. 18b: independent t -test: $t=2.323$; $df=84.628$; $p=0.023$).

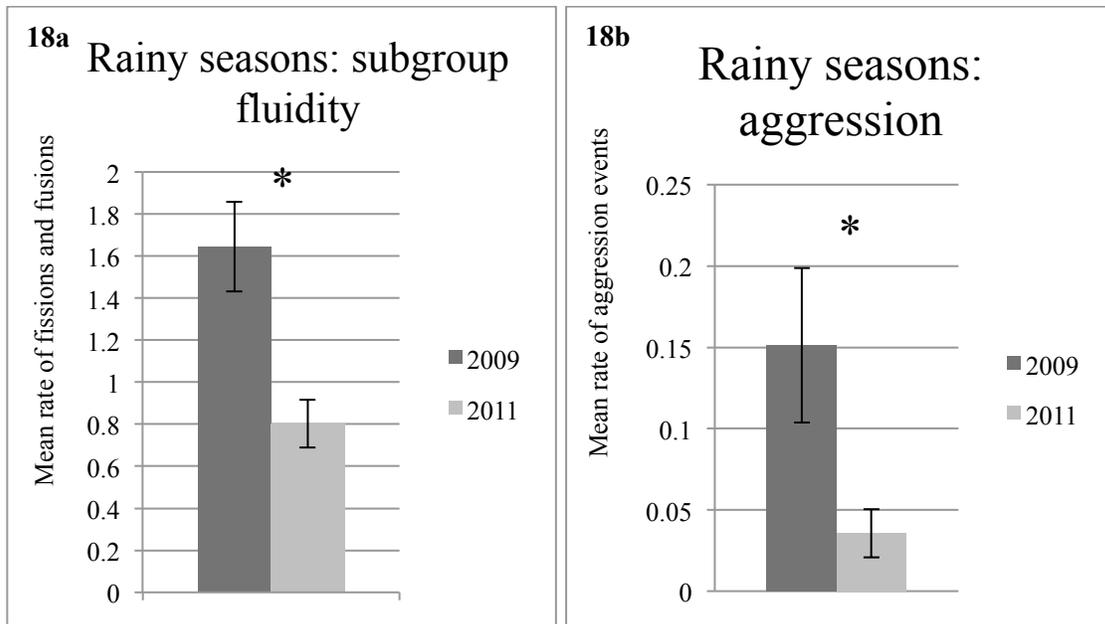


Fig. 18a Mean (\pm SE) rate of fission and fusion events per hour of contact time compared between the rainy seasons before and after Hurricane Richard (independent *t*-tests). * $p < 0.05$. **Fig. 18b** Mean (\pm SE) rate of aggression events per hour of contact time compared between the rainy seasons before and after Hurricane Richard (independent *t*-tests). * $p < 0.05$.

3.4.2. Dry season comparison

The activity budget of dry seasons before and after the hurricane and fire differed (Fig. 19): the monkeys decreased the time spent feeding (paired *t*-test: $t=2.835$; $df=19$; $p=0.011$) in the 2012 dry season and increased the time spent inactive (paired *t*-test: $t=-2.938$; $df=19$; $p=0.008$).

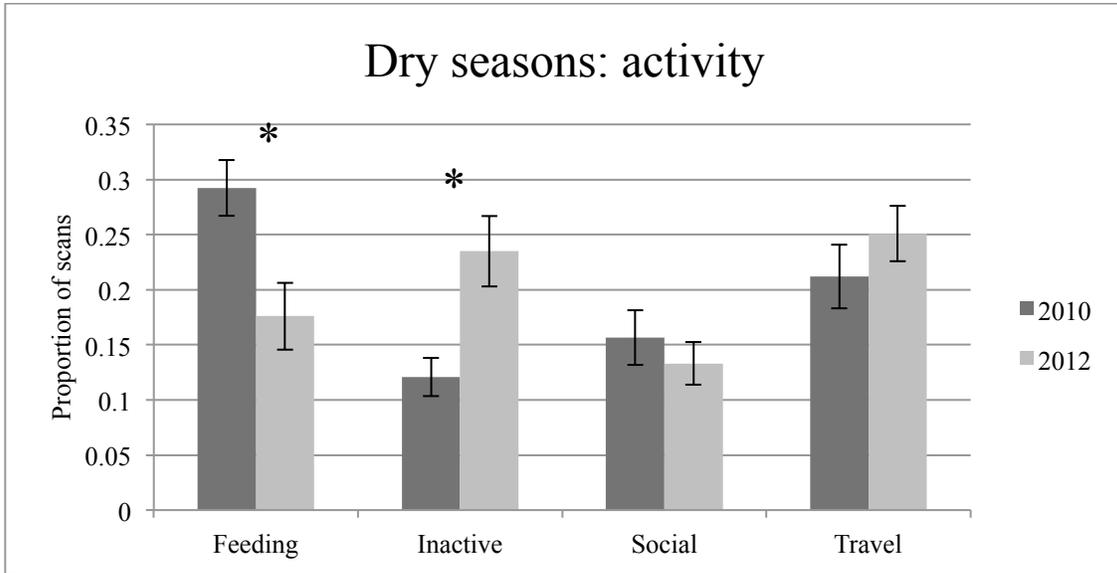


Fig. 19 Mean (\pm SE) proportions of scans in different activities between the dry seasons before (2010) and after (2012) Hurricane Richard and the subsequent fire (paired t -tests). * $p < 0.05$.

There were no statistically significant changes in the dry season comparison of diet (Fig. 20). This was considerably different from the rainy season comparison, which showed an increase of proportion of leaves and unripe fruit with a decrease in the proportion of ripe fruit consumed (Fig. 16).

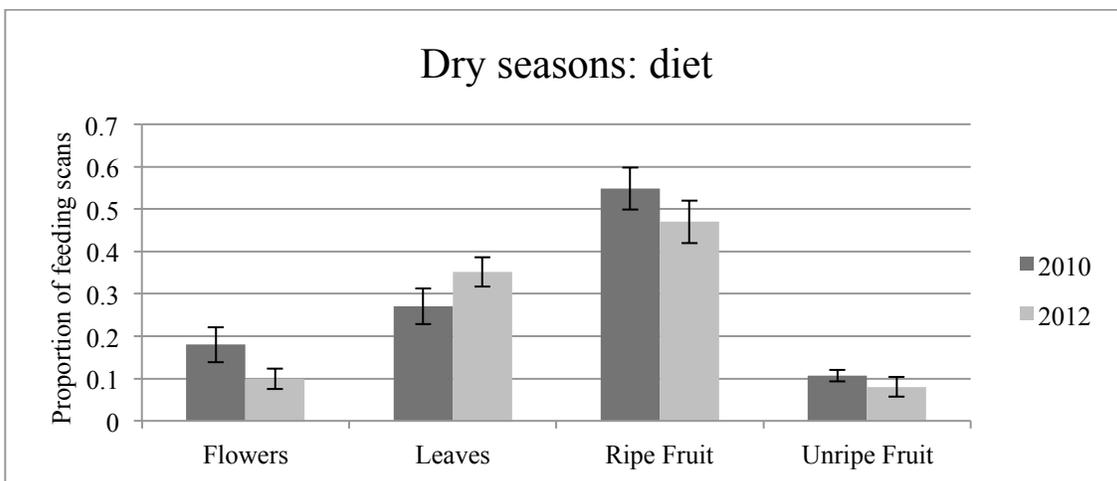


Fig. 20 Mean (\pm SE) proportions of feeding scans for different food types between the dry seasons before (2010) and after (2012) Hurricane Richard and the subsequent fire (paired t -tests).

There were no significant differences in daily subgroup size nor daily subgroup spatial cohesion in the dry seasons of 2010 and 2012 (Figs. 21a and 21b).

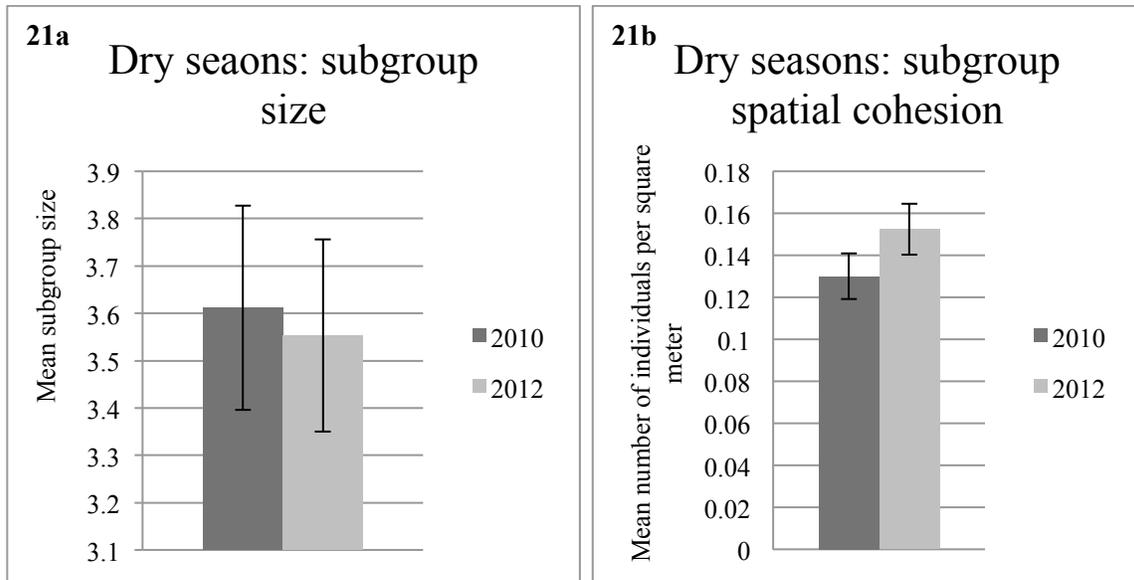


Fig. 21a Mean (\pm SE) daily subgroup size compared in dry seasons before and after Hurricane Richard (independent t -tests). **Fig. 21b** Mean (\pm SE) number of individuals per square meter of subgroup area compared in dry seasons before and after Hurricane Richard (independent t -tests).

The only significant change in grouping patterns was an increase in the rate of fission and fusion events (independent t -test: $t=-4.117$; $df=152.876$; $p<0.0005$), the opposite result as the rainy season analysis where the results showed lower levels of fission and fusion events after the disturbances. Aggression rates between sets of dry seasons did not reveal significant results (22b).

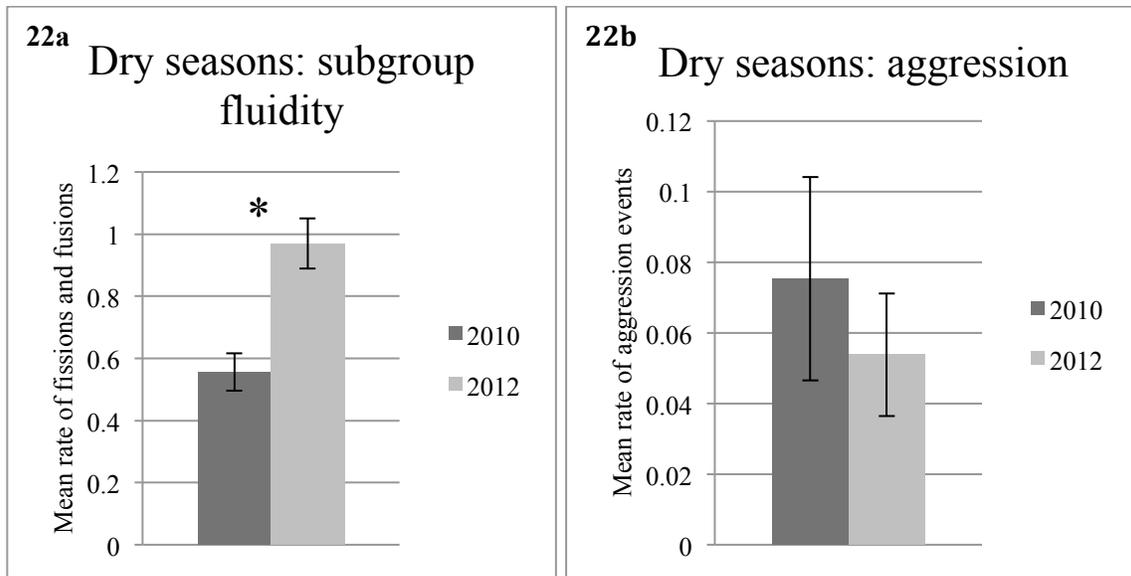


Fig. 22a Mean (\pm SE) rate of fission and fusion events per hour of contact time in the dry seasons before and after Hurricane Richard (independent *t*-tests). * p <0.05. **Fig. 22b** Mean (\pm SE) rate of aggression events per hour of observation time in the dry seasons before and after Hurricane Richard (independent *t*-tests).

CHAPTER FOUR: OVERALL DISCUSSION

5.1.1. Summary of results

Variable		22 months pre and post-hurricane	8-weeks pre and post-hurricane	6 month comparisons			Rainy seasons 2009-2011	Dry seasons 2010-2012
				1 & 2 Pre-hurricane and in-between	2 & 3 In-between and post-fire	1 & 3 Pre-hurricane and post-fire		
Activity	Feeding	↓	↑	↑	↓			↓
	Inactive				↑	↑		↑
	Social							
	Travel		↓					
Diet	Flowers							
	Leaves	↑	↑	↑		↑	↑	
	UF	↕	↕	↕	↓	↕	↕	
	RF	↕	↕	↕		↕	↕	
Subgroup size				↓			↑	
Subgroup spatial cohesion		↑		↑	↓		↑	
Subgroup fluidity			↓	↓			↓	↑
Aggression rate		↓	↓			↓	↓	

Table 2 Summary of significant results. See Appendix 3 for means of significant results.

5.1.2. Discussion of study

This analysis examined a group of spider monkeys that experienced both a hurricane and forest fire over a period of six months during the course of a longer-term study. I aimed to document changes the monkeys' activity budgets, diet, subgroup size, spatial cohesion, fluidity, and aggression over the course of 44 months, including the two natural disturbances. The spider monkeys showed both dietary and behavioural flexibility after the disturbances. In addition, the monkeys coped with habitat changes through high levels of fission fusion dynamics: altering subgroup size, spatial cohesion, and subgroup fluidity.

Storm damage can cause trees to abandon energetically expensive fruit and flower production (Barone 1998; Vandermeer *et al.* 1998) and increase new leaf production (Brokaw and Walker 1991). These altered resources, along with structural damage, can alter primate diet and behaviour. Primates in general, and ripe-fruit specialists in particular, are expected to be exceedingly sensitive to forest disturbances, even experiencing high mortality rates (Johns and Skorupa 1987). In previous instances of storm-damaged sites, it was shown that the survival of resident primate populations was linked to flexibility in diet, activity, and grouping patterns (Behie and Pavelka 2005; LaFleur and Gould 2009; Ratsimbazafy 2007; Schaffner *et al.* 2012).

As expected, there were several changes in spider monkey activity, diet, and grouping dynamics following Hurricane Richard. There was less ripe fruit consumption in most comparisons but the monkeys adjusted by consuming more leaves and unripe fruit in lieu of ripe fruit. Overall, the monkeys spent less time feeding after the hurricane. Grouping patterns and agonism are thought to be related to food supply in spider monkeys (Aureli *et al.* 2008; Aureli and Schaffner 2007) and the results of this study support this; the monkeys were less aggressive and more cohesive overall when their diet switched to leaves. I analyzed several time periods to take into account normal patterns of seasonality as well as detect possible lagged responses versus very temporary responses.

In the 8-weeks immediately following the hurricane, the monkeys spent less time travelling. They increased time spent feeding, presumably because their diet consisted of many more leaves, which are a less energetic food source than their normal frugivorous diet (Milton 1981 a, b). Leaves are also more evenly distributed than patches of ripe fruit, which require more significant travel costs to exploit (Felton *et al.* 2009; Chaves *et al.* 2011a).

Therefore, the monkeys probably did not need to travel far to forage; indeed, travel may have been initially impeded because normal travel routes were likely altered in the storm. Changes in diet and activity after the storm may have led to subgroups that were more stable in their membership. It is possible that the monkeys were not fissioning to travel to fruit patches and as a result were less likely to fuse with other subgroups. In the 8 weeks immediately after the hurricane results showed that there was less fluidity in grouping patterns. Similar grouping patterns were found after Hurricane Emily in Punta LaGuna, Mexico (Schaffner *et al.* 2012). 8-weeks immediately following that storm, the spider monkeys in the forest had fewer fusions per hour as it was suggested that they decreased time spent travelling in order to reduce subgroup fusions with other monkeys and therefore, larger foraging groups.

These immediate trends occurred during the 8-weeks following the hurricane did not last in longer time intervals analyzed. The short-term trends did not hold, perhaps due to recovery processes but the forest was further disturbed by the 2011 fire, which burned for two months of the 2011 dry season. Fires are common in the dry season and usually burn the savannah bordering the karst hills. Hunters have been seen setting these fires to promote new grass growth, which attracts grazing animals. The thick broad-leaf forest usually naturally stops the fire, but with the hurricane deadfall in the forest acted as a natural fire fuel and the fire of 2011 did not stop at the forest edge but instead burned deep into the forest. The fire burned strong for about two weeks until the first heavy precipitation of the 2011 rainy seasons started. The spider monkeys displayed different responses in the aftermath of each natural disturbance. Like the immediate comparison, time spent feeding increased after the hurricane but decreased after the fire. A decrease in feeding after the fire was coupled with a

significant increase in time spent inactive. It is possible that the monkeys were trying to conserve energy in a stressful environment, rather than trying to increase their calorie intake. Previous studies have also noted more inactivity or resting following a natural disturbance. Schaffner *et al.* (2012) hypothesized that more resting time allowed hurricane-affected spider monkeys in Mexico to better digest highly fibrous leaves (Gonzalez-Zamora *et al.* 2009; Korstjens *et al.* 2010). In addition, shade loss and increased temperatures could have also been cause for increased time spent inactive (Fernandez and Fletcher 1991; Korstjens *et al.* 2010).

In the time following the hurricane and leading up to the May 2011 fire, the average size of subgroups was smaller, more spatially cohesive, with fewer changes in membership. Unexpectedly, all grouping variables showed some sort of recovery in the six months after the fire to levels closer to those found in the six months before the storm. This result was unexpected given worsening forest conditions and presumably more limited resources. High quality resources, including fruits and flowers, may be scarce after tropical storms or hurricanes (Behie and Pavelka 2005; Zimmerman and Covich 2007; Schaffner *et al.* 2012) and ensuing forest fires magnify the damage of a storm (Whigham *et al.* 1991). Surprisingly, it appears that the fire did not have the immediate impact on spider monkey grouping patterns that was expected and did not appear to interfere with a return to pre-hurricane grouping patterns. The effects of the fire on the monkeys' may have only manifested itself in longer-term consequences.

In longer-term comparisons, the monkeys spent less time foraging after the hurricane than they did in the 8-weeks and 6 months after the storm. This was surprising because their diet continued to indicate increased folivory, requiring them to consume more to achieve the

same caloric intake as a frugivorous diet. They may have compensated for a less preferred diet by increasing time spent inactive, thereby reducing energetic output. Indeed, increased folivory in highly frugivorous species has been linked to more time spent inactive in order to digest (Chapman and Chapman 1991; Wallace 2005).

Spider monkey activity, diet, and social patterns vary greatly throughout any given year and are highly influenced by seasonality. They rely heavily on other food items in their diet rather than the preferred ripe fruit during dry seasons (Chapman *et al.* 1995; Wallace 2005; Chaves *et al.* 2011a). However, ripe fruit availability is at its highest at RCNR during the months of April and May, the end of the dry season (Hartwell 2010). Hurricane Richard occurred during the rainy season of 2010 and may have caused some fruiting trees to temporarily abandon ripe fruit production. In the following rainy season of 2011, the monkeys were still eating leaves and unripe fruit, suggesting that the forest was still not producing as much ripe fruit as it had before the storm. Preliminary analysis of vegetation data suggest that this was the case (unpublished data).

The monkeys at RCNR showed both short and long term dietary flexibility in the aftermath of Hurricane Richard. Consumption of leaves and unripe fruit increased while consumption of ripe fruit decreased in most of the time periods analyzed. Several other primates species affected by tropical storms have also showed dietary flexibility (Behie and Pavelka 2005; Tsuji and Takatsuki 2008) and shifted diets to include less preferred foods (Ratsimbazafy 2002; LaFleur and Gould 2009; Schaffner *et al.* 2012). Although spider monkeys have a range of diets between sites and dietary flexibility within sites (Chapman 1987; Chaves *et al.* 2011a; DiFiore 2008; Felton *et al.* 2009; Gonzalez-Zamora *et al.* 2009), it is unknown how sustainable a highly folivorous diet is (Korstenjens *et al.* 2010). The

digestive system of a spider monkey, short gut passage and small hindgut, is well adapted for ripe fruit and not for high-fiber leaves (Milton 1981a). In all comparisons where leaf consumption was significant, there was an increase in the amount of leaves consumed after the hurricane and fire. Similarly, increased folivory was found in both howler monkeys (Behie and Pavelka 2005) and a different population of spider monkeys in the aftermath of more severe hurricanes. Berenstain (1986) found that fire-affected long-tailed macaques in Borneo consumed more leaves, which were previously only a small portion of their diet. Different types of natural disturbances can result in a boost of leaf production due to canopy gaps and increased light availability (Barone 1998). The ability of primates to exploit new food resources can be an effective way to cope the changes brought about by natural disturbances. Throughout this study, when dietary changes were significant, the results showed an increase of unripe fruit and a decrease of ripe fruit. The monkeys may have compensated for lack of ripe fruit in their diet by consuming those that were not yet ripe. Similar results were found in a group of long-tailed macaques that ate noteworthy quantities of unripe seeds following a drought and fire (Berenstain 1986).

As time passed after Hurricane Richard, the spider monkeys fluid social structure may have provided more flexibility than their activity budget. Spider monkeys display a high degree of fission fusion dynamics (Van Roosmalen and Klein 1988; Aureli *et al.* 2008), which might allow them to rapidly respond to changes in habitat and food resources. In this study, data showed many changes in subgrouping patterns after the hurricane and fire. Aureli *et al.* (2008) identified three variables of fission-fusion dynamics: group composition, group size, and spatial cohesion. Any of these variables or interaction between them may be altered as a result of a habitat disturbance.

One factor that may influence subgroup size in spider monkeys is food availability, specifically ripe fruit availability (Aureli *et al.* 2008; Asensio *et al.* 2009). Multiple studies have found the degree of folivory is highest during dry seasons and average number of individuals in subgroups is lower (Asensio *et al.* 2009, Chapman *et al.* 1995, Shimooka 2003, Wallace 2008). Surprisingly, there was little change in subgroup size in the Hurricane Richard comparisons. Although consumption of leaves was higher in several post-hurricane time periods, smaller groups were more temporary and only found in the six months after the hurricane.

Immediately after the storm subgroups changed membership less often but remained the same in size and density. Six months after the hurricane, the daily subgroups were on average smaller, spatially more cohesive and more stable in membership. As the forest and monkeys continued to adjust and recover, by the 2011 rainy season, subgroup size was larger for the first time since the hurricane but they were still more cohesive. This could reflect the continued heavy reliance on leaves, which are evenly distributed, and cause of less contest competition for access to food. There were fewer changes in subgroup composition in the 2011 rainy season but as the forest continued to improve in the first post-hurricane and fire dry season of 2012, rate of fissions and fusions was higher.

Following two hurricanes in the Yucatan peninsula, Schaffner *et al.* (2012) found spider monkeys' highly fluid social system allowed for the group to adapt to the forest damage without any loss in the benefits of sociality. Interestingly, other primates with less fluid social systems have had significant and drastic changes in group dynamics following natural disturbances. Ratsimbazafy *et al.* (2002) found more solitary lemurs after a cyclone hit their forest. Following a drought and a fire, the normally cohesive long-tailed macaques

in Borneo reduced group cohesion and formed subgroups (Berenstain 1986). After an ENSO related fire in Borneo, a decrease in fruit led to siamangs forming smaller subgroups (O'Brien *et al.* 2003). In southern Belize, Hurricane Iris caused significant population losses and the howler monkeys were found more often as solitary individuals and in smaller groups after the storm (Pavelka *et al.* 2003).

Agonism is rare in spider monkeys (Asensio *et al.* 2008; Van Roosmalen and Klein 1988; Feidgan and Baxter 1984; Slater *et al.* 2009), including the study group at RCNR and they became even more so after the hurricane and fire. In all comparisons where rate of aggression events was significant, it was always lower post hurricane. In the 8-weeks following the hurricane, researchers did not witness any aggression. While the rarity of this behaviour in general may have led to significant differences that were tied to sample size, the lack of aggression may also reflect changes in diet and grouping patterns. Ripe fruit grows in patches which may be defended by aggressive behaviours. Post-hurricane, these ripe fruit patches may have been less common or less accessible than leaves, which are a non-defensible, evenly distributed resource. Especially in the immediate comparison, subgroups were travelling less and changes in subgroups were less frequent. Fission and fusion events have been associated with aggression events in spider monkeys. Thus, aggression events were less common after the hurricane and fire when subgroups were more stable.

As mentioned earlier, following a fire event, often non-native or invasive species of plants move in, in this case one of these species included the woodrose vine (*Ipomoea sepacuitensis*), previously uncommon to RCNR (Fig. 23). Fire opportunistic and pioneer plant species can be beneficial as they can be an important food resource after disturbances (Ratsimbazafy 2002; Kowalzik *et al.* 2010). In addition, pioneer species tend to contain

fewer secondary compounds, a byproduct of rapid growth and little investment into such defenses (Behie *et al.* 2010). As a result, a primate population may benefit from exploiting new, invasive species that grow quickly after a disturbance. The monkeys at RCNR were observed to forage closer to the forest floor on new shoots of the woodrose vine. This was alarming because spider monkeys prefer the upper canopy and are rarely seen near the ground (Youlatos 2008; Wallace 2008). The monkeys at RCNR have never been seen on the forest floor and on the rare occasions when they are near the ground, they are noticeably nervous.



Fig. 23 Series displays the invasion of the woodrose vine (*Ipomoea sepacuitensis*) after the fire. Pictures taken from the same location from left to right: June 23, July 17, and August 14, 2011.

There were no deaths documented as a direct result of the hurricane or fire and all group members were accounted for in the first several weeks following each event. However, in the 22 months reported in this project following Hurricane Richard, there were several disappearances and presumed deaths of group members. The first of the disappearances occurred over one year after the hurricane. Two adult females disappeared in early 2012. Several months later, their respective offspring, a juvenile male and a juvenile female, also disappeared and were presumed dead. Another juvenile female, approximately four years of age, disappeared in early 2012. At the time they went missing, all three juveniles were occasionally nursing and spending the majority of time with their mothers,

although no longer clinging to their mothers to travel. Although these deaths cannot be directly connected to Hurricane Richard and the fire, they may be a delayed result of damage to the forest and food supply or predation due to foraging low to the ground.

Other studies have shown more direct links to tropical storms and significant impacts on a non-human primate's population, reproduction or genetics. Hurricane Iris caused an immediate population reduction of 88% (Pavelka *et al.* 2007) and no infants were born for over a year following the storm (Pavelka and Chapman 2006). A cyclone in Southeastern Madagascar destroyed a large portion of fruit trees, which caused a nutritional deficiency in a population of sifaka lemurs and subsequent reduction in genetic diversity (Louis *et al.* 2005). A different cyclone in Madagascar caused a reproductive collapse of red variegated lemurs (Vasey and Borgerson 2009). Depending on the species and severity of the storm, population losses may not be apparent for several years after the event takes place.

A natural experiment presented itself when a hurricane and fire hit a primate research site, providing an excellent opportunity to document responses to the events in an effort to determine possible coping mechanisms to habitat damage. Examining several time periods allowed for the opportunity to compare short and longer-term responses, control for seasonality, and look at individual disturbances. The spider monkeys at Runaway Creek Nature Reserve were able to maintain a more folivorous diet than seen before the hurricane. Activity budgets and subgrouping patterns were altered to the disturbed habitat and, based on diet, different resources available in the forest. Although this study found spider monkeys were able alter dietary, behavioural, and grouping patterns in response to habitat disturbances, negative consequences, further research may find lagged responses and dietary and behavioural adjustments may not be sustainable with repeated major disturbances.

5.1.3. Direction for future research

It remains to be seen if the spider monkeys at RCNR experience any longer term consequences from Hurricane Richard and the fire. The disappearances and suspected deaths at this point cannot be directly linked to the storm. In a model examining how ENSO related events affect four *Ateles* genera, Wiederholt and Post (2010) found a delayed response in spider monkeys. Animals that live in the hurricane belt are subject to storms on average every 4.6 years (Walker *et al.* 1991) and have evolved with the pressure of tropical storms. Spider monkeys have frequently been considered one of the most sensitive new world monkeys, especially to human modified landscapes and habitat fragmentation (Garber *et al.* 2006). However, when not under anthropogenic pressures and habitat alteration, they may not be as sensitive to natural disturbances, such as hurricanes and fires. Spider monkeys are endangered (Rylands *et al.* 1997) and habitat destruction is the largest threat to their survival (Ramos-Fernandez 2003). The fragile state of spider monkey populations puts them in a vulnerable position when a hurricane hits and causes significant damage to their habitat (Brokaw and Walker 1991). Since 1995, the number of major hurricanes in the Caribbean has increased and is expected to continually increase in frequency/intensity as a result of climate change (Goldenberg *et al.* 2001; Saunders and Lea 2008; Webster *et al.* 2005). Although hurricanes are a common occurrence in much of the spider monkey's range, including Belize, they are expected to increase in frequency and/or severity (Saunders and Lea 2008). The response and flexibility of spider monkeys, already vulnerable due to anthropogenic pressures, to these climatic disturbances is important for the study of their ecology and conservation.

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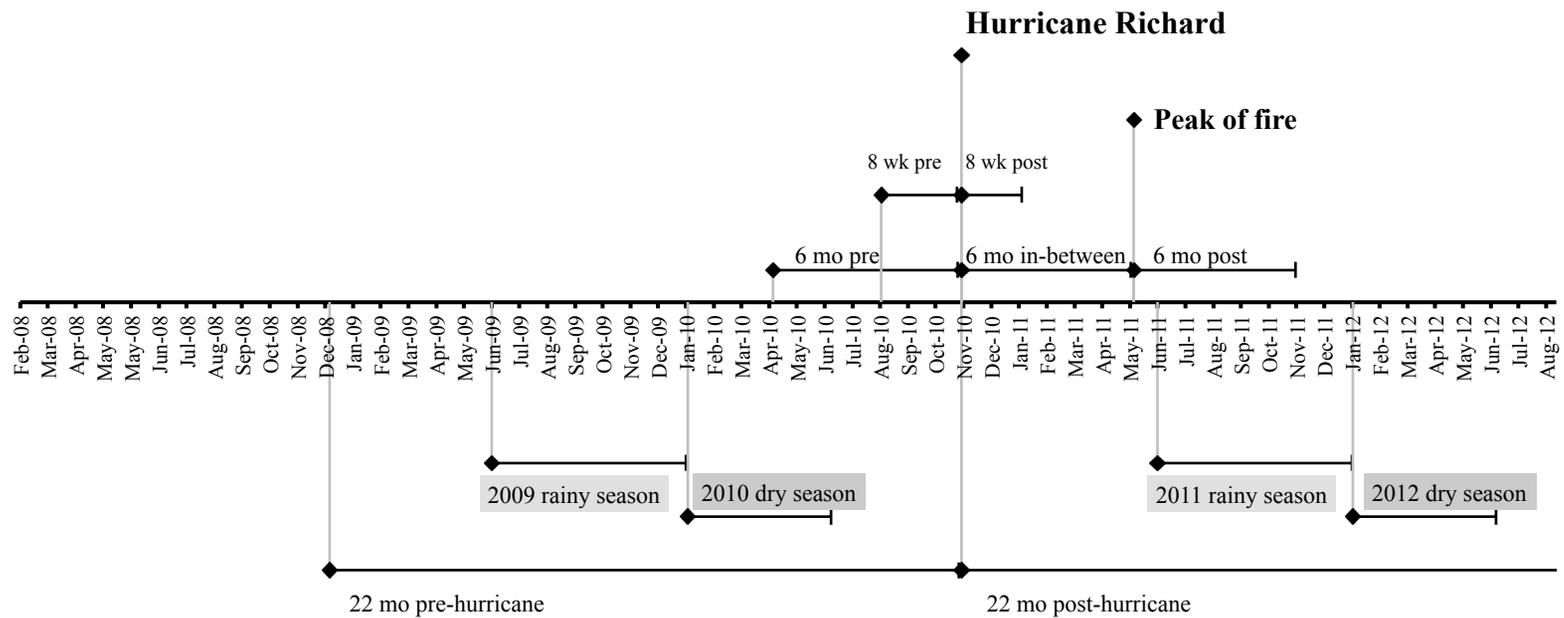
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Appendix 1: Project Timeline



Appendix 2: Ethogram

Ethogram used at Runaway Creek (Hartwell 2010)

SOLITARY BEHAVIOUR		
F	Feed/ Forage	Focal eats or actively searches for food items (also includes smelling fruits). Indicate plant species and plant part consumed.
DK	Drink	Focal consumes water. Indicate where (tree hole, palm, etc.) and how (i.e. dunks hand in water source and drips water into mouth off of knuckles, fingers, wrists or sucks water off fingers, collects water in palm of hand and brings to mouth, brings head to water source and drinks directly).
I	Inactive	Focal sits, lies down or hangs (eyes can be open or closed).
T	Travel	Focal moves (does not include moving around in a tree while foraging for food).
AUG	Auto groom	Focal grooms itself (does not include scratching).
NSP	Non-social play	Solitary play, i.e. swinging from tail, playing with broken branch
PLS	Place sniff/lick	Focal touches nose or tongue to branch/substrate. Usually performed by males directly after a female got up from sitting on a branch/substrate (if known, indicate who was sitting there prior to place sniff). Also indicate if place sniffing/licking urine (rare behaviour).
CR	Chest rub	Focal rubs chest back and forth against substrate/branch (rare behaviour).
GR	Genital rub	Focal sits and rubs ano-genital region back and forth along branch (rare behaviour).
VG	Vigilance	More alert then just scanning an area, usually in response to potential danger, i.e. large raptor flies over (rare behaviour).
SOCIAL BEHAVIOUR (indicate d and r)		
d	Direct	Focal animal initiates action.
r	Receive	Another animal initiates action to focal animal.
SN	Sit Near	Focal is within 2 meters (2 arms reach) of other individual(s). Record ID or age/sex class of other individual(s).
SC	Sit Close	Focal is within 1 meter (but not in contact) with other individual(s). Record ID or age/sex class of other individual(s).
SIB	Sit in Body Contact	Focal is in physical contact with other individual(s). Record ID or age/sex class of other individual(s).
a	Approach	Focal directs (or receives) an approach within 2 meters of other individual. Record ID or age/sex class of other individual(s) involved and director/receiver.
l	Leave	Focal directs (or receives) a leave, i.e. one individual

		distances itself from another individual. Record ID or age/sex class of other individual(s) involved and director/receiver.
pb	Pass By	Focal directs (or receives) a pass by, i.e. one individual passes within 2 meters of another and keeps on moving without stopping. Record ID or age/sex class of other individual(s) involved and director/receiver.
ALG	Allogroom	Focal directs (or receives) allogroom from other individual (5 sec break between bouts). Record ID or age/sex class of other individual involved and director/receiver.
SG	Solicit Groom	Focal directs (or receives) solicitation to allogroom, i.e. one individual presents body part (usually lifts arm up to present armpit area) to another individual for grooming. Record ID or age/sex class of other individual involved and director/receiver.
SP	Social Play	Focal plays with other individual (chasing, wrestling, mock biting and usually accompanied by play vocalizations). Record ID or age/sex class of other individual(s) involved.
NU	Nurse	Focal nurses their offspring.
PSE	Pectoral Sniff and Embrace	Focal wraps one or two arms around another's shoulder, head, or waist and places its nose near to the other's pectoral gland (around the neck/chest or arm pit region). Usually accompanied by a guttural whinny-like vocalization. Can vary in intensity and last up to several seconds. Pectoral sniff and embrace can also occur independently from one another. Record ID or age/sex class of other individual involved and director/receiver.
WC	Wound Clean	Focal directs (or receives) cleaning of wound by touching and licking. Record ID or age/sex class of other individual involved and director/receiver (rare behaviour).
GRP	Grapple	Focal engages in sustained contact (usually lasting several minutes up to over an hour) with another individual and behaviour may contain, but is not limited to: facial greeting/touching, embracing, tail wrapping, pectoral sniffing, and genital contact. Animals may also move apart, maintaining intense face to face visual contact then move together. Usually accompanied with high pitch whistles, pants, and soft growl vocalizations. Usually observed between subadult and adult males or occasionally subadult males and adult females. Record ID or age/sex class of individuals involved, and director/receiver if obvious (rare behaviour).
ALC	Allocarry	An individual (other than mother) carries an infant/juvenile while traveling. Record ID or age/sex class of individuals involved (rare behaviour).
IH	Infant Handle	An individual (other than mother) sits and handles an infant, letting infant climb on and/or cling to them. Record ID or age/sex class of individuals involved (rare behaviour).

SIH	Solicit Infant Handle	Individual (other than mother) presents chest/stomach area to infant for it to climb on (rare behaviour).
CP	Copulation	Self-explanatory. Record ID or age/sex class of individuals involved (rare behaviour).
KF	Kissy-Face	Focal gazes in direction of other and purses lips outward in a wide kiss-like gesture, usually accompanied with a guttural whinny vocalization. Record ID or age/sex class of other individual involved and director/receiver (rare behaviour).
GT	Genital Touch	Focal (directs or receives) touches/sniffs/licks the anogenital region of another individual. Record ID or age/sex class of other individual involved and director/receiver (rare behaviour).
FS	Finger sniff	Focal (directs or receives) touches genitals of another individual and sniffs their fingers. Record ID or age/sex class of other individual involved and director/receiver (rare behaviour).
SCO	Solicit copulation	Focal directs or receives invite to copulate (copulation may or may not follow) (rare behaviour). Record ID or age/sex class of other individual involved and director/receiver (rare behaviour).
OS	Out of Site	Focal is out of view.
AGGRESSION		
AGG	Aggression	Record ID or age/sex class of other individual(s) involved and director/receiver. Indicate if aggression was in the form of a coalition and describe intensity: 1=lunge, open mouth threat, vocalizations (growling, screams), short in duration 2= same as above, but continued chase with no physical contact 3= same as above with physical contact (slaps, hits, grabs, bites) but no serious injury 4= same as above with noticeable injury (wounds, bleeding, limping)
TD	Threat display	Focal threatens observer, potential predator (or nothing obvious) by growling and/or shaking/breaking branches.
PBT	Piggy Back Threat	2+ individuals pile on top of each other in a threat display
DP	Displacement	Individual displaces another. Record ID or age/sex class of other individual involved and director/receiver (rare behaviour).
AV	Avoid	Individual moves out of the way when another individual approaches. Record ID or age/sex class of other individual involved and director/receiver.
VOCALIZATIONS		
WHV	Whinny	most common vocalization, wavelike frequency modulation that varies in length tone and harshness

THV	Tee-Hee	similar sound to a whinny but a shorter 2 note call
OBV	Ook-Bark	Alarm call, harsh short notes varying in intensity.
SCV	Scream	given when individual is under attack or physical threat
GRV	Growl	Harsh noisy sound vocalized during threat display or aggression and rough physical contact play.
LCV	Long Call	Very loud and long call given in an attempt to re-establish contact with other sub-groups.
PLV	Play Vocalizations	Light or heavy panting and growling used during social play. Can vary in intensity
CHV	Chirps	High pitch short notes given repeatedly, usually during threat display or aggression.
TSV	Tschool	Similar to a long call but less intense, harsh gurgle in the throat.
HPWV	High-Pitch Whistle	a flat high pitch vocalization held for 2-3 seconds and usually repeated – kind of like a whine

Appendix 3: Mean values for significant results.

Activity and diet scores represent the mean proportion of time spent in that activity and proportion of time feeding by plant part; subgroup size is the daily mean size of subgroups observed for that time period; subgroup spatial cohesion is the daily mean number of individuals per subgroup area; subgroup fluidity is the daily mean rate of fission and fusion events per hour of observation; aggression is the daily mean rate of agonistic behaviours per hour of observation.

Variable		22 months		8-weeks		6 month comparisons						Rainy seasons		Dry seasons	
						1 & 2 Pre-hurricane and in-between		2 & 3 In-between and post-fire		1 & 3 Pre-hurricane and post-fire					
		Pre	Post	Pre	Post	1	2	2	3	1	3	2009	2011	2010	2012
Activity	Feeding	0.292	0.213	0.310	0.481	0.248	0.329	0.329	0.155					0.292	0.176
	Inactive							0.173	0.357	0.170	0.357			0.121	0.235
	Social														
	Travel			0.281	0.148										
Diet	Flowers														
	Leaves	0.202	0.426	0.139	0.392	0.150	0.358			0.150	0.460	0.238	0.484		
	UF	0.029	0.167	0.000	0.357	0.001	0.247	0.247	0.096	0.001	0.096	0.025	0.112		
	RF	0.645	0.346	0.854	0.177	0.825	0.290			0.825	0.434	0.718	0.394		
Subgroup size						0.413	0.312					5.644	3.581		
Subgroup spatial cohesion		0.134	0.184			0.168	0.245	0.245	0.152			0.089	0.164		
Subgroup fluidity				4.405	3.692	1.120	0.572					1.644	0.802	0.556	0.969
Aggression rate		0.099	0.035	0.130	0.000					0.158	0.036	0.151	0.036		