Dispersal Behavior and Habitat Use in an All-male Group of White-faced Capuchins at Lomas Barbudal Biological Reserve in Costa Rica

by

Kristin L. Fisher

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Thesis Committee:

Professor Bobbi S. Low, Chair
Dr. Susan E. Perry

Dedication

For my family

and Dakota Sur

Abstract

Key words: male migrants; natal dispersal; habitat quality; predator risk; conspecific influence.

In white-faced capuchin monkeys (*Cebus capucinus*), males typically disperse from their natal group when they reach reproductive age. Here I seek to gain more information about the dispersal patterns of these males. Specifically, I ask how their dispersal is affected by habitat quality, predation risk, and conspecific (social) influences. I examined the social and foraging behavior of an all-male group of habituated, wild white-faced capuchins over a 4-month period during their dispersal at Lomas Barbudal Biological Reserve in Costa Rica. I used a Generalized Linear Model and other tools to identify factors that predict time spent in specific areas during the dispersal period. Habitat quality was important: migrants spent significantly more time in horticultural and mixed habitats than deciduous and savanna habitats. They also spent more time at sites with greater forest maturity, coverage, vegetation, and water available, though the number of fruiting trees at a habitat was not a significant predictor of time spent in that habitat. Despite the fact that all horticultural sites had non-researchers present (a type of predation risk), migrants still spent the most time there, suggesting that these migrants weigh predation costs less heavily at this point in their dispersal than the costs of conspecific aggression. In contrast, migrants quickly left sites where non-human predators were present and where intergroup encounters occurred. This particular group of migrants appeared to weigh risks of interactions with other groups more heavily than potential reproductive opportunities during this period in their dispersal. These data provide insight to the daily complexities, stressors, and life-history tradeoffs of a migrant. Because dispersal is crucial to wild primate populations, affecting such things as population dynamics and gene flow, these data may prove useful to conservation efforts at Lomas Barbudal and nearby sites.

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Introduction

Dispersal, or permanent emigration from an individual's natal home range, occurs in most organisms at some point in their lifetime (Baker, 1978; Dobson, 1982; Greenwood, 1980; Hamilton & May, 1977; Holekamp & Sherman, 1989; Lidicker, Jr., 1975). We can understand dispersal from the complementary perspectives of ultimate and proximate factors (Holekamp & Sherman, 1989; Tinbergen, 1963) as a nonrandom movement (Cheney & Seyfarth, 1983).

One way in which individuals can increase reproductive opportunities is by reducing competition for mates with older individuals (Clarke et al., 1997; Dobson, 1982; Endler, 1977; Howard, 1960; Moore & Ali, 1984). Another includes avoiding incest with closely related individuals (Alberts & Altmann, 1995; Clarke et al., 1997; Cockburn et al., 1985; Harcourt, 1978; Greenwood, 1980; Itani, 1972; Packer, 1979; Pusey & Packer, 1987).

Proximate endogenous mechanisms of influences on dispersal, such as an increase in body size and hormonal changes at the onset of reproductive maturity, have been well studied and explored (Caldwell, 1974; Caldwell & Rankin, 1972; Holekamp & Sisk, 2003; Johnson, 1969; Meier & Fivizzani, 1980). Proximate *exogenous* mechanisms, such as the influences of habitat, predation, and social factors (primarily intergroup encounters), may also have a large effect on dispersal in highly social species like non-human primates (Jack et al., 2012); these are only just beginning to be studied. Habitat and resource pressures can often cause or have effects on dispersal in many species (Dobson, 1979; Lin & Batzli, 2001; Matthysen, 2005), while costs of predation can be higher during the dispersal period (Isbell, 1994). Social factors, such aggression towards individuals (Gerlach, 1990; Gerlach, 1996), and maternal rank (Colvin, 1983; Koford, 1963) can affect the timing of dispersal events, too.

Here I seek to learn more about these influences of habitat, predation, and social factors during the dispersal period of an all-male group of white-faced capuchins (*Cebus capucinus*) in the tropical dry forest.

It is difficult to summarize dispersal mechanisms and strategies in primates; they are often highly dynamic, individualized, and variable, just as the social lives that heavily influence natal dispersal across primate species are (Jack et al., 2012; Jack & Isbell, 2009; Pusey & Packer, 1987). Because of this, investigating what social factors affect the decisions of an individual to stay or leave its natal group (and potentially select a new group after dispersal) continues to be studied in depth in capuchins (Jack et al., 2012; Perry et al., 2012).

Focusing only on what influences the timing of dispersal events may be limiting. Dispersal ultimately affects the size, structure, genetic composition, and social organization of populations (Cheney & Seyfarth, 1983; Hamilton, 1972; Howard, 1949, Lidicker, Jr., 1975; MacArthur & Wilson, 1967; Shields, 1982; Taylor & Taylor, 1977). Further, it is one of the most enduring and intense changes that a migrant will experience in its life (Smale et al., 1997), demonstrating considerable costs (Alberts & Altmann, 1995). Certain dispersal patterns may have social advantages even though they appear to carry genetic costs like inbreeding (Cheney & Seyfarth, 1983). Questions also should seek information regarding habitat quality and predation risk during dispersal. Here I attempt to gain more information about just what happens in the day-to-day life of an individual once it has permanently dispersed from its natal group and before it finds a new group successfully. I examined habitat quality and predation risk, as well as conspecific (social) influences.

Habitat quality is an important factor to dispersal patterns (Frantz et al., 2010; Lin & Batzli, 2001). Dispersal habitats are often lower habitat quality than areas occupied after dispersal or areas occupied by resident individuals (Palomares et al., 2000). Also, long-distance dispersers, such as white-faced capuchins, disperse in directions influenced by local habitat preference (Selonen & Hanski, 2004).

The risk of predation also is an important factor during dispersal. Primates in unfamiliar areas can be at high risk for predation, and arboreal primates are at greater risk of predation when they are in more exposed locations (e.g., at forest edges and tops of canopies) than in more concealed ones (Isbell, 1994). Enhancing our understanding of responses to particular behavioral and ecological variables like habitat quality and predation risk, as well as conspecific influences, specifically during this period will provide insight to daily complexities, stressors, and life-history tradeoffs of a migrant. Such understanding will also prove useful to the conservation of tropical dry forest habitats (in which little forest remains intact and even less is under protection [Stoner & Timm, 2004]) and their resident wildlife, such as local white-faced capuchin populations.

White-faced capuchins are a female-philopatric species (Fragaszy et al., 2004; Jack & Isbell, 2009; Perry, 2012): males disperse out of their natal group. In some primates, males may disperse to avoid mating with closely related kin (Pusey & Packer, 1987) and/or potentially to find a new group with a more reproductively favorable male-female sex ratio where their mating opportunities might increase (Jack & Isbell, 2009). In white-faced capuchins, group instability can trigger natal dispersal (Jack et al., 2012). The existing literature focuses on the *timing* of these first dispersal events in white-faced capuchins currently; depending on the study population, the timing of first dispersal has been shown to be quite variable (Jack et al., 2012). At Lomas Barbudal males first disperse from their natal group at an average age of approximately 7 years (range of 20 months – 12 years of age [Perry et al., 2012]); the average

age of dispersal of the nearby Santa Rosa National Park site’s capuchin population is much younger (4.5 years; range of 19 months – 11 years [Jack et al., 2012; Jack & Fedigan, 2004 a, b]). Social factors also can influence the timing of dispersal in both populations: slightly less than half of all males first disperse after the death of a migrant’s father or when a male takeover event occurs at Lomas Barbudal (Perry et al., 2012). Males are approximately 18 times more likely to disperse after a male takeover event at Santa Rosa (Jack et al., 2012). Furthermore, once dispersal does occur at Lomas Barbudal, most (~80%) males migrate with at least one other male (Perry et al., 2012). Yet beyond timing and social influences of dispersal events in these study populations, little is known of the actual dispersal range period (i.e., the day-to-day life of an individual once it has permanently dispersed from its natal group and before it finds a new group successfully) and its social and environmental influences.

For many species, environmental influences such as habitat quality can have a large impact on the timing of dispersal events. Dispersal events vary depending on habitat quality characteristics; generally, when all suitable habitat is occupied (e.g., due to high population densities), dispersal is delayed, and its timing is constrained by this lack of a suitable habitat. Fragmented landscapes can also cause barriers to dispersal (Cox & Kesler, 2012). It is unknown whether these factors have a similar influence once individuals permanently leave their natal groups, because the dispersal period has its own costs and benefits compared to those of a resident individual in a multi-male, multi-female group (Johnson & Gaines, 1990). For example, the movement of multi-male, multi-female groups is affected by the locations of edible fruit and water (personal observation); these areas are often more desirable and already occupied by bisexual groups (and, thus unavailable to migrants avoiding intergroup encounters). Because migrants are often pushed to areas of relatively low quality (Hiebeler et al., 2013; Selonen &

Hanski, 2004) other stressors (e.g., predation risk) may have unusually high impacts during the dispersal period.

Factors such as a small group size and relatively high risk of predation, may intensify the importance of energy needs and uses in migrants during the dispersal period (Clarke et al., 1997; Isbell, 1994). Here I seek to provide insight to such stressors and life-history tradeoffs, and to enhance the understanding of demographic responses to particular behavioral and ecological variables like habitat quality, predation risk, and conspecific influences during the dispersal period.

Predictions

I investigated the social and foraging behavior of an all-male group of habituated, wild white-faced capuchins during a portion of their dispersal period at Lomas Barbudal Biological Reserve. I predicted that the dispersal range of this all-male group is influenced by one or more of the following three factors: 1) habitat quality, such as the availability of fruiting trees and water, and the canopy coverage of the area, 2) predator (both non-human and human) risk, and/or 3) conspecific influences, such as intergroup encounters and mating opportunities. Specifically, I predicted:

1. Migrants will prefer high quality habitats (e.g., riparian rather than savanna), areas with available fruiting trees and water, relatively numerous trees with high average diameter of breast height (a measure of canopy coverage and forest maturity), and a higher Normalized Difference Vegetation Index (NDVI [a measure of live, green vegetation]).
2. Migrants will prefer habitats with no predators, whether non-human or human.

3. Migrants will prefer habitats characterized by a high density of reproductively mature females. Thus, they will maximize the duration of time spent in habitats that are likely to increase mating opportunities in the near future (e.g., a territory with a more favorable male-female sex ratio), and when faced with intergroup encounters, although at risk, they will spend more time fighting for access to females.

Why Study Dispersal?

Dispersal is crucial to wild primate populations; it affects population dynamics, community structure, gene flow, local adaptations, speciation, and evolutionary life-history traits (Cheney & Seyfarth, 1983; Clarke et al., 1997; Greenwood, 1980). Understanding behavioral responses and habitat use during dispersal should provide insight to the daily complexities, stress, and life-history tradeoffs of a migrant.

Lomas Barbudal is a part of the endangered tropical dry forest, where habitat fragmentation and anthropogenic impacts continue to occur (Stoner & Timm, 2004), and may disrupt behavior (Boydston et al., 2003; Wielgus & Bunnell, 1994) that affects capuchin foraging efficiency and dispersal patterns. For migrant males to disperse as far as might be desirable for maintaining gene flow over large areas, they often have to pass through disturbed and fragmented habitats (such as pastures, farms, and tiny forest fragments in zones heavily populated by humans). It is important to understand the limits of migrant tolerance to such fragmentation, and to understand how it affects dispersal patterns. Such understanding will prove useful to the conservation and management (e.g., what types of terrain are adequate and what habitat features are preferred by this species to serve as biological corridors) of endangered tropical dry forest habitats, this wild primate population, and potentially other resident wildlife.

Methods

The Lost Boys and the Lomas Barbudal Study Site

I collected data from one habituated all-male group of wild, migrating white-faced capuchin monkeys, named the “Lost Boys”, in the Lomas Barbudal Biological Reserve (10°29–32′N, 85°21–24′W) and adjacent public and private lands located in the Guanacaste province of Costa Rica (Figure 1). The site is part of the Pacific Basin, characterized by a dry and rather harsh (Stoner & Timm, 2004) heterogeneous seasonal climate, and is part of the Pacific Lowland watershed (Frankie et al., 1988; Mata & Echeverría, 2004). This area had heavy hunting pressures, and the loss of tropical dry forest due to cattle ranching, the timber and tourism industry, and agricultural development (Stoner & Timm, 2004). These factors also rapidly influence the density of the mammal population (Stoner & Timm, 2004).

The Lomas Barbudal Biological Reserve is approximately 2400 hectares in area; it can be broadly defined as a tropical deciduous forest. Trees in the reserve form a discontinuous canopy with no distinct stratification; they attain heights of 20-25 meters, and occasionally reach 30 meters. Six plant communities or habitat types are found within the reserve: dry deciduous, riparian and spring, savanna, mesic, extreme deciduous, and regenerative (Frankie et al., 1988). The dry deciduous and riparian habitat types are most frequently visited by the Lomas Barbudal capuchin population (personal observation).

The Lost Boys’ group is an all-male group that is a subset of the larger Lomas Barbudal population (in which groups vary in size from 5 to 40 individuals and typically consist of 1-15 adult males and 3-12 adult females). This population has been studied since 1990 (with continuous monitoring since January 2001) by Dr. Susan E. Perry of the University of California at Los Angeles and her team of researchers (Perry et al., 2012). This research team also continuously monitors other multi-male, multi-female groups, collecting census data, ranging data, and behavioral data.

Beginning in the fall of 2009, many of the Lost Boys males began to exhibit dispersal behaviors in their natal group (“Rambo’s”): hanging around the periphery, lurking near neighboring groups, and disappearing for a portion of the day to several days (Perry, personal communication). Eventually, after a series of several brief visits to other groups, the Lost Boys fissioned from Rambo’s group in February 2010, with one member returning to Rambo’s group in April 2010. One juvenile member visited back and forth between Rambo’s and the Lost Boys before permanently joining the all-male group in May of 2010 (Perry, personal communication). At this time, the group consisted of seven males, but by February of 2011, when data collection for this project commenced, only six variably-aged individuals: two juveniles age 5 years, 9 months and four adults age 7 – 13 years. All individuals were sons, grandsons or great-grandsons of the same alpha male. Two pairs were maternal half brothers, and one pair was paternal half brothers (Figure 2 [Perry, personal communication]). I collected observational data on these six individual members from January 2011 through April 2011. No members of the group have been sighted since June 2011.

Field Data Collection

I used several techniques to document a variety of behaviors (e.g., male-male aggression, sexual behaviors, etc.) and vocalizations (e.g., other monkey alarms), as well as intergroup encounters. I collected group scans, in combination with focal follows and *ad libitum* data (Altmann, 1974) to gain general information about the Lost Boys’ ranging patterns and to perform activity budgets using the methods described in the “General Data Analysis” section (below). Group scans have the same format as the point samples in focal follows (below); males were scanned at the moment in which they were first seen, and observers rotated through the Lost Boys' group attempting to scan as many monkeys as possible. Ten minutes or more separated group scans for any individual to reduce the problem of non-independence of data points.

To assess the influence of habitat quality on the Lost Boys' ranging behavior, I followed the group (*N* = 36 days) from January through April 2011 with a Garmin GPSMAP 60CSx GPS. The GPS was programmed to create automatically a daily digital travel track, which provided a visual representation of each follow day's dispersal pattern (Marshall, 2009). A "follow day" consists of approximately two to 14 hours of observation, including all hours during which at least one observer was in sight of the monkeys. At a later date (varying from 1 day to approximately 1.5 months after the tracks were created), I conducted a series of habitat transects from these daily tracks. A habitat transect measured 30 meters x 2 meters and ran south to north. (During most observations the Lost Boys were grouped within a 30-meter radius.) Transects were conducted from the start of the track (when monkeys were first sighted) at 100 meter intervals along the track.

I also noted the habitat type (savanna, deciduous, riparian, horticultural, or mixed), any anthropogenic disturbances (e.g., a road, a canal, gravel pit, pasture, etc.), and water availability. I also recorded the locations and diameter at breast height (DBH) of 42 species of fruiting plants (Appendix 1) greater than or equal to 10 centimeter DBH. These species comprised 95 percent of the Lomas Barbudal study population's diet in December 1992 – May 1993 (Perry & Ordoñez Jiménez, 2006). I later created a Normalized Difference Vegetation Index (NDVI) for each transect, which is a measure of the amount of live-green vegetation that can be interpreted as coverage of the habitat, using the methods described in the "Geospatial Analysis" section (below).

I recorded behavioral data to assess the influence of predator risk on the Lost Boys' dispersal range while following the group. Individual males (i.e., focal males) were observed using a 10-minute focal follow protocol (Altmann, 1974) with a Psion Workabout MX handheld computer and, occasionally, a digital recorder (when the rate of behavioral data collection became too rapid to type codes into the Psion). Human observers rotated among monkey focal subjects to prevent biased sampling. Once a follow was complete, the next focal follow subject was someone who had not interacted with the previous focal during the last 2.5 minutes of the follow, in order to prevent double-counting interaction bouts. On occasion, due to the separation of the Lost Boys' group (and the small group size), lengthier focal follows were conducted (1 hour – all day).

Ad libitum (Altmann, 1974) and commentary data documented a variety of behaviors, such as specific predator call for snakes (e.g., boa constrictors and neotropical rattlesnakes), birds of prey (falcons, owls, etc.), and terrestrial mammalian predators (dogs, ocelots, etc.) and group size composition (i.e., the normal group size or any deviations of it, such as separations or intergroup encounters). Because poaching by recreational hunters is a major source of monkey mortality, I also noted non-researcher human presence. Inter-observer reliability tests were administered at the start of data collection until 97% reliability was achieved for similarity of behavioral records and 100% reliability was achieved for recognition of monkeys. Monthly retests were conducted for behavioral codes and vocalization recognition.

To assess conspecific influences (i.e., intergroup encounters, and female presence and mating opportunities) on the Lost Boys' ranging patterns, the onset of these interactions were noted as a comment in the behavioral data. The timestamps of these comments were then used to identify the location of the interaction. The Lost Boys' daily travel tracks and other travel tracks collected from researchers as a part of the larger team observing multi-male, multi-female study groups were used to assess territory overlap between multi-male, multi-female groups' territories and the Lost Boys' dispersal range. At a later date, a male-female sex ratio for each transect was calculated from the other tracks and the census data collection of the other study groups, using the methods described in the "Geospatial Analysis" section (below).

General Data Analysis

For general data descriptions and activity budgets involving the day-to-day lives of the Lost Boys males, I performed simple descriptive statistics and log-transformed independent samples t-tests ($\alpha \leq 0.05$) in IBM SPSS Statistics for Windows version 20.0 (IBM Corp., Armonk, NY.) A statistical model was also created to test my three predictions (i.e., habitat quality, predator risk, and conspecific influence) using the methods described in the "Statistical Methods" section (below).

Geospatial Analysis

Additional data were collected and analyzed in ArcGIS version 10 (Environmental Systems Research Institute, Redlands, CA) and Erdas IMAGINE Professional (Leica Geosystems, Atlanta, GA) to test further my predictions regarding habitat quality. A Normalized Difference Vegetation Index (NDVI), a measure of the amount of live, green vegetation, biomass, and coverage scaling from -1 to +1 at the transect sites, was calculated (Carroll et al., 2010). I obtained this value for each transect by creating 30-meter radius buffer zones around the center of transect sites (i.e., proximity analysis). (During most observations the Lost Boys were grouped within a 30-meter radius around transect sites.) I then calculated the NDVI value for each transect using raster analysis calculations of a dry season landsat data image collected during my study period (Figure 3 [USGS/EROs L4-5 TM, Path 15, Row 53, March 2011]).

To assess the influence of conspecifics, specifically female presence and/or mating opportunities, on the Lost Boys group's ranging patterns, I also collected other data and analyzed them in ArcGIS version 10 (Environmental Systems Research Institute, Redlands, CA). Previous researchers at Lomas Barbudal had already analyzed the ranging data of multi-male, multi-female study groups from June 2009 – May 2010 using Hawth's Analysis Tools (Beyer, 2004) to create Minimum Convex Polygons of each group's ranging patterns (Berl, personal communication). I made the assumption that these group's home ranges remained the same in January through May 2011 as they were in June 2009 – May 2010. To obtain a male-female sex ratio for each transect, I created 30-meter radius buffer zones around the center of transect sites (i.e., proximity analysis). I then used an overlap operation, or spatial join analysis, with geospatial union tools. This generated the territory overlap between the Lost Boys' area of use and multi-male, multi-female groups' territories. In this way, if the Lost Boys' dispersal range overlapped with another study group, a new minimum convex polygon was created. This new polygon included census data collected from both multi-male, multi-female groups (i.e., how many adult males and adult females were in each multi-male, multi-female group and thus, were in each group territory each study month) and the Lost Boys' group (i.e., how many Lost Boys were at a particular transect site). From this new territory overlap polygon, I calculated a male-female sex ratio for each transect site.

Statistical Analysis

To examine my three hypotheses (i.e., habitat quality, predator risk, and conspecific influence) I used a Generalized Linear Model (GLM) with a Negative Binomial distribution to find predictors of the amount of time spent at a transect site. I used the negative binomial distribution because the outcome was a count (i.e., the count of the number of 5-minute intervals spent in a transect), and the distribution of the outcome was highly skewed (Hilbe, 2011). Because there were multiple observations made on the 36 days of the study, I used a Generalized Estimating Equations (GEE) approach to take into account the possible correlations among observations that were made on the same day (Diggle et al., 2002). All analyses were carried out using IBM SPSS Statistics for Windows version 20.0 (IBM Corp., Armonk, NY).

The model also included control variables deemed *a priori* likely to be important. I assessed each of these variables (i.e., month, time of day, relative group size, age distribution, and whether or not the transect was a sleepsite) individually in a GLM to see which were significant predictors ($P \leq 0.05$) of time spent at a transect site. I included in the final prediction model only those that were individually significant (i.e., time of day, relative group size, and age distribution [Table 1]).

I assessed each predictor individually in a GLM with the significant control variables to see which were significant predictors ($P \leq 0.05$) of time spent at a transect site, and included in the final model only those that were individually significant. If covariates were found, I selected those that were likely to be important (i.e., habitat type, non-human predator presence, and intergroup encounter [Table 2]).

The final model included the control variables: time of day, relative group size, and age composition as dummy variables, plus the predictors of interest: habitat type, presence of non-human predator, and intergroup encounters, also as dummy variables (Table 3). Note that time spent was analyzed on the natural log scale, which is the canonical link for the negative binomial distribution (Figure 4).

Results

A Day in the Life of a Lost Boy

The following general descriptions of daily activities in the lives of the Lost Boys' group males comes from the following data set: 36 days of data (approximately 372 contact hours) collected in the dry season of 2011, which incorporates the months of January (*n* = 2 days), February (*n* = 6 days), March (*n* = 22 days), and April (*n* = 6 days). Of these 36 total follow days, 1,579 group scans and 915 transects, and the transect's related data points and variables, make up the total data set that is used in these general descriptions and the GLM results.

What Do Migrants Do?

Individuals in the Lost Boys' group spent most of their time sleeping and resting (38% of their time), but also spent approximately a quarter of their time foraging (26.1%) and a quarter of their time travelling during their dispersal period (24.2%). Individuals also engaged in social activities, such as grooming, sex, or play, 11.7% of their time. These percentages did not vary greatly with month; however, there were some differences. For example, the occurrence of social activities continuously increased during the months of February (2.3% of time), March (12% of time), and April (18.6% of time).

Individuals also spent approximately one third of their time foraging in the months of January through March (January, 31%; February, 29.8%; March 28%). This amount of time decreased in April (18.4% of time). Sleeping and resting did not vary much across months, though it slightly increased during the month of February (January, 37.9%; February, 46.5%; March, 35.5%; April, 38%). Lastly, individuals spent more time travelling during January and February (January, 31%; February, 31%) compared to the months of March and April (March, 24.5%; April, 24.9%), although it can be said that approximately one third of a Lost Boys' time was devoted to this activity.

As a group, the Lost Boys spent significantly more time at transects (i.e., a 30-meter radius where transects were performed on the daily GPS track) during the afternoon ($n = 300$) than the morning ($n = 391$; $P < 0.0001$; Morning, $M = 15.392$, $SE = 1.5663$; Afternoon, $M = 29.531$, $SE = 3.077$) and evening ($n = 211$; $P < 0.0001$; Evening, $M = 20.649$, $SE = 3.4004$). They also spent significantly more time at transects if individuals were all together and not separated from one another ($N = 896$, $P = 0.002$; Less than Group Size [separated], $M = 17.374$, $SE = 1.9747$; Group Size, $M = 24.771$, $SE = 2.0267$) or with additional individuals during an intergroup encounter ($P = 0.002$; More than Group Size [in an intergroup encounter], $M = 12.135$, $SE = 2.3327$).

They spent more time at transects if the group was of mixed ages ($M = 22.838$). The age composition of the Lost Boys' group was of mixed ages, and if separated, often only juveniles or only adults were followed due to how the group separated. If juveniles were left on their own, they moved significantly more quickly than the group moved when it included older individuals ($N = 902$; $P < 0.0001$; Juvenile(s), $M = 6.678$, $SE = 0.4117$; Adults, $M = 18.987$, $SE = 3.5021$; Mixed Ages, $M = 22.838$, $SE = 1.7850$). The migrants did occasionally seem to be in search of a group into which to migrate ($n = 123$ transects with intergroup encounters); 13.4% of transects had intergroup encounters occurring. However, they generally went through long periods when they appeared to focus only on eating and resting and potentially avoiding other groups ($n = 765$ transects with no intergroup encounters); that is, 83.6% of transects had no intergroup encounters occurring.

Collectively, the Lost Boys showed little conflict and there was no apparent dominant individual, although there were sometimes vocal disputes regarding the proposed direction of travel. The majority of their time during the 36 total follow days was spent together as a stable bachelor group (*n* = 30 days or 83.3% of the total follow days). They were separated from each other for only six days (16.7% of days) during my observations. Very few interactions occurred between other groups and the Lost Boys' group in the beginning months of the dry season (January and February had only seven intergroup encounters, 5.7% of the total or ~0.08 intergroup encounters per contact hour). The majority of interactions with other groups occurred in the later months of the dry season (March and April had 116 intergroup encounters, 94.3% of the total or ~0.40 intergroup encounters per contact hour). This is possibly because I did more follow days in March and April (*n* = 28; 77.8% of total follow days or ~287.66 contact hours).

Great disorder often erupted when there were intergroup encounters; the Lost Boys ran from the other group's males in 112 of 123 (~93%) encounters, scattering and separating from each other. The rest of the day(s) following these intergroup encounters were usually spent in an effort to re-unite. From my personal observation, most intergroup encounters seemed to take the Lost Boys by surprise; they would be traveling, resting, and/or foraging and suddenly noticed another group, usually running away instantly. On four days they lingered not far from the periphery of a multi-male, multi-female group ("Pelon" Group), and had five intergroup encounters with Pelon males (1.25 intergroup encounters per day). An older adult Lost Boy male, "Hada", occasionally would interact and exhibit sexual behaviors with the Pelon males, while the rest of the Lost Boys ran. However, on one occasion (when "Pelon" group was already undergoing an intergroup encounter with another multi-male, multi-female group, "Rafiki" group) the entire Lost Boys' group appeared to attempt to engage in an intergroup encounter rather than scattering.

The two youngest males ("Dakota Sur" and "Chambon") never approached other monkeys during any of the intergroup encounters, and often exhibited cooing vocalizations that are generally produced by only infant capuchins. The Lost Boys did take over another study group, “Newman” group, on one occasion; however, the group’s males were missing at the time and the take-over lasted less than 12 hours. When the Newman males returned they chased the migrants away. During the take-over, the Lost Boys interacted almost exclusively with the juveniles of Newman group and ignored the females in their excitement.

Where Do Migrants Go?

The Lost Boys’ group may have had a few safe areas located in different multi-male, multi-female home group territories during their dispersal period. For example, they spent nine follow days (25% of time) at a popular site with a mango grove, named Abran’s farm. Here they commonly ignored non-researchers in close proximity to the site. They also spent three days at a river site out of the Lomas Barbudal study groups’ home ranges, and three days on a river site commonly populated by the Lomas Barbudal primary study groups, called Rita’s Farm.

At Rita’s Farm, the migrants became trapped on the river between two multi-male, multi-female study groups. There was open pasture on either side of the river and little forest to travel through if the males wanted to leave this area and avoid intergroup encounters with these two other groups. Often, the Lost Boys stayed at these sites for many days, and only left for another safe area by crossing a significant distance quickly in one day. A more favorable male-female sex ratio in these different home group territories did not appear to influence the movement of the Lost Boys’ group: they did not spend significantly more time at transects that were in territories with relatively more females (N = 860, P = 0.661, M = 0.7054, SE = 0.0046).

During the dry season, there is little available water; precipitation is low and temperatures are high (Mata & Echeverría, 2004). Because of this, male and female groups often congregated on the rivers, where both food and water are more readily available. These sites then became less available to migrant males. While the Lost Boys sometimes found areas in which to stay in these riparian habitats ($n = 51$; 5.6% of transects), the time they spent at these sites with drinking water was slightly less ($n = 40$; 4.4% of transects) than at riparian sites. Also, slightly less than a quarter of their total time was spent at sites where there was such drinking water available ($n = 195$; 21.9% of transects), but once the Lost Boys were in these areas, they maximized the time spent there. Significantly longer time periods were spent at transects with drinking water available ($N = 889$, $P < 0.0001$; No Water Available, $M = 13.174$, $SE = 1.3233$; Water Available, $M = 24.125$, $SE = 3.5287$), although this variable was not incorporated into the final GLM due to co-variance with habitat type (Figure 5).

The following variables also did not affect the amount of time migrants spent at a transect: anthropogenic disturbances in the habitat, such as a road or canal ($N = 888$, $P = 0.154$; No Disturbance, $M = 15.136$, $SE = 1.050$; Disturbance, $M = 12.593$, $SE = 1.6358$), the amount of fruiting trees available in the transect ($N = 867$, $P = 0.079$, $M = 8.878$, $SE = 0.2616$), and the total number of trees in the transect ($N = 867$, $P = 0.072$, $M = 13.475$, $SE = 0.3192$). However, the Lost Boys' group spent significantly more time at sites with a greater average diameter at breast height (DBH) of the total number of trees ($N = 867$, $P < 0.0001$, $M = 69.26$, $SE = 1.596$ [Figure 6]). They also spent significantly more time at sites with a greater Normalized Difference Vegetation Index ($N = 896$, $P = 0.001$, $M = 0.4054$, $SE = 0.0042$ [Figure 7]). Both variables are a measure of the habitat's coverage, but were not incorporated into the final GLM due to co-variance with habitat type.

Unlike some male-female groups (personal observation), the Lost Boys often did not respond to the presence of non-researchers at transect sites. Most sites were without humans

(69.3% of transects); the Lost Boys were around humans only in 30.1% of transects. Most of this time migrants were around humans occurred in the month of March (*n* =198 or 72% of transects). However, the presence of humans did not significantly predict the amount of time the Lost Boys spent at sites (*N* = 890, *P* = 0.307; No Humans, *M* = 14.024, *SE* = 1.2790; Humans, *M* = 16.014, *SE* = 1.5789), although sites without humans had significantly more fruiting trees available than sites with humans (T-Test: *N* = 852, *P* < 0.0001 [Figure 8]).

Final Model Results: What Predicts the Lost Boys' Days?

The final prediction model included the effects of the significant control variables, plus the effects of habitat type, non-human predator presence, and whether or not an intergroup was occurring at the transect (Table 1; Table 3). In the individual GLM models run to create the final prediction model, time of day, relative group size, and age composition were significant (Table 1). Month and whether or not the transect was at a sleepsite were not significant, and so were not included in the final model (Table 1).

Migrant males spent the most time in (relatively high-quality) riparian and horticultural habitats (Table 3). The Lost Boys spent significantly longer durations of time in horticultural habitats compared to savanna (*P* < 0.0001) and deciduous habitats (*P* = 0.05 [Table 3]). They also spent more time at transects that were of mixed habitat compared to savanna (*P* < 0.0001) and deciduous habitats (*P* = 0.017 [Figure 9; Table 3]).

With regard to predation risk, migrant males spent significantly less time at transects where non-human predators were present, compared to sites where there were no predators present (Figure 10; Table 3). Finally, the Lost Boys' group spent significantly less time at transects where intergroup encounters occurred, compared to sites with no intergroup encounters

(Figure 11; Table 3). Migrant males often immediately ran away when encountering another male-female group.

Discussion

This all-male group, the Lost Boys, is currently the largest known and longest documented, stable all-male group at Lomas Barbudal. Although all-male groups are quite common at Lomas Barbudal (14 of the 24 males who have been study subjects from the time of their birth through their 12th year of life have spent some time in all-male groups [Perry et al., 2012]), little was known about how all male groups' ranging behaviors are affected by habitat quality, predation risk, and encounters with extra-group conspecifics. This is because habituated all-male groups are extremely difficult to find and monitor: they are composed of individuals who rarely vocalize, and they have larger home ranges than do multi-male, multi-female groups (Perry et al., 2012).

Some previous generalizations about all-male groups at Lomas regarding social behavior hold for the present study: males in the Lost Boys' social life involved much less conflict than among males in multi-male, multi-female groups; they also showed little dominance striving. Their daily behaviors thus involved more foraging and resting, and less social interaction, than males in a multi-male, multi-female group (Perry et al., 2012). However, unlike other previous observations (Perry et al., 2012), the Lost Boys during this particular study period almost always fled any encounter with a bisexual group. Perhaps this is related to these males spending a longer period of time as an all-male group with little reproductive success. In the 20 months of their dispersal period, the Lost Boys only succeeded in invading two groups; one takeover event lasted less than a month and occurred very early on in their dispersal period, and the other takeover event lasted less than 12 hours and occurred when the other group's males were not present.

Males in bisexual groups are almost always hostile to migrants, and thus any encounter between a male in a bisexual group and a migrant will often result in serious risk and wounding of males (Perry et al., 2012).

The dispersal period is one of the most intense periods an individual will experience in its life with many costs (Alberts & Altmann, 1995; Smale et al., 1997), both to an individual and to a population (Hamilton & May, 1977). Thus, a period of such high stress may well influence behavior differently as time progresses (Pusenius & Viitala, 1993; Sommer, 2003); and the benefits of dispersal may change through time (Cheney & Seyfarth, 1983). The Lost Boys' group had a dispersal range that overlapped with the home ranges of at least 17 other groups, far more than the 3-6 neighboring groups that overlap in home range with a typical multi-male, multi-female group (Perry et al., 2012). Also, after migrants suffered severe wounds in intergroup encounters, they would often spend time resting in areas where the rates of intergroup encounters were low. For example, only one intergroup occurred at Abran's Farm; the activity budget while there comprised approximately 50% of time sleeping and resting.

If such resting areas are important to migrants as a means of intergroup recovery (Perry et al., 2012) or avoidance of conflict (only approximately 10% of transects were the location of intergroup encounters), environmental influences at these areas should have a large part in the dispersal range of a migrant. My first prediction regarding habitat use (i.e., migrants will prefer habitats that have a higher habitat quality) was only partially supported by my results. The Lost Boys migrants did appear to prefer habitats that were relatively somewhat high in habitat quality: they spent longer periods of time at sites that had drinking water available, had higher average DBH (a measure of coverage and forest maturity) of total trees, and higher NDVI (a measure of coverage and live vegetation) of the habitat. However, the number of fruiting trees, the total number of trees available, and anthropogenic disturbances did not affect how much time they spent at a site. While they did spend significantly longer durations of time at sites with water availability, most (*n* = 195 or 21.9% of transects) of the sites they spent time at had no drinking water available, including Abran's Farm, a potential refuge site where the Lost Boys spent the most consecutive days.

It appears that canopy coverage weighs more heavily in migrant habitat preference than fruit availability and the risk of anthropogenic disturbances. It is also possible that the Lost Boys were pushed out of sites with higher total measures of habitat quality, as they are more desirable sites (personal observation), to avoid risk of wounding in intergroup encounters with more stable multi-male, multi-female groups (less than 1% of intergroups occurred at these sites). For example, I know that the Lost Boys spent significantly longer periods of time in horticultural and mixed habitats compared to savanna and deciduous habitats. Horticultural habitats primarily have horticultural fruiting trees within them (which have a high water and sugar content) even though there are fewer total fruiting trees available in these habitats compared to non-horticultural habitats. These horticultural habitats might seem unappealing; they often do not have drinking water available (92.9% of horticultural sites had no water), and non-researchers are always at these sites. Thus, it seems that these migrants preferred horticultural habitats, and were willing to be in these despite little water and limited fruits. This may be due to the types of fruits they were eating and the safety these areas provided; these habitats had more cover as well.

Further, even though all horticultural sites had non-researchers present (a type of predation risk), migrants still spent the most time there, suggesting that migrants weigh predation costs as less important than the costs of conspecific aggression (at least during this study which was later in their dispersal period). It is possible that capuchins can distinguish between dangerous and non-dangerous humans; the Lost Boys would first give alarm calls at the non-researcher(s)' presence, but after many days with increased exposure, the males would give alarm calls less and less (personal observation).

In my study, it seems that at this point in a migrant's dispersal period, somatic effort was spent on seeking and staying in refuge habitats, rather than seeking a new group in which reproductive opportunities might increase. Unfortunately, without explicit quantitative comparisons between the Lost Boys' group and multi-male, multi-female groups, it is difficult to argue that migrant males do trade predation risk and other measures of habitat quality for access to higher quality food or nutrition, compared to large multi-male, multi-female groups that can defend access to food in low-predation risk zones.

Future studies should focus on comparative analyses of environmental and habitat influences on migrants versus male-female groups, and should perform nutritional analyses on study populations' diets.

Nonetheless, it is likely that migrants maximize the amount of time they spend at sites with high habitat quality if they foresee no risk of an intergroup encounter, even though these opportunities are rare (only approximately 5% of transects appeared to have a high habitat quality). During the dry season, when little water is available and temperatures are the highest, the likelihood of dangerous intergroup encounters is heightened.

While my second prediction regarding predator risk (i.e., migrants will prefer habitats with no predators [non-human and human] present) was only partially supported by my results, migrants did leave quickly areas when there was a non-human predator present and spent longer periods of time in areas where there were no non-human predators. It is not surprising that migrants spent more time at safe sites, but such a significant result is, perhaps, surprising. In multi-male, multi-female groups, the gathering of individuals around a predator while performing aggressive antipredator behaviors (Curio, 1978) usually occurs during certain types of predator sightings (Meno et al., 2013); groups spend relatively long periods of time engaging in this behavior. However, such behavior rarely happened in the all-male study group. Migrants may be leaving sites with non-human predators quickly because such areas are unfamiliar (and can result in higher predation rates [Isbell, 1994]) and their group size is relatively small (also resulting in high risks of predation [Cheney & Wrangham, 1987; Miller & Treves, 2007), resulting in high risk aversion. They may also have a lower tendency than larger groups to mob.

The Lost Boys' social behaviors followed some previous generalizations; however, contrary to predictions, they did not prefer areas characterized by higher female-to-male ratios, perhaps because larger numbers of females were also defended by larger numbers of males who could pose a risk to the Lost Boys. Migrants actually spent significantly less time in habitats with intergroup encounters, leaving such sites quickly. It also seems that migrants may have used intergroup encounters to assess who is in the other group, only to flee when they realized their chances of winning the encounter and gaining access to reproductively capable females were low. Such assessment of costs and benefits may be unique to migrant males, but I need comparative data from multi-male, multi-female groups, before I can infer this.

Conclusions

Some previous predictions were supported: migrants did spend significantly more time in horticultural and mixed habitats compared to dry deciduous and savanna habitats, and spent more time at sites with greater measures of forest maturity, coverage, vegetation, and drinking water available. However, such habitats are not necessarily a measure of higher habitat quality and may indicate cost and benefit tradeoffs during a specific point in the dispersal period. Some measures of a better habitat quality did not seem to influence migrants' dispersal routes. Migrants did spend significantly less time at sites where non-human predators were present; yet, contrary to predictions, presence of non-researcher humans did not negatively impact their habitat choice. Migrants also were not influenced by more favorable male-female sex ratios, often immediately fleeing intergroup encounters.

The Lost Boys' ranging behavior during this study suggests that the migrants are avoiding bisexual groups and potential mating opportunities, rather than finding a new group to immigrate into; it seems that they seek safe refuges, even though these refuges do not necessarily have higher measures of habitat quality. Cost and benefit tradeoffs, as well as habitat preferences, likely shift during the high-stress dispersal period (Smale et al., 1997) and during an individual's life (Cheney & Seyfarth, 1983). These tradeoffs also may shift at different points in the dispersal period due to constant assessment and risk evaluation, and potential forms of alternative strategies based on past events that occurred prior to this study in their dispersal period.

I still do not know what the typical ranging patterns are for an all-male group, or even for individual migrants dispersing alone, because the Lost Boys are the only migrant group that has been monitored continuously for long periods of time (Perry et al., 2012). The fact that they are unusual in some ways (being of an unusually large size and breadth of age ranges, and failing to integrate themselves into a bisexual group for a longer time than is typical) may mean that at least some of the males in this group are of lower competitive ability than typical capuchin males, which could have implications for their habitat preferences. The Lost Boys' group may or may not provide good predictors of dispersal in other primates. To examine whether migrants compared to settled groups are influenced differently by habitat quality, predator risk, and conspecific influences, I need comparative studies of males in bisexual groups versus all-male groups. Studies of stress hormones during the dispersal period would also enhance my understanding of the role the endocrine system plays at different points in the highly stressful dispersal period (Smale et al., 1997); sources of stress can come from both environmental (Rosenblum & Paully, 1985) and social factors (Lonsdorf & Ross, 2012) and have been shown to influence reproduction (Alberts & Altmann, 1995; Roberts et al., 2012), social behaviors (Bardi et al., 2005; Bardi & Huffman, 2005; Schneider & Moore, 2000; van Noordwijk & van Schaik, 1985), and dominance (Colvin, 1983; Koford, 1963; Onyango et al., 2008). It is likely that environmental and social stresses cause different alternative strategies and fitness effects during a migrant's dispersal period, and at different points.

In habitats where resource availability is diminishing due to habitat fragmentation and other anthropogenic causes, such as the Lomas Barbudal study site (Stoner & Timm, 2004), environmental factors and the role of habitat potentially have even more of an effect (and may be the strongest drivers [Boydston et al., 2003; Wielgus & Bunnell, 1994]) on wild primate dispersal behaviors.

Thus, gaining more knowledge of the connection between dispersal behavior and habitat use in rapidly changing forest environments is crucial to future conservation decisions. Such information can enhance future forest management designs (e.g., forest corridor connections), conservation of wildlife, and encourage the study of dispersal as a management tool in order to potentially increase biodiversity (Ben-Zion et al., 2012; Zuberogoitia et al., 2009) as dispersal is crucial to the genetic structure and possible genetic diversity in wild populations (Cox & Kesler, 2012).

Figures

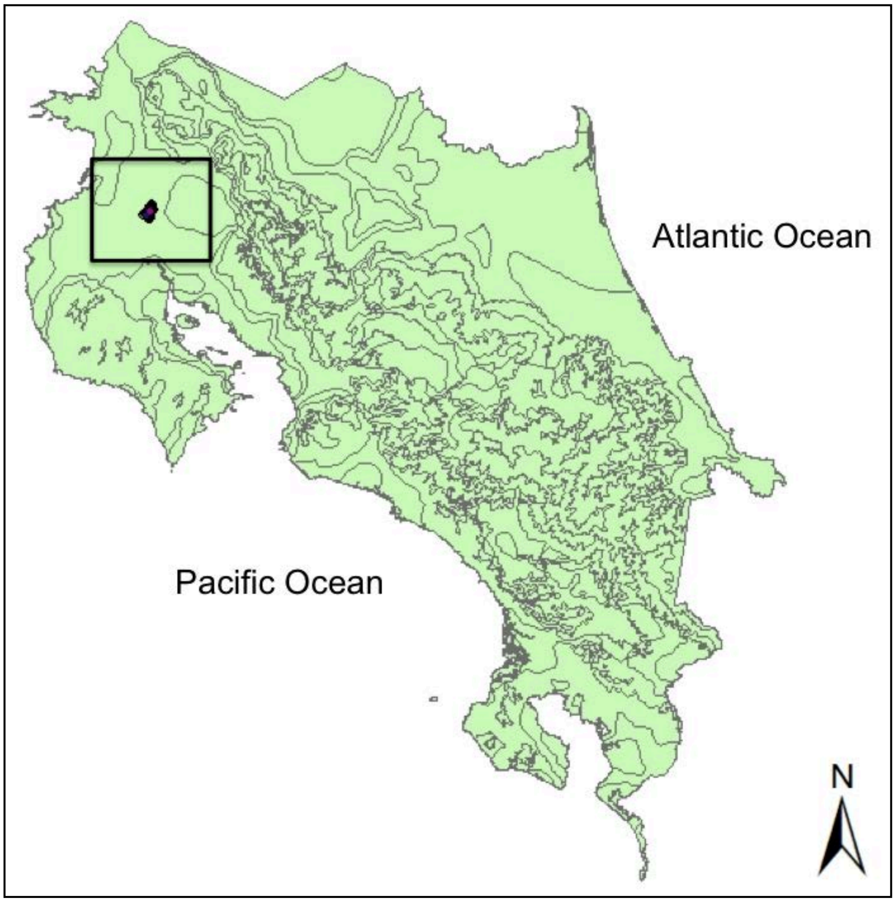

Figure 1: Data were collected in the Lomas Barbudal Biological Reserve (10°29–32′N, 85°21–24′W) and adjacent public and private lands in the Guanacaste province of Costa Rica (Ramos, 2004). The site consists of a highly disturbed tropical dry forest (classified as endangered) and includes riparian forest, dry deciduous forest, mesic forest, and regenerative forest habitat. It receives 1,000–2,200 mm of rain annually between the months of May – November (Frankie et al., 1988). During the dry season (December – May) when precipitation is low and temperatures are high, fires are common. The Lomas Barbudal monkey population most frequently visits the dry deciduous and riparian habitats (personal observation). The lines on the map denote different biotic life zones in the country.

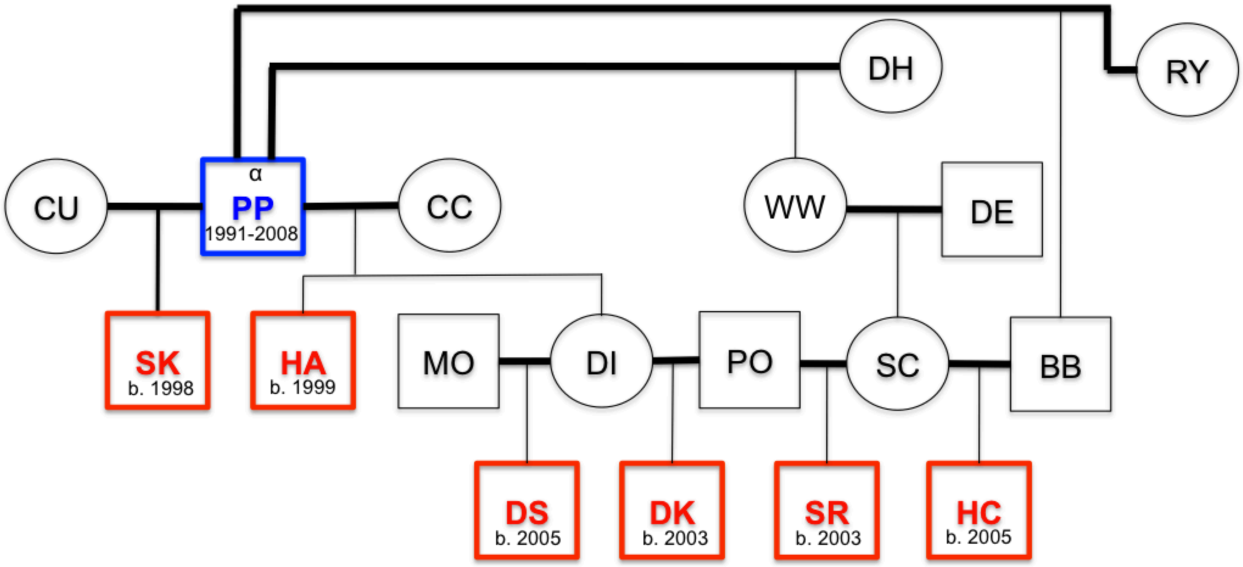

Figure 2: The Lost Boys' group migrant males are all members of the natal group Rambo's and descendents of the alpha male Pablo (PP). Skippy (SK) is the oldest member and son of PP, followed closely by Hada (HA), who is also PP's son; the pair are paternal half brothers. Dashiki (DK) and Dakota Sur (DS) are grandsons of PP, and are also maternal half brothers. Finally, although Scrappy (SR) is two years older than Chambon (HC), he is a great grandson of PP through the maternal line, while HC is a grandson of PP through the paternal line; thus, they are related through the paternal line in addition to being maternal half brothers. Beginning in the fall of 2009, many of the Lost Boys males began to exhibit dispersal behaviors in Rambo's. After a series of many dispersal events, they fissioned from Rambo's group in February of 2010, with one member returning to Rambo's group in April of 2010 and HC transitioning back and forth between Rambos' group and the Lost Boys' group before permanently joining the all-male group in May of 2010 (Perry, personal communication). By February of 2011, only these six individuals remained (personal observation).

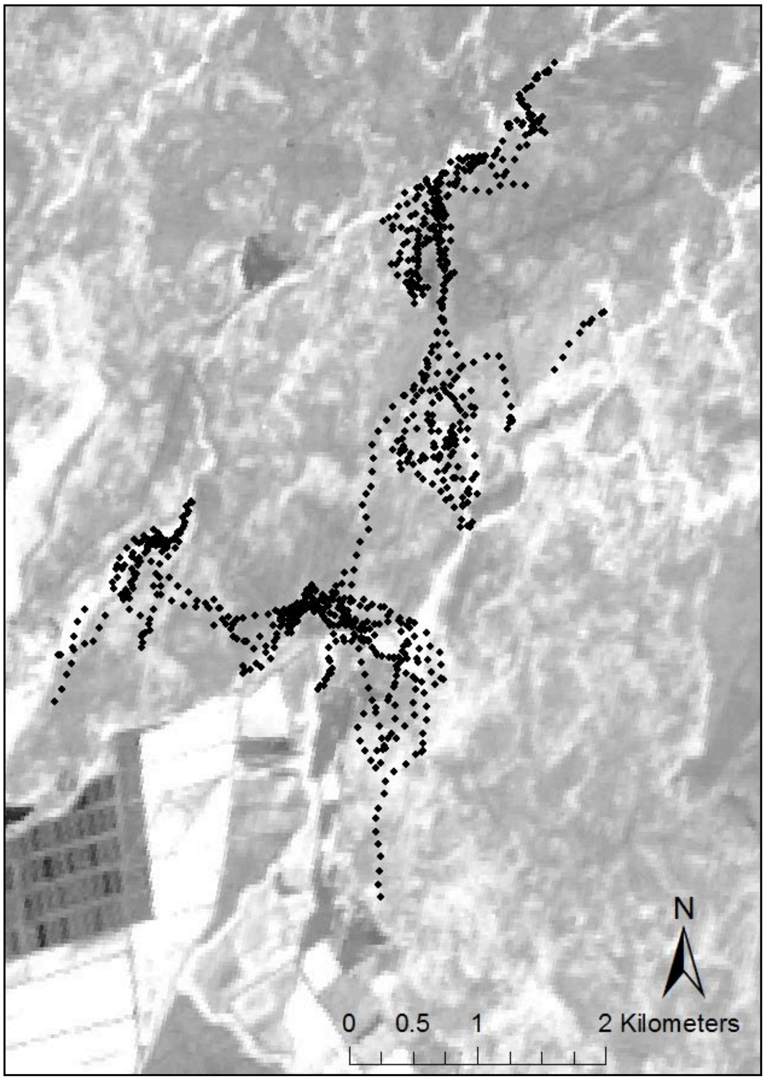

Figure 3: A detailed Normalized Difference Vegetation Index (NDVI) measuring the amount of live, green vegetation, biomass, and coverage scaling from -1 to +1 was calculated using proximity and raster analysis of a dry season landsat data image (USGS/EROs L4-5 TM, Path 15, Row 53; March 2011) in ArcGIS version 10 (Environmental Systems Research Institute, Redlands, CA) and Erdas IMAGINE Professional (Leica Geosystems, Atlanta, GA). The black dots on the figure are transect sites; the lightest areas of the figure represent full coverage and the most live, green vegetation, while the darkest areas represent sites with little to no coverage. During the dry season of 2011, the Lost Boys males primarily congregated at transects that had greater NDVI values.

$$\begin{aligned}\text{Ln(Minutes Spent in Transect)} = {} & \beta_0 + \beta_1\text{Evening} + \beta_2\text{Morning} + \beta_3\text{Less\_than\_Group} + \\ & \beta_4\text{Group\_Size} + \beta_5\text{Adults} + \beta_6\text{Mixed\_Age} + \\ & \beta_7\text{Deciduous} + \beta_8\text{Horticultural} + \beta_9\text{Riparian} + \\ & \beta_{10}\text{Mixed} + \beta_{11}\text{No\_Predator} + \beta_{12}\text{No\_Intergroup}\end{aligned}$$

Figure 4: The final Generalized Linear Model (GLM) showed that significant control variables that predicted minutes spent in a transect were time of day, group composition, and age distribution. Significant predictors were habitat type, non-human predator presence, and occurrence of intergroup encounters.

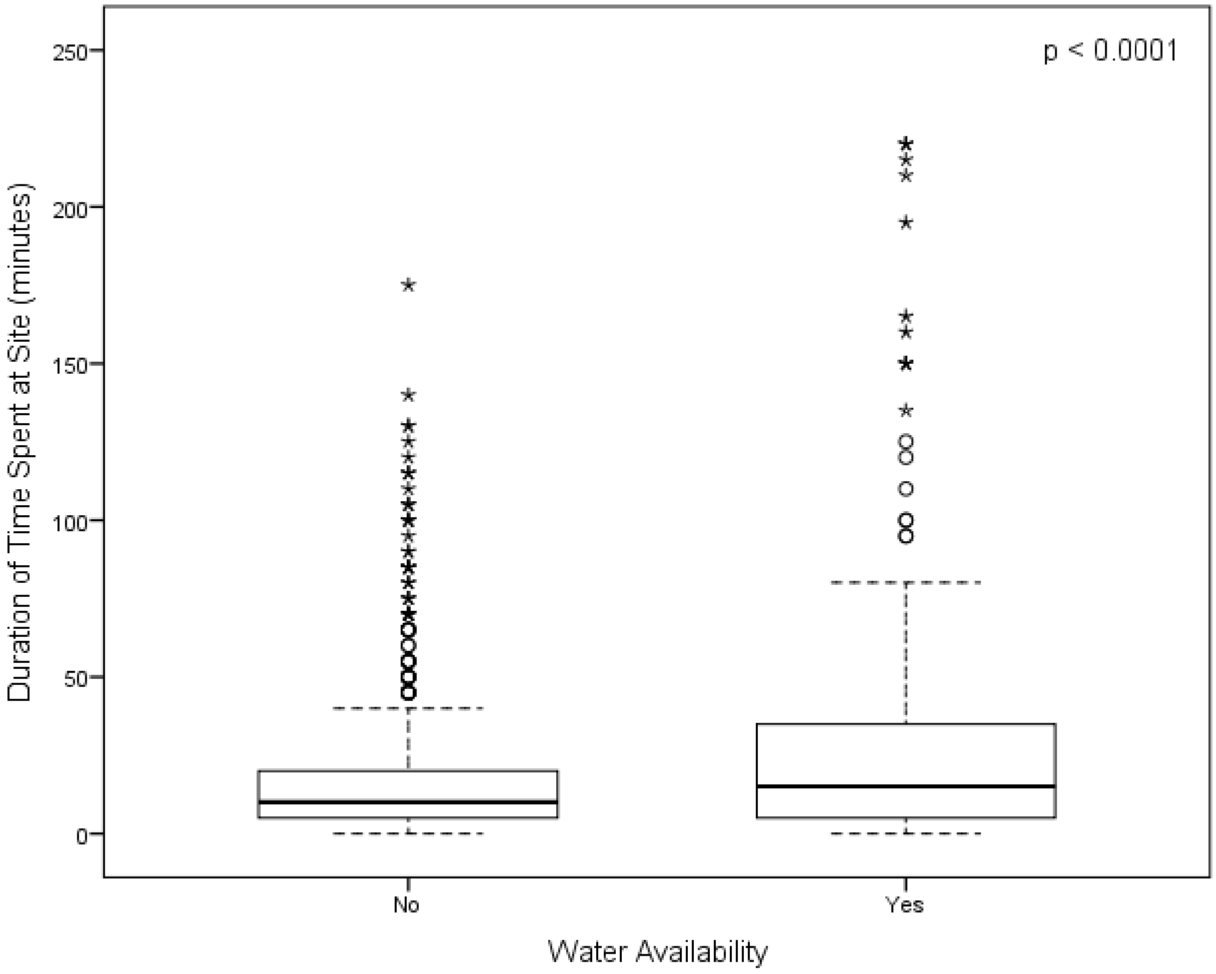

Figure 5: The Lost Boys' group spent significantly more time at transects where there was water available (*n* = 191 transects) compared to sites with no water available (*n* = 704, *N* = 889, *P* < 0.0001; No Water Available, *M* = 13.174, *SE* = 1.3233; Water Available, *M* = 24.125, *SE* = 3.5287). Although most of the sites (78.7% of transects) were sites without water, it seems that the migrants maximized the amount of time they spent at sites with water once they found themselves at such a territory.

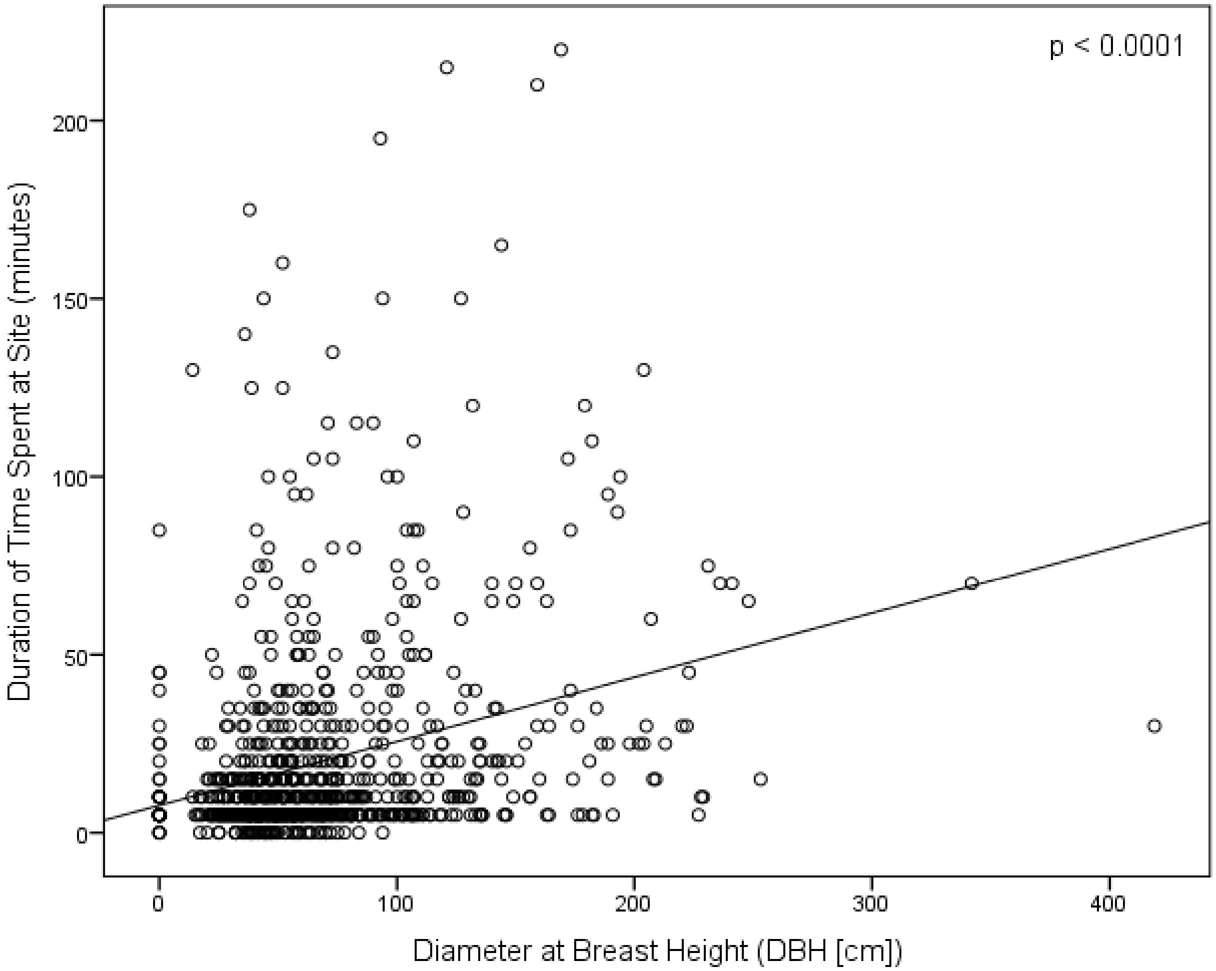

Figure 6: The Lost Boys' group spent significantly more time at transect sites where trees had a greater average diameter at breast height (cm [$N = 865$, $P < 0.0001$, $M = 69.08$, $SE = 1.589$]). This predictor is potentially a measure of canopy coverage and forest maturity and was not incorporated into the final Generalized Linear Model (GLM) due to co-variance with habitat type, but may indicate migrant preferences for a more mature forest with greater coverage.

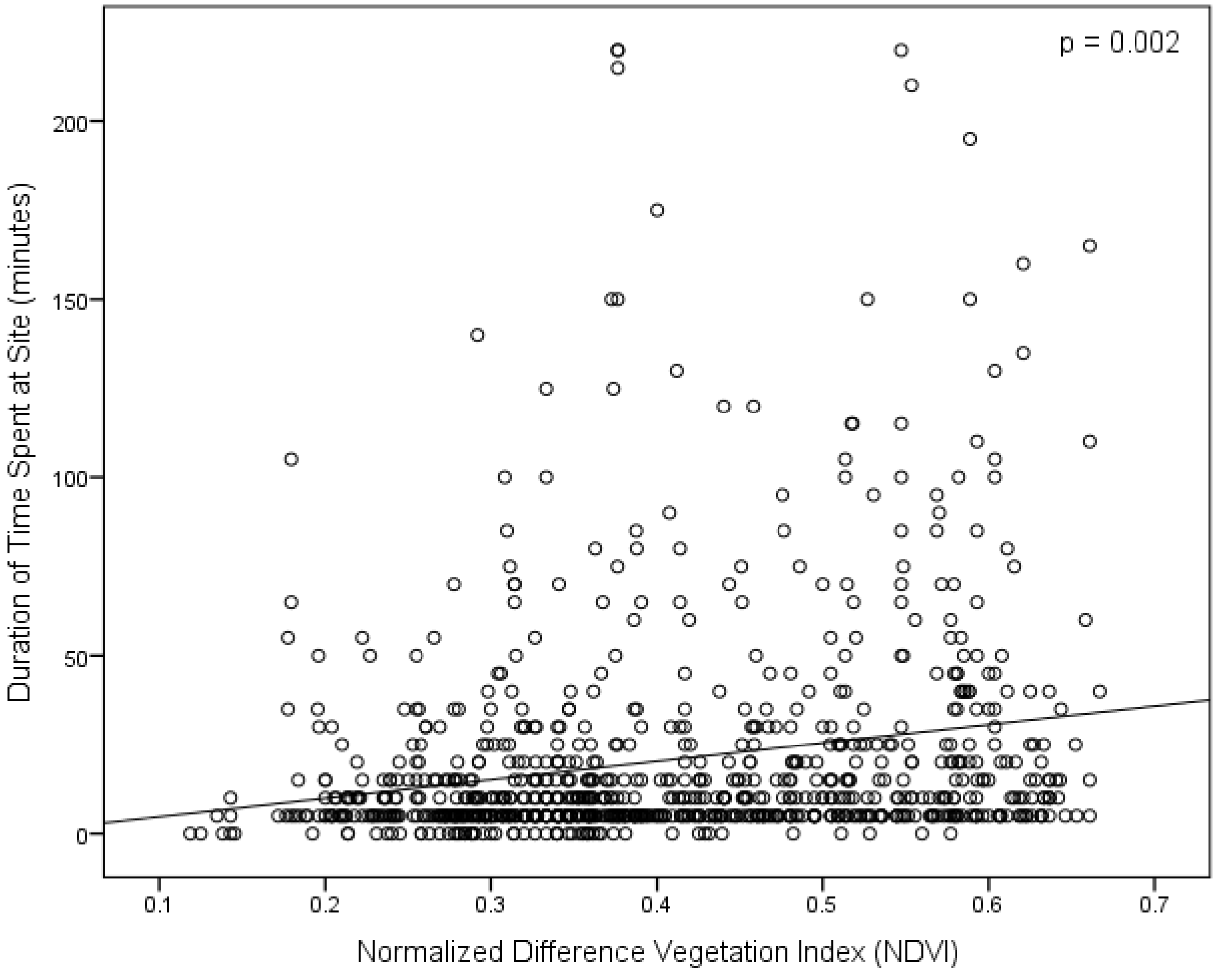

Figure 7: The Lost Boys' group spent significantly more time at transect sites with a greater Normalized Difference Vegetation Index (NDVI [*N* = 894, *P* = 0.002, *M* = 0.4053, *SE* = 0.0042]). This predictor is a measure of canopy coverage and was not incorporated into the final Generalized Linear Model (GLM) due to co-variance with habitat type, but may show migrant preferences for habitats that have greater canopy coverage and an increase in live, green vegetation.

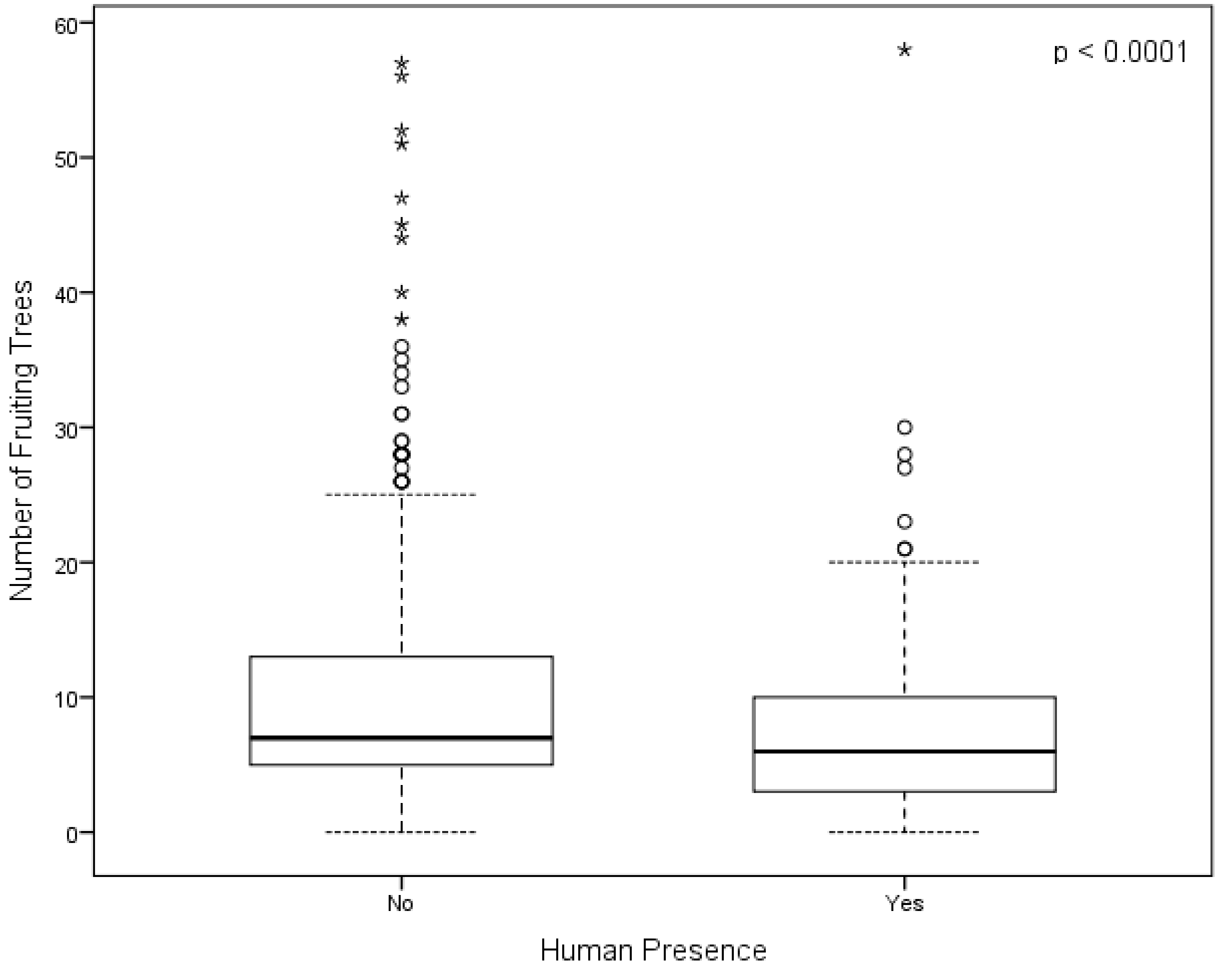

Figure 8: The Lost Boys' group did not spend significantly more time at transects where there were more fruiting trees available, nor at sites where there was no human presence; however, sites that did not have a human presence (*n* = 611) had significantly more fruiting trees available than sites that had a human presence (*n* = 275; T-Test: *N* = 852, *P* < 0.0001). Such results may indicate that migrant males have different tradeoffs than individuals in multi-male, multi-female groups. Migrants may be pushed out of areas with more fruiting trees and less risk of predation in order to avoid the risk of intergroup encounters. They may trade this type of predation risk for fruits that are higher in water and sugar content.

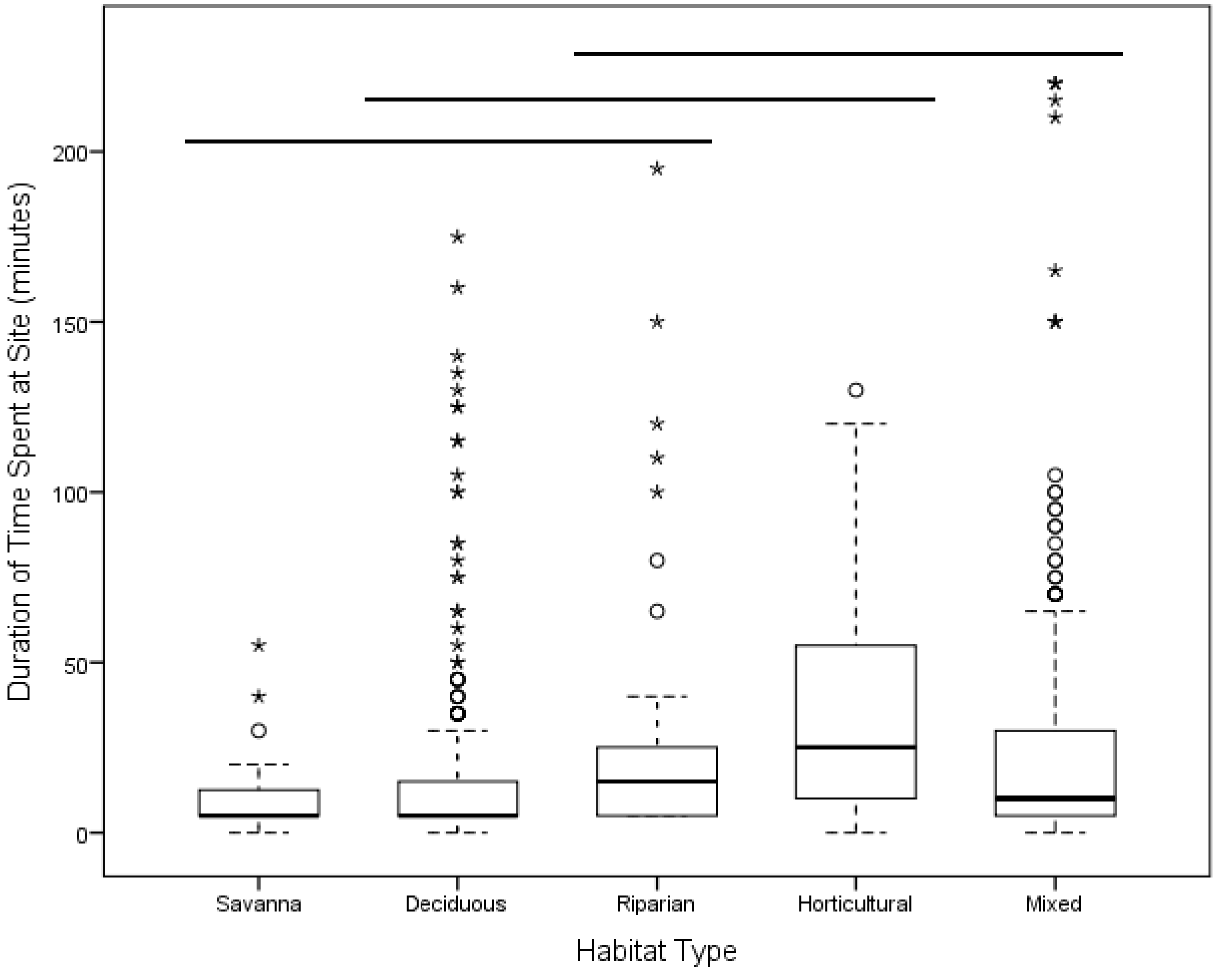

Figure 9: The Lost Boys' group spent significantly more time in horticultural habitats compared to savanna (*n* = 114 transects, *P* < 0.0001; Horticultural, *M* = 16.792, *SE* = 2.6397; Savanna, *M* = 6.868, *SE* = 1.7094) and deciduous habitats (*n* = 489 transects, *P* = 0.05; Deciduous, *M* = 9.732, *SE* = 0.7669). They also spent significantly more time in mixed habitats compared to savanna (*n* = 334 transects, *P* < 0.0001; Mixed, *M* = 15.017, *SE* = 1.7895) and deciduous habitats (*n* = 707 transects, *P* = 0.017). While horticultural habitats contain fruiting trees that have fruits higher in sugar and water content, these habitats also have a greater presence of non-researchers, a potential predation risk. Migrant males may differ from bisexual groups in that they trade this type of predation risk for access to high quality food or nutrition, and large bisexual groups that can defend access to food in low-predation risk zones do so.

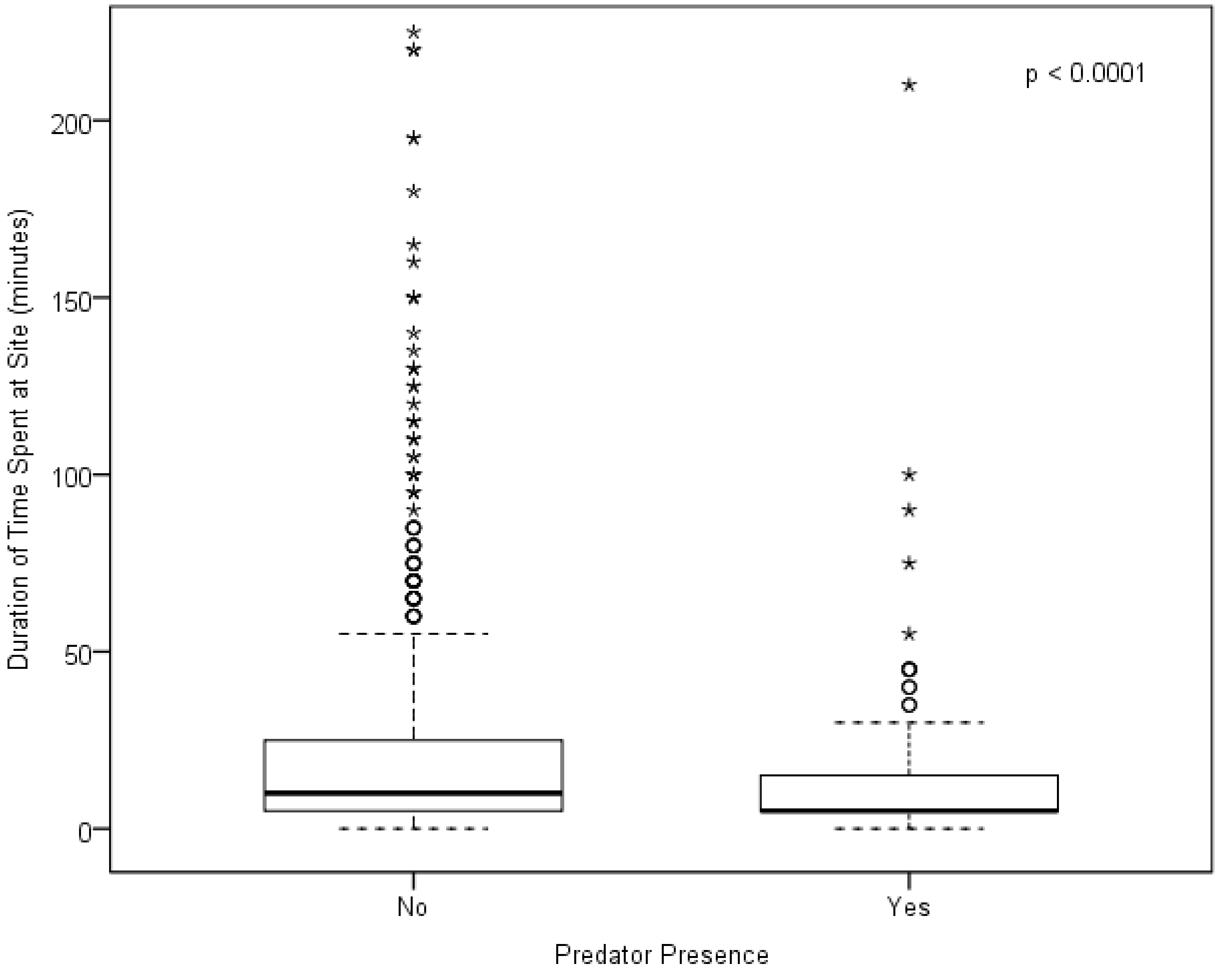

Figure 10: The Lost Boy's group males spent significantly less time at transects where non-human predators were present (*n* = 755 transects) compared to sites where there were no predators present (*n* = 110 transects, *N* = 865 transects, *P* < 0.0001; No Predator, *M* = 15.278, *SE* = 1.5818; Predator, *M* = 10.005, *SE* = 1.3700). This may vary from multi-male, multi-female groups, where often predator presence results in extended predator alarming and anti-predator behavior (e.g., mobbing behavior) against the predators (Meno et al., 2012).

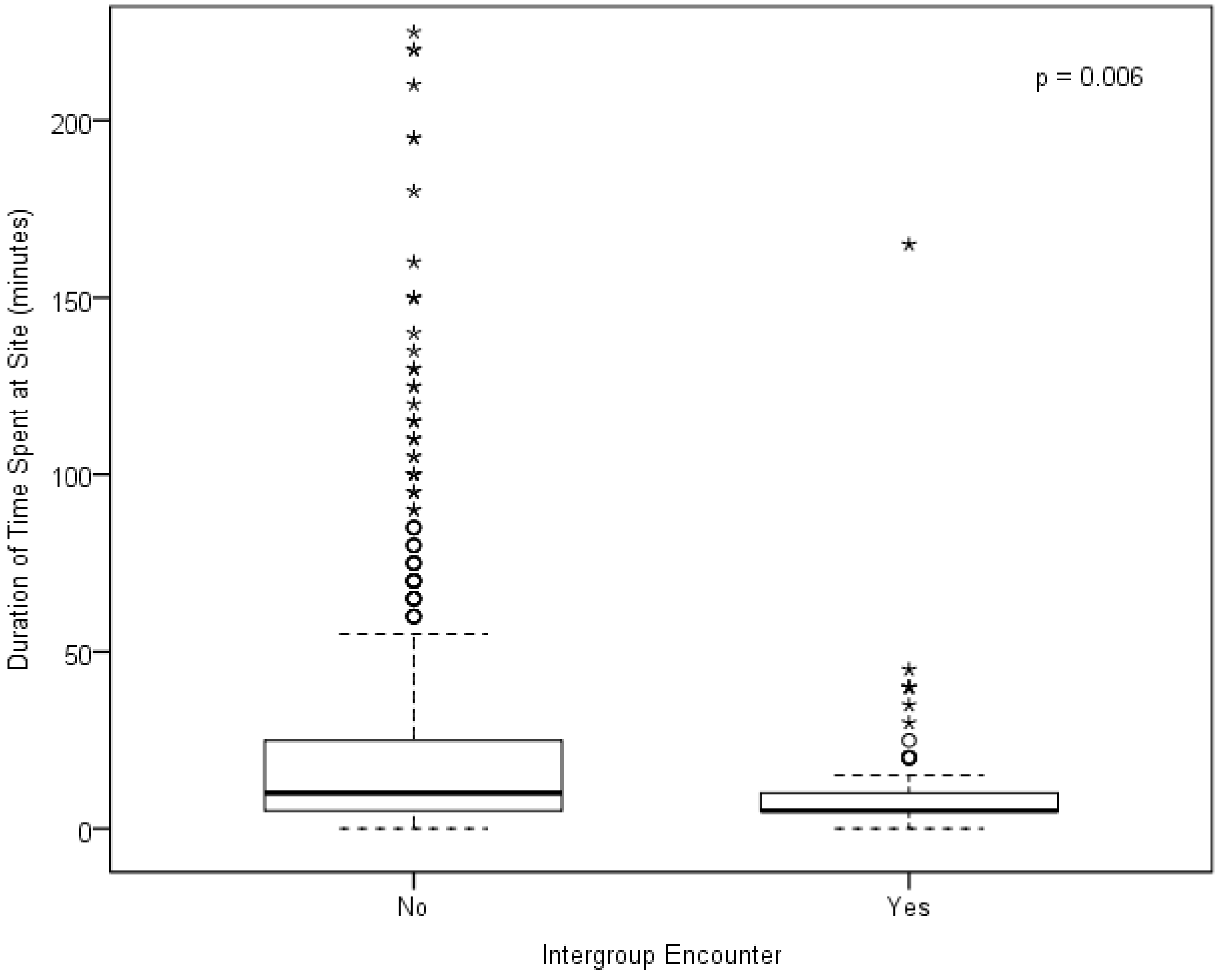

Figure 11: The Lost Boy's group spent significantly less time at transects where there were intergroup encounters occurring (*n* = 114 transects) compared to sites where intergroup encounters are not occurring (*n* = 751, *N* = 865 transects, *P* = 0.006; No Intergroup, *M* = 16.171, *SE* = 1.8659; Intergroup, *M* = 9.453, *SE* = 1.6986). Migrant males often immediately ran away when encountering another multi-male, multi-female group.

Tables

Table 1: Control variables tested individually in the GLM for statistical significance. Time of day, relative group size and age composition were highly significant and were incorporated into the final prediction model.

	Mean	Std. Error	Significance
Month (*N* = 902)			0.467
January (*n* = 28)	24.583	2.1995	
February (*n* = 184)	24.053	4.1090	
March (*n* = 535)	20.213	1.8276	
April (*n* = 155)	22.172	3.3462	
Time of Day (*N* = 902)			< 0.0001
Morning (*n* = 391)	15.329	1.5663	
Afternoon (*n* = 300)	29.531	3.0770	
Evening (*n* = 211)	20.649	3.4004	
Relative Group Size (*N* = 896)			0.002
Less than Group (*n* = 301)	17.374	1.9747	
Group Size (*n* = 563)	24.771	2.0267	
More than Group (*n* = 32)	12.135	2.3327	
Age Composition (*N* = 902)			< 0.0001
Juvenile(s) (*n* = 30)	6.678	0.4117	
Adult(s) (*n* = 160)	18.987	3.5021	
Mixed Ages (*n* = 712)	22.838	1.7850	
Sleepsite (*N* = 902)			0.624
No (*n* = 889)	21.436	1.5448	
Yes (*n* = 13)	24.406	5.8248	

Table 2: Significant and non-significant predictors tested individually in the GLM with significant control variables. Due to covariance, only the significant variables habitat type, non-human predator presence, and intergroup encounter were incorporated into the final prediction model.

		Mean	**Std. Error**	**Significance**
Significant Variables				
Habitat Type (*N* = 902)				< 0.0001
	Savanna (*n* = 30)	9.491	2.0889	
	Deciduous (*n* = 403)	11.819	0.8712	
	Riparian (*n* = 44)	20.461	5.9917	
	Horticultural (*n* = 84)	20.687	3.0559	
	Mixed (*n* = 304)	17.205	1.8031	
Water Availability (*N* = 902)				0.001
	No (*n* = 699)	13.174	1.3233	
	Yes (*n* = 190)	24.125	3.5287	
Diameter at Breast Height (*N* = 867)		69.26	2.3522	< 0.0001
Normalized Difference Vegetation Index (*N* = 867)		0.4054	0.0042	0.001
Non-human Predator Presence (*N* = 886)				< 0.0001
	No (*n* = 774)	15.805	1.2298	
	Yes (*n* = 112)	10.739	1.0086	
Intergroup Encounter (*N* = 878)				0.025
	No (*n* = 764)	18.361	1.8601	
	Yes (*n* = 114)	11.522	2.1136	
Non-significant Variables (dropped from overall model)				
Anthropogenic Disturbances (*N* = 888)				0.154
	No (*n* = 688)	15.136	1.0500	
	Yes (*n* = 200)	12.593	1.6358	
Fruiting Trees (*N* = 867)		8.878	0.2632	0.079
Total Trees (*N* = 867)		13.475	0.3192	0.072
Human Presence (*N* = 890)				0.312
	No (*n* = 616)	14.024	1.2790	
	Yes (*n* = 274)	16.014	1.5789	
Male-Female Sex Ratio (*N* = 860)		0.7054	0.0046	0.661

Table 3: Final predictor variables in the GLM. Migrants spent more time at horticultural and mixed habitat types than savanna and deciduous habitats. Migrants also left quickly when there was a predator present or when an intergroup encounter occurred.

		Mean	**Std. Error**	**Significance**
Habitat Type (*N* = 902)				< 0.0001
	Savanna (*n* = 30)	6.868	1.7094	
	Deciduous (*n* = 403)	9.732	0.7669	
	Riparian (*n* = 44)	17.141	4.6815	
	Horticultural (*n* = 84)	16.792	2.6397	
	Mixed (*n* = 304)	15.017	1.7895	
Non-human Predator Presence (*N* = 865)				< 0.0001
	No (*n* = 304)	15.278	1.5818	
	Yes (*n* = 304)	10.005	1.3700	
Intergroup Encounter (*N* = 865)				0.006
	No (*n* = 751)	16.171	1.8659	
	Yes (*n* = 114)	9.453	1.6986	

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Appendices

Appendix 1: Fruiting plants that compose 95% of a white-faced capuchin's diet composition in the dry season, including Genus and species, type of plant, and what months it fruits during the dry season (Perry & Ordoñez Jiménez, 2006). When transect data were collected, only these species were noted.

Genus and Species	Type	Months in Fruit
Allophylus occidemtale	Tree	June-Sept
Anacardium excelsum	Tree	Feb-May
Anacardium occidentale	Tree	Feb-May
Ardisia revoluta	Shrub	Jan-May
Bauhinia sp.	Liana	Mar-May
Bixa orellana	Shrub	Apr-May
Bromelia pinguin	Bromeliad	Year round
Brosimum alicastrum	Tree	Jun-July
Bursera simaruba	Tree	Jan-Mar
Byrsonima crassifolia	Tree	Jun-July
Casearia arguta	Tree	Apr-Jul
Casearia tremula		
Chomelia spinosa	Shrub	Nov-Jan
Cissus sp.	Vine	Sep-Nov
Cupania guatemalensis	Shrub	Mar-Apr
Curatella americana	Tree	Mar-Jun
Diospyros salicifolia (nicaraguensis)	Tree	Sept-Feb
Eugenia sp.	Shrub	Feb-Apr
Eugenia hiraeifolia (salamensis)	Tree	Aug-Oct
Ficus sp.	Tree	Variable
Guazuma ulmifolia	Tree	Jan-Jun
Guettarda macrosperma	Tree	Jun-Oct
Hirtella racemosa	Tree	Feb-Apr
Jacquinia nervosa (pungens)	Shrub	Sep-Jan
Luehea candida	Tree	Jan-May
Maclura tinctoria	Tree	May-Aug
Mangifera indica	Tree	Feb-April
Manilkara chicle	Tree	

Muntingia calabura	Shrub	Jan-Jun
Musa sp	Banana	Feb-Apr
Passiflora sp.	Vine	Jun-Sep
Prockia crucis	Shrub	May-Aug
Randia subcordata	Tree	Dec-Jan
Sapranthus palanga	Tree	Mar-Sept
Sciadodendron excelsum	Tree	May-July
Sideroxylon capiri	Tree	Jan-May
Simaruba glauca	Tree	
Sloanea terniflora	Tree	Feb-June
Stemmadenia obovate	Tree	Jun-July
Sterculia apetala	Tree	Jan-Feb
Tabebuia ochracea	Tree	Jan-Jun
Tetracera volubilis	Liana	Jan-Apr